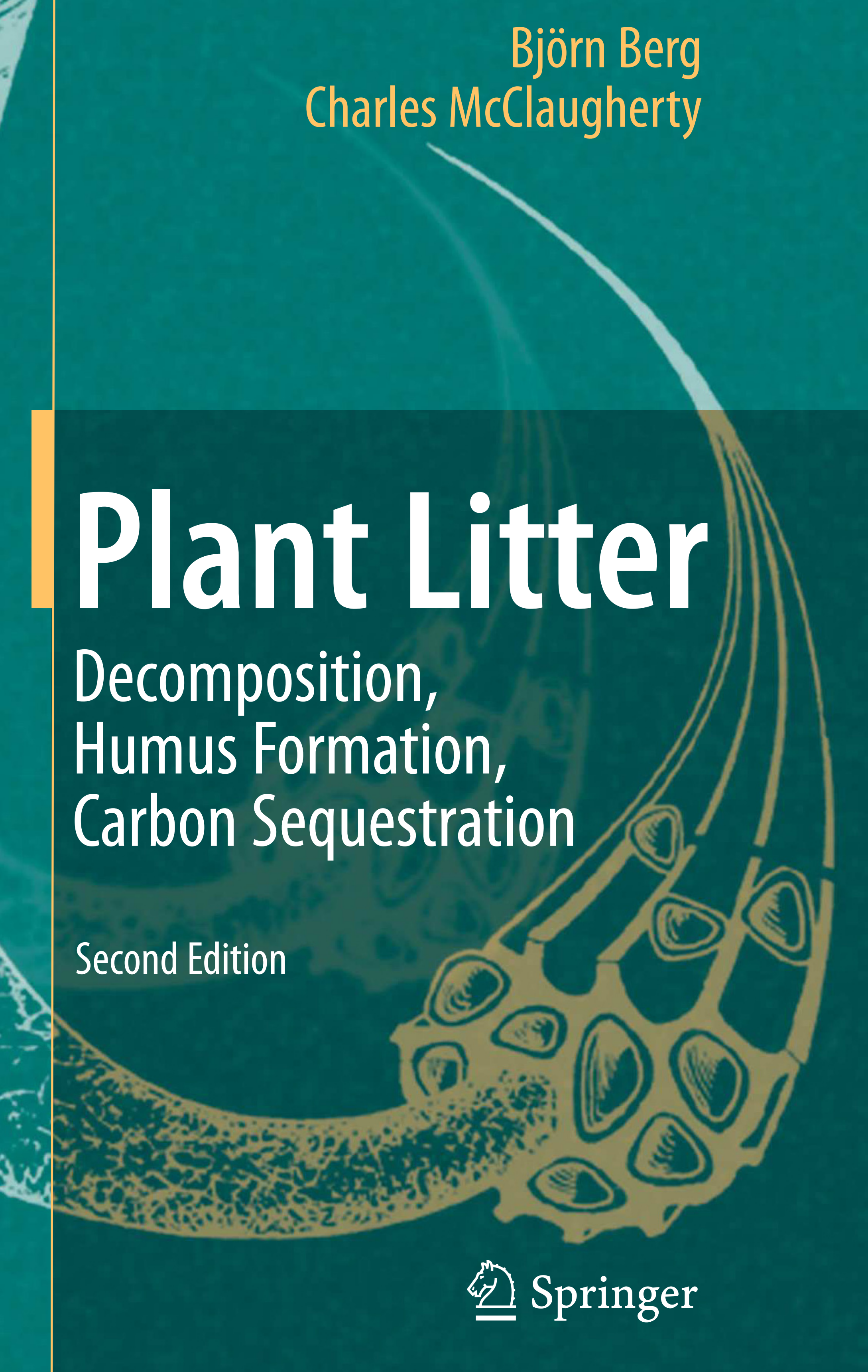

Björn Berg
Charles McClaugherty

Plant Litter

Decomposition, Humus Formation, Carbon Sequestration

Second Edition

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Preface

When starting our work on this book, we intended to summarize and synthesize the new information that had developed in the last 20–30 years in the field of plant litter decomposition. It turned out, however, that the main part of more recent work was directed toward boreal and temperate forest systems, and therefore with a focus on these ecosystems, we finally concluded a synthesis that has a similarity to a case study. Still, we hope that a deeper insight into the behavior of a limited number of litter species will be of value for a generalization, and also for the identification of process systems that deviate from those presented here.

We have written the book focusing on the transfer from newly shed litter to recalcitrant humus, describing and explaining the system of chemical changes taking place in the process both on a mechanistic basis, and on a more general and regional level, considering different climates and species.

As a synthesis, this book gives some new aspects on decomposition that to some of us may be controversial. Thus, the fact that we emphasize the dominant role of microorganisms in the process may not appeal to some readers, as well as the strong emphasis we give to the fact that humus layers actually do grow over millennia, and that at a considerable rate, and thus really sequester, e.g., C and N.

This book is based primarily on data and conclusions made from field studies. We have focused on undisturbed forest systems in an attempt to create a basic understanding of, and present basic mechanisms for the decomposition and transformation processes. Its emphasis is on boreal systems for the obvious reason that there appears to exist more data about these systems that could be synthesized. The information from temperate systems has largely supported and extended the conclusions, suggesting that the synthesis so far may be applicable to at least both types of systems.

On the topic of litter decomposition and transformations, we can not yet identify different schools of thought; it appears that this field of research has not yet developed far enough. We would rather consider different directions of the research work. Thus, some scientists have attempted to understand the mechanisms of degradation, whereas several groups have searched for indices for the prediction of long-term decomposition rates.

The synthesis that we present has clearly benefited from the work of other scientists and research groups that we wish to acknowledge here. Thus, the papers emerging from the group around Dr. Marie-Madeleine Couteaux, CNRS, Montpellier, have been important to us; likewise, those from Prof. John Aber, University of New Hampshire, and Dr. Jerry Melillo, The Ecosystems Center, MBL, Woods Hole. Many other persons have been helpful in the process of collecting and developing the information that makes up the backbone for this book. We wish to thank all of them, and hope they appreciate that all cannot be listed here.

For this second edition of Plant Litter, we have used much of the data and the views on regionalization under different climates that have been developed by Prof. Vernon Meentemeyer, University of Georgia, Athens, which has proved extremely valuable. We have been allowed to use unpublished data by, and express our gratitude to, Drs Cecilia Akselsson, Maj-Britt Johansson, Anna Hagen-Thorn, Per Gundersen, and Åke Nilsson.

Now that the second edition has been completed, we wish to express our appreciation also of other fruitful inputs we have received along the way. Thus, we thank Prof. Carl-Johan Westman, Dept. of Forest Ecology, University of Helsinki, and Prof. Amalia Virzo De Santo, Dipartimento Biologia Strutturale e Funzionale, University of Naples Federico II, for their extensive support of this book. That of the Brumbaugh Center for Environmental Science, Mount Union College, Alliance, Ohio, is also gratefully acknowledged. Substantial financial support for the first edition came from the Commission of the European Union, through the CNTER project (QLK5-2001-00596), and is acknowledged here.

Finally, before handing over the book to the reader, we would like once again to congratulate each other for such an excellent cooperation.

Helsinki and Napoli, June 2007
Alliance, June 2007

Charles McClaugherty

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Contents

Chapter 1
Introduction

1.1 Overview of Plant Litter Decomposition

Decomposition and photosynthesis are processes that account for a vast majority of the biological carbon processing on planet Earth. Photosynthesis has been studied extensively at levels ranging from biochemical to ecological. Relatively speaking, photosynthesis is well understood. Its importance to the functioning of the biosphere, as well as its agronomic significance, is well established. Furthermore, photosynthesis occurs in aboveground tissues in organisms that are often large and aesthetically pleasing.

Decomposition accounts for the transformation of nearly as much carbon as does photosynthesis. However, it occurs mainly on or below ground. As such, decomposition is largely “out of sight”. It is carried out primarily by bacteria and fungi, and is sometimes associated with products that are “unappealing”. The biochemistry of decomposition is incredibly multifaceted, compared to that of photosynthesis. Thus, it should be no surprise that decomposition is the less well-studied of the two major carbon-transforming processes on the planet. In the last two decades, the need to gain a better understanding of decomposition has become increasingly apparent. Decomposition of organic matter is responsible for huge amounts of the carbon dioxide returned to the atmosphere. It is also responsible for the formation of humic substances that contribute to soil fertility as well as the long-term storage of carbon.

Decomposition is closely tied to nutrient cycling, and is essential for the regeneration of organically bound nutrients.

Decomposition is more difficult to define than photosynthesis. In broad terms, decomposition includes physical, chemical, and biological mechanisms that transform organic matter into increasingly stable forms. This broad definition includes physical fragmentation by wet–dry, shrink–swell, hot–cold, and other cycles. Animals, wind, and even other plants can also cause fragmentation. Leaching and transport in water is another important physical mechanism. Chemical transformations include oxidation and condensation. Biological mechanisms involve ingestion and digestion, along with extracellular enzymatic activity. Much of decomposition is ultimately accomplished by aerobic metabolism. The process is far from linear, and many meta-stable products are created and accumulated during decomposition.

B. Berg and C. McClaugherty, *Plant Litter*,

Scientists have long been familiar with negative exponential models. These describe the extinction of light intensity at increasing depths in the water column. They define the decline in radioactivity of a radioactive isotope over time. They have also been used to describe the loss of mass from decomposing organic matter in natural systems. As much as we would like Occam's razor to prevail, the simple linear decay function is not universally applicable to the decay of organic matter, though it often provides an excellent first approximation, especially during early stages of decay. Equation (1.1) is the basic exponential decay with time (*t*):

$$X_t = X_0 \mathrm{e}^{(-kt)} \tag{1.1}$$

Unfortunately, neither the total biomass nor the constituent nutrients of decaying organic matter follow this simple function well enough to make it predictive. As a result, decomposition studies have taken two basic tracks. Along one track, scientists have relied on mathematical abstractions and a variety of models, both theoretical and empirical, to predict – or at least simulate – the decomposition process. Along another track, the intention has been to study decomposition experimentally in the field and in the laboratory, in an attempt to extract general principles of the process. Both approaches have merit, yet neither has been able to completely explain the complex process of decomposition.

Decomposition is so complex that it requires the attention of numerous scientific disciplines. Studies on litter decomposition and humus formation may encompass different branches of science, including chemistry, microbiology, climatology, geology, and systems ecology.

The objective of this second edition of *Plant Litter* is to illustrate the importance of decomposition as a major ecological process, and to review and summarize our current understanding of decomposition processes in natural systems. We rely heavily on work that has been done in temperate and boreal forests, but we also refer to other ecosystems.

1.2 A Short Retrospective

In 1929, Tenney and Waksman postulated that decomposition rates of soil organic matter are controlled by four distinct factors: (1) the chemical composition of the substrate; (2) a sufficient supply of nitrogen for the decomposer organisms; (3) the nature of the microorganisms involved; (4) environmental conditions, especially aeration, moisture supply, pH, and temperature. As a general statement concerning factors that control decay, this is still valid more than 70 years later.

During the intervening 70 years, we have progressed in understanding many of the details of decomposition. We have gained a deeper insight into the effects of substrate quality and environmental factors, both on a local and regional scale. Studies have begun to show us more about the implications of decomposition on nutrient cycling. We have learned something about the microbial enzymes involved in degrading complex organic substrates. Moreover, we have begun to view decomposition as more than simply the breakdown of organic matter, but also as the formation of stable humic substances.

In the 1970s, several scientists reviewed the state of knowledge relating to plant litter decomposition. Singh and Gupta (1977) reviewed studies on plant litter decomposition with a focus on soil respiration. Schlesinger (1977) approached decomposition from the perspective of carbon balance, and brought together a large body of literature that describes carbon pools and fluxes in ecosystems of the world. His review emphasized the importance of long-term carbon storage in soils. At about the same time, Swift et al. (1979) produced a book that reviewed what was then known about decomposition in terrestrial ecosystems.

Mindermann (1968) was among the first to challenge the idea of simple negative exponential kinetics. He proposed that, as litter decomposes, the readily decomposable materials would disappear first, leaving the more recalcitrant substances behind. As a result, decay should occur at a decreasing, rather than a constant rate. As we will see, even this approach is not entirely correct, but it is closer to reality than the simple, constant-rate loss model.

Nitrogen and lignin were soon recognized as major variables that influence the rate and pattern of decomposition (Fogel and Cromack 1977; Melillo et al. 1982). During the 1980s, numerous investigators focused on the role of these two substances in regulating the decomposition process. These studies laid the foundation for our current understanding of the decay process, and are described extensively in subsequent chapters.

1.3 The Ecological Significance of Litter Decomposition and the Formation of Humus

At the biosphere level, an understanding of decomposition is important for two main reasons. First, significant amounts of carbon dioxide, methane, and nitrogen-based gases are released as products of decomposition. Currently, these so-called greenhouse gases are of great interest because of their roles in potential global climate change. Thus, factors that increase the rate of decomposition could serve to increase the amounts of carbon-based gases in the atmosphere. Second, soils represent a major sink for carbon. To the extent that carbon is stored in soil as humus and related stable organic compounds, it is not being circulated through the atmosphere. Thus, an understanding of the factors influencing the amount of humus formed, and the stability of that humus are also important in predicting global atmospheric carbon budgets (Schlesinger and Andrews 2000).

At the ecosystem level, decomposition is important for somewhat different reasons. Nutrient cycling is clearly related to decomposition. The availability of nutrients in a given soil is due in large part to the decay dynamics of the organic matter in that soil. In addition, the accumulation of organic matter in soil can greatly increase the cation exchange capacity, and have positive impacts on the nutrient holding capacity of that soil. Decomposition can influence the pH of soil; pH may be increased if plants pump basic cations up from the mineral soil to be released during the leaching and decay of litter. Soil pH can be lowered through the release of CO_2 and the formation of carbonic acid. Finally, during initial stages of decay, nutrients are immobilized and taken out of the general circulation for a while, thereby temporarily reducing nutrient availability.

Another impact of decomposition is on the diversity and stability of the ecological community. Entire food webs are based on decomposition. In fact, detrital food webs process more carbon and energy than do the better-known grazer food webs. Only a small amount of primary production is grazed by herbivores and passed onto higher trophic levels. In contrast, all ecosystem production ultimately becomes detritus.

The ecological significance of decomposition and humus formation can also be viewed from the perspective of microbial ecology. The decomposition of the litter substrate can be subdivided into phases, in which different parts of the substrate give energy to different groups of the microflora. This process supports diversity in the microbial population by supplying a rich set of intermediate degradation products, serving as energy and nutrient sources for different microbial subpopulations.

Decomposition influences other soil processes, too. For example, part of the litter forms humus and organic acids, which in part are responsible for weathering in the mineral soil, thus supporting the supply of plant nutrients. Humus may also act as a carbon source for microorganisms that subsequently produce acids and contribute to weathering. Nutrients are stored in humus. In practice, this creates a reserve of nutrients for plants that may be mobilized through a variety of mechanisms, such as fire or by stress signals from trees to their mycorrhizae.

In addition to weathering, decomposition and humus formation are involved in storage and the controlled release of nutrients to the plant and microbial communities, as well as the storage dynamics of carbon compounds. Furthermore, the decomposition of litter and humus may produce precursors for pathways other than the common one that leads to carbon dioxide. Well-known examples would be the fermentations that produce methane, and the ones that produce organic acids.

1.4 Factors Influencing Decay and Humus Formation

Decomposition begins with complex plant detritus, and produces carbon gases and humus. The process can be characterized by the rate of mass loss, and the rates of nutrient immobilization and release. In addition, the chemical composition of decaying litter changes during decay. These changes are not, in all cases, linearly associated with mass loss. Neither are the changes in composition the same for similar litter substrates decomposing under different environmental conditions. Thus, there is a complex and interacting set of factors that regulate mass loss, humus formation, nutrient dynamics, and patterns of change in chemical composition of decomposing plant litter.

In this book, factors that influence either rates or patterns of decay will be introduced: litter chemical composition, climate, nutrient availability, communities of soil organisms, and site-specific factors. The relationship between human activities and decomposition will be presented. Although there is an emphasis on boreal and temperate ecosystems, reflecting the relatively large amount of data from these systems, we have attempted to create a basic image for decomposition and dynamics of plant litter/soil organic matter (SOM).

The chemical composition of litter differs among plant species and tissue type, thus creating unique environments as regards both the larger chemical components and nutrient composition. The importance of these substances in regulating decay varies among litter types, under different climates, and at different sites. These possibilities increase dramatically when we consider a wider range of nutrients (e.g., N, P, S, K, Ca, Mg, Mn, Cd, Pb, Zn, and Cu). In addition, litter pH may have a regulating effect, both directly on the microorganisms involved in the decomposition processes, and indirectly on the solubility and thus availability of the individual nutrients. Nikolov and Helmisaari (1992) listed 58 dominant tree species for boreal Eurasia and North America. Of these, 14 species dominate in Fennoscandia and Russia/Siberia, and 15 in North America. We know the chemical and nutrient composition for only a few of these species, so that it is difficult to generalize to entire forest communities.

1.5 Accumulation of Humus and Nutrients

The nature, rate, and amount of carbon storage vary greatly among ecosystems. We know, for example, that anaerobic environments conserve their carbon compounds in peat or humus, and we normally find more carbon stored there than in drier environments. Thus, anaerobicity may be one factor, but is it the dominant one? Could the chemical composition of the litter also have an influence? Even among aerobic systems with similar vegetation, we can find varying amounts of stored humus, from almost bare mineral soil with about 200–300 g humus m^{-2} on top of the mineral soil, to layers nearly 150 cm thick and with ca. 50 kg humus m^{-2}. Therefore, there may be mechanisms for long-term humus accumulation that can explain the wide range of accumulated humus. Disturbances such as fire, harvesting for forestry, or agriculture and cultivation can clearly reduce soil organic matter content. A natural question is thus what could such a mechanism be? Is there only one or does a series of coincidences rule whether, and to what extent humus will accumulate?

A humus layer of ca. 50 kg humus m^{-2} accumulated over ca. 3,000 years (Wardle et al. 1997) represents, on average, an annual accumulation of ca. 17 g humus m^{-2}. Such a powerful mechanism for storage of C could mean a long-term storage of 0.1 to 0.3 Pg (petagram = 10^{15} g) $year^{-1}$, considering the whole boreal forest zone of 1–2 billion ha (UNECE/FAO 2000), which accounts for 10 to 20% of the currently estimated 1–2 Pg unidentified sink for carbon (Woodwell et al. 1998; Houghton 2001).

There is often a rather resistant part of the litter remaining, one that may be stored on a long-term basis (e.g., millennia) and be regarded as humus. This long-term storage encompasses both carbon and nutrients. For carbon, amounts of the magnitude of 50–108 kg humus m^{-2} have been found in the form of organic layers (Berg et al. 1993c; Wardle et al. 1997). For nutrients such as N and P (see Chap. 11), amounts of 760 and 39 g m^{-2} have been measured, respectively. A long-term storage, and in such amounts, raises doubts about the concept of a steady state suggested by a number of authors, such as Schulze et al. (1989).

Plant litter contains nutrients at differing concentrations, and is thus a carrier of nutrients that are released largely when the organic matter is being decomposed. The release of nutrients may take place in different ways, depending on the type of litter. Foliar litters may leach nutrients, with particularly mobile ones such as K being leached to a high extent. Other nutrients may be partially leached, which may depend on their concentrations in litter. The major nutrients, such as N, P, and S, can be partially leached immediately at litter fall. This immediate leaching may be followed by an accumulation or a net uptake of nutrients to the litter, with a later net release. The release of such structural nutrients is often proportional to litter mass loss, and thus regulated by the same factors that regulate the rate of litter mass loss. Normally, all nutrients are not released. Available studies indicate that some components, such as most heavy metals, are not released from litter, even in clean, unpolluted systems, but rather accumulate so that when the decomposition process becomes extremely slow, close to the humus stage, the remaining part has a rather high concentration of such nutrients.

The boreal forest has a multitude of different storage pools of carbon, in dead organic matter, not only in the form of numerous chemical compounds of which we will never know more than a fraction, but also on a larger scale in the form of different ecosystem niches. On an even larger scale, we may distinguish between living forests with soil systems that are more or less aerobic and more or less anaerobic. Both soil system types would be expected to store carbon on a long-term basis unless disturbed by, for example, fire, ditching, or site preparation.

1.6 The Contents and Organization of the Book

This book brings together much of the current understanding of the decomposition process as it occurs in forested ecosystems, using examples primarily from boreal and temperate forests. The book begins with a presentation of decomposition as a process (Chap. 2). Terminology related to decomposition is briefly introduced, including litter, humus, mineralization, and immobilization (also see Glossary). The overall process of decomposition is reviewed from the input of fresh litter, through the dynamics of microbial and physical decay to the formation of meta-stable humic substances. An examination of litter quality includes a presentation of the cellulose, hemicellulose, and lignin structures, and the enzymes attacking these. A simple conceptual model is introduced that illustrates the decomposition processes and identifiable functional steps. The model, which is used as an organizing principle, encompasses three stages of litter decomposition with contrasting functional properties.

The book then moves to examine the biological agents of decay (Chap. 3). The most important groups of decomposer organisms are fungi and bacteria, which in boreal coniferous forests may be responsible for more than 95% of the decomposition. Their importance in deciduous forests is somewhat less (Persson et al. 1980). Even in tropical forests and grassland communities where herbivores may consume larger proportions of net primary production, they are notably inefficient, and microorganisms are still the major decomposers. The chapter, therefore, has an emphasis on the microflora. It emphasizes functional roles of organisms, rather than their taxonomy. The main groups of fungi and some bacterial genera will be mentioned, but with an emphasis on function and activity.

With this biological background, the next two chapters (Chaps. 4 and 5) examine the importance of initial and changing chemical composition of decaying litters. The initial substrate for decomposition is newly shed litter. Its chemical composition determines both the composition of the microbial community, and the course and pattern of the decomposition process. Both the organic and the nutrient composition of litter vary not only with species, but also with climate and site properties. Generally, deciduous foliar litters are richer in nutrients than are coniferous ones. Organic components are also highly variable; lignin concentration may vary from a few percent in some litters, up to about 50% in some others.

As the decomposition process proceeds, chemical changes take place in the decomposing litter, such as increases in the concentrations of some nutrients and most heavy metals. The concentration of the organic component lignin increases, too, whereas changes in concentrations of the main carbohydrates vary. A basic pattern of chemical changes, and an overview of how such changes vary depending on initial chemical composition are discussed.

In Chapter 6, attention is shifted to the influence of changing litter quality on the decay processes. This chapter shows that the influences of selected litter components change dramatically during the process, sometimes even reversing the direction of the effect. For newly shed litter, differences in initial N, P, and S levels influence the rate of the decomposition process. In a later stage of decay, the increasing lignin levels suppress the decomposition rates in ways that interact with N concentration and climate. Finally, the decomposition process normally reaches a stage at which decomposition goes so slowly that the stage may be approximately described by an asymptote or a limit value. Factors that influence this limit value are reviewed and evaluated.

Decomposition occurs in a natural environment where climate (Chap. 7) and other site factors (Chap. 8) can have a profound influence on the decay dynamics. Climate is a powerful regulating factor for litter decomposition, as shown on a larger scale using actual evapotranspiration (AET; Meentemeyer 1978), and will directly influence litter decomposition rate, especially that of the newly shed litter. This effect of climate will decrease as decomposition proceeds. We will use the conceptual model introduced in Chapter 2 and developed in Chapter 6 to describe how these effects change with the phase of decomposition. The other major environmental factors that influence decomposition are edaphic: soil texture, nutrient availability, and soil chemistry. For example, a site factor that may have an influence is the parent rock material. Granite parent material, being nutrient-poor, gives a poor litter substrate, whereas one of limestone often increases the nutrient content of the litter. The texture of the soil (sand and clay content) influences nutrient mobility and hydrology, which can affect the decomposition rate both indirectly and directly.

Some litter types, notably wood and roots, behave differently from foliage, and these substrates require treatment in a separate chapter (Chap. 9). Woody debris and roots may represent a large proportion of the total litter input into an ecosystem. The decay of these substrates is often very different from that of foliar litter, and the course of the decomposition process is directly dependent on whether the wood is attacked by white-rot or brown-rot fungi. Although much less data are available on these litter types than for foliar litter, it appears that the attack by white-rot or brown-rot fungi is an important factor for determining both the rate and course of decomposition, and for the long-term accumulation of soil organic matter.

As knowledge of decomposition has grown, scientists have created a number of models to describe or predict decay (Chap. 10). These models vary in intent and complexity. Simple mathematical models have been used (e.g., a linear one, and simple exponential ones) that can describe the process, including rates of decomposition, and that are in agreement with conceptual models. Four such models are discussed – single exponential, double exponential, an advanced triple exponential, and an asymptotic model – and are evaluated in terms of recent findings.

Many ecosystem properties and processes are closely related to decomposition, and these are briefly reviewed in Chapter 11. Topics closely related to decomposition include nutrient cycling, soil organic matter formation, and carbon sequestration and efflux. A major rationale for studying decomposition is the strong link to carbon and nutrient cycling and storage. Large amounts of nutrients may be stored in the soil organic matter of an ecosystem, both as integral components of organic residues and as attached ions on organic colloids. In addition, the role of humus in soil structure and function, as well as the potential importance of forest soils for long-term carbon storage are discussed.

A survey of how selected human activities influence decomposition processes is the topic of Chapter 12. Ecosystems will respond differently to climate change. For example, a change in humus accumulation is predicted for part of the taiga belt. Forestry and agricultural practices, including fertilization and site preparation, will cause changes in the decomposition process.

The book concludes with a chapter that focuses on carbon sequestration rates. This chapter reviews three case studies covering the same forested area, with each case study based on a separate method. This is a logical step building upon the accumulation of organic matter discussed in Chapter 11. New data appearing in recent years make it possible to present different approaches to calculate carbon sequestration in forest soils. In Chapter 13 we describe and compare these three approaches, and validate them based on independent studies on carbon sequestration. We also place these values within the context of other studies of carbon dynamics in forest soils.

The terminology used in decomposition studies is sometimes confusing, or even misleading. In order to make our text as clear as possible, we have provided a glossary that explains and defines terms used in this book. We have also provided an appendix that gives Latin names together with English names for all vascular plant species that we discuss. We have used the plant names as they were given in the original articles. As some species have different common names in American and European English, we have given both names.

1.7 Motives for the Present Synthesis

We hope this book will help aim research efforts toward furthering our understanding of decomposition. During the past several decades, numerous investigators have studied many aspects of the decomposition process. At the same time, both scientists and the public have become concerned about the increasing concentrations of carbon gases in the atmosphere, and the implications for global climate change. As a result, we felt the need to compile existing recent information on boreal forest litter and humus, with the aim of giving a new basis for understanding what regulates the buildup and stability of humus. Much of the book focuses on the processes and controls of the early stages of decay, but these early stages influence the long-term carbon dynamics of each ecosystem. A number of basic questions are raised, including:

- Is there a long-term buildup of humus?
- Do forest systems exist with very high, or very low buildup rates?
- Can we influence the humus buildup rate?
- Are there any large-scale threats to the natural course of the process?

This book is based primarily on data and conclusions made from field studies. We have focused on undisturbed forest systems in an attempt to create a basic understanding, and basic mechanisms for the decomposition and transformation processes. The book focuses on boreal systems for the obvious reason that there are more data about these systems available for analysis. Of course, we have used information from temperate systems when applicable, and there have not been any conflicting conclusions, suggesting that the synthesis so far may be applicable to both kinds of systems.

On the topic of litter decomposition, we have not identified different schools of thought, as it appears that this field has not yet developed far enough. We would rather consider different directions of the research work. Thus, some scientists have attempted to understand the mechanisms of degradation, whereas several groups have searched for indices for prediction of long-term decomposition rates.

1.8 New Developments Included in the Second Edition

Since the first edition was written, the interest in carbon sequestration, and in the release of carbon gases with relevance for global climate change have both increased. Additional studies on the factors that regulate the decomposition process have allowed us to develop a number of novel sections.

The importance of manganese as a factor that influences lignin decay has become more obvious. In Chapter 2 we develop a new section on the role of Mn, and also expand our conceptual model to include a role for it in the decomposition of plant litter. The tools of molecular biology are being increasingly used in the life sciences, including decomposition studies. These tools show promise for studying the composition of microbial communities, and we have developed a new section in Chapter 3 devoted to the use of molecular techniques for the study of organisms involved in decomposition. Novel findings about relationships between the N content of litter and climatic variables on a global scale have been added to Chapter 4, allowing us to extend to a nearly global scale some of the observations described in the first edition. In addition, we review new data on nutrient retranslocation prior to leaf abscission. We also expand on our discussion of lignification in the light of data from species that follow decomposition patterns that differ from the general model. In Chapter 8, we have added a discussion of data on carbon accumulation in forest floors relative to soil properties of the site. Finally, Chapter 13 is a completely new chapter that demonstrates the potential for carbon accumulation in forest soils using three different case studies from Sweden.

Chapter 2
Decomposition as a Process

2.1 Litter Decomposition – a Set of Different Processes

Decomposition of plant litter involves a complex set of processes including chemical, physical, and biological agents acting upon a wide variety of organic substrates that are themselves constantly changing. Due to the immense diversity of possible factors and interactions, decomposition in a natural setting can be described in general terms only. In spite of this complexity, several major processes are commonly involved, and general trends can be outlined.

Litter, when shed by the plant, is in its simplest state. From this initial state, litter chemical composition changes, with some litter components disappearing rapidly, some slowly, and some beginning to disappear only after a time delay. Perhaps non-intuitive, but very significant, is the fact that some substances, particularly nutrients, are imported into the decomposing substrate, and new organic compounds are synthesized during decomposition. Due to the heterogeneity in both litter composition and factors influencing decay, decomposition of litter is far more complex than decay of, for example, a radioactive isotope.

The bulk of plant litter consists of varying amounts of several major classes of organic compounds. The relative proportions of these compounds vary with plant part (for example, leaves, stems, roots, bark), and among species (see Chap. 4). These major groups of compounds can be classified according to their molecular size, their solubility, and their primary constituents. Some materials, notably sugars, low-molecular-weight phenolics, and some nutrients, are readily lost from litter through dissolution and leaching, combined with the action of rapidly growing opportunistic microorganisms. Larger macromolecules, including cellulose, hemicelluloses and lignin, are degraded more slowly. During decay, condensation of phenolics and lignin degradation products, combined with the import of nutrients, results in the net accumulation of newly formed substances. The relative magnitudes of the main flows (Fig. 2.1) are thus different among litter types, and are influenced by litter chemical composition (see Chap. 6).

We regard “litter mass loss”, or “decomposition”, as the sum of CO_2 release and leaching of compounds, including both C compounds and nutrients. Leaching is simply the loss of nutrients and incompletely decomposed organic compounds transported out by water from the remains of decomposing litter (see Glossary).

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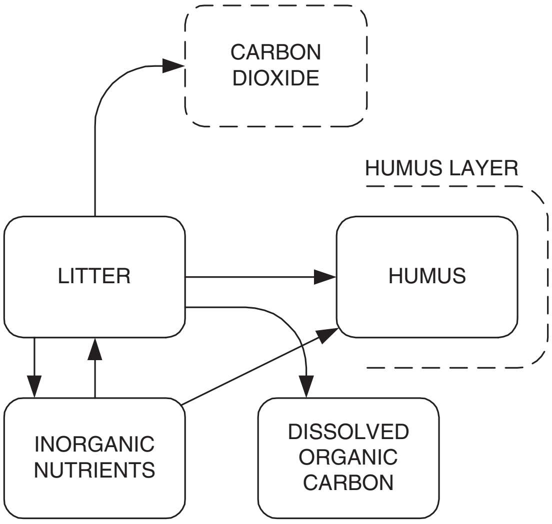

Fig. 2.1 Generalized pathways for transformation of litter to humus and inorganic C. When the litter is shed and its decomposition has started, the microorganisms begin forming carbon dioxide, and soluble compounds that are initially present may be leached out. Newly formed compounds that are stable but water-soluble are also leached out (dissolved organic carbon, DOC), and long-term stable remains form humus

The interpretation of mass-loss data during the initial stages of decay may be influenced by a high leaching rate of water-soluble material that is not physiologically modified by microorganisms until after leaving the litter (McClaugherty 1983). These dissolved materials may be lost from litter, and subsequently sequestered by humus or clay particles. In such cases, the materials are lost from a particular substrate, but are retained in the soil ecosystem.

Under aerobic conditions, microbial decomposition results in a release of CO_2 that exits the system. Under more anaerobic or oxygen-limited conditions, such as in a temporarily waterlogged organic matter layer, anaerobic decomposers may produce organic acids, rather than CO_2. This may also happen with aerobic decomposers that suffer from a lack of oxygen. For example, acetic acid may be released instead of CO_2, and either be decomposed outside the cell, or be stored and fulfill another role (see Chap. 11).

In later stages of decomposition, recalcitrant substances become more abundant in the residue, and in some cases the rate of decomposition approaches zero. In 1974, Howard and Howard estimated limit values for the decomposition of some species of leaf litters that were incubated in an animal-free environment. Using litter decomposition data from nutrient-poor forest systems, Berg and Ekbohm (1991) also estimated such limit values, indicating a stage at which the decomposition rate nears zero (Fig. 2.2A, B).

This chapter describes and explains the principal microbial processes associated with litter decomposition that results in mass loss or CO_2 release. We present basic

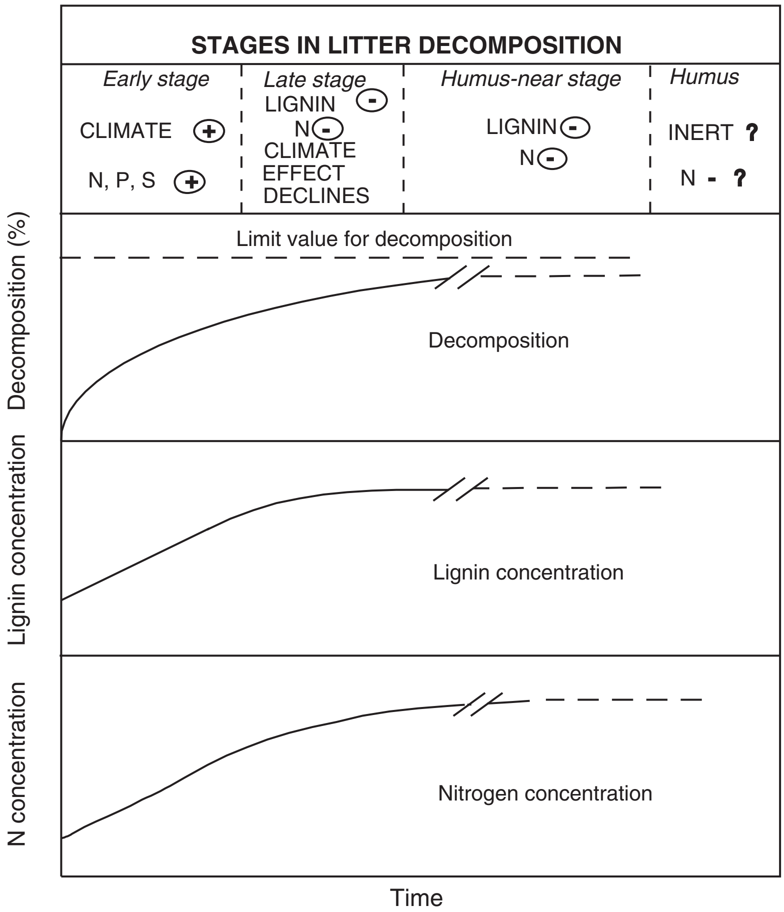

Fig. 2.2 **A** Stages in litter decomposition. We may distinguish three phases before humus is formed (*top*), which have different properties in terms of decomposition (and CO_2 release). In the *early stage*, decomposition of solubles, and of unshielded cellulose and hemicelluloses takes place, in a process influenced by climate. In the *late stage*, the influence of climate on decomposition gradually decreases to essentially zero. In the same late stage, N may have a negative influence on lignin degradation through a repression of de novo ligninase synthesis and/or by creating a barrier based on chemical bonds between lignin remains and N. Finally, in a *humus-near stage*, the decomposition reaches a limit value. From the onset of decomposition, the concentrations of N and lignin increase. The + and – *signs* indicate positively and negatively related effects, respectively, to increased concentrations of nutrients and lignin

principles about the microbial degradation of the main components of litter, such as cellulose, different hemicelluloses, and lignin. The process of litter mass loss is described in some detail for one litter type, namely, Scots pine needles. We organize our description using a conceptual model that separates the decomposition process *of this species* into different phases. As litter passes through these phases,

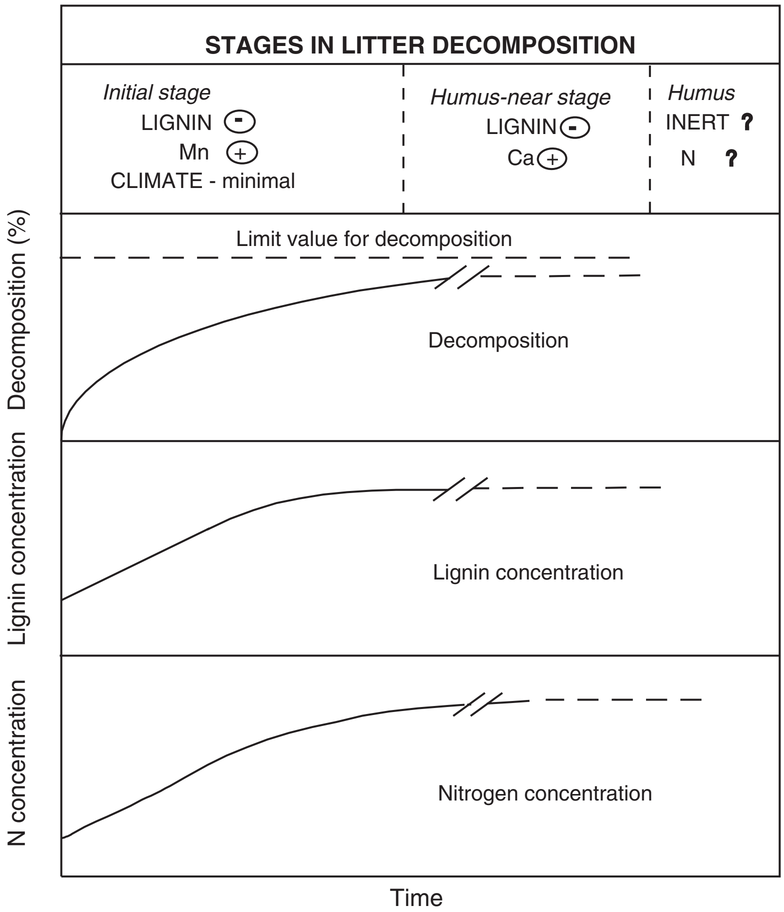

Fig. 2.2 B Stages in litter decomposition. We may distinguish two phases before humus is formed (*top*), which have different properties in terms of decomposition (and CO_2 release). Initially, decomposition of lignified tissues takes place, a process that is minimally influenced by climate but moderately influenced by Mn concentration in the litter. In comparison to the three-stage model, we view this such that the early stage is absent or nearly nonexistent. Later, in a *humus-near stage*, the decomposition approaches a limit value. From the onset of decomposition, the concentrations of N and lignin increase. The + and – *signs* indicate positively and negatively related effects, respectively, to increased concentrations of nutrients and lignin

the factors that regulate the decay process change. The model connects the various developmental processes, beginning with newly formed litter and continuing to the formation of humus. Differences in the importance of substrate properties (for example, the influence of N, Mn, and lignin) as the decay process unfolds are emphasized. Recent development has allowed us to introduce a further model (Fig. 2.2B), which today encompasses a few species that deviate in a few particular cases from the basic model described above.

2.2 Definition of Litter Decomposition

Litter decomposition may in part be defined by the method used to study it. A very common method is the litterbag, used for incubations in the field or in laboratory microcosms. Another variety of direct incubation is tethered litter. With these kinds of measurements, decomposition is evaluated in terms of loss of mass, and studies normally do not distinguish between what is respired as carbon dioxide, and what is leached out of the litter or lost due to fragmentation, unless these processes are investigated separately. In terms of mass, mobile nutrients such as K and Mn are also part of the loss. Ingrowth of microbial biomass, and the transport of nutrients into the litter result in the movement of mass into the litter that was not there originally. Thus, what is often called “litter mass loss”, or “decomposition”, is a *net mass loss*, although the ingrowth of mycelium normally is negligible in terms of mass. As we will see later, the in situ incubation of intact litter is, from several points of view, preferred to laboratory incubation methods but may still be compared with laboratory studies.

When litter decomposition is measured as respiration, only part of the mass-loss process is quantified. No specific term has been suggested for this more specific process, but terms such as “release of CO_2”, “C mineralization”, and “litter respiration” are used. We will use “litter CO_2 release” (see Glossary in Appendix I) in this book. Thus, the two processes of “litter CO_2 release” and “leaching” together should correspond to “decomposition” as the term is used today (Fig. 2.1), although loss to fragmentation could influence mass-loss measurements.

Distinguishing litter-based respiration from other respiration in the field is difficult. Methods to separate other sources of respiration – for example, root and faunal respiration that are not directly associated with litter decomposition – need further development, although some first steps have indeed already been taken (cf. Högberg et al. 2001).

In boreal forest systems, microorganisms carry out more than 95% of the litter decomposition (Persson et al. 1980). Before it falls, some microorganisms are present on the litter. Most of these are not involved in decomposition, unless they are pathogens. After litter fall, fungi are generally the first invaders, penetrating the leaf through openings and thus invading the fresh substrate. The less mobile bacteria appear later, and there is also a succession of fungal species with different physiological properties, depending on the decomposition stage and thus the substrate quality of the litter.

2.3 Degradation of the Main Groups of Compounds in Litter

2.3.1 Degradation and Leaching of Soluble Organic Substances

Foliar litter may contain considerable levels of soluble substances. For example, concentrations of water-soluble substances between 7% in Scots pine needles and 30% in grey alder leaves have been recorded (see Chap. 4). Part of these substances may be leached out of the litter (McClaugherty 1983; Bogatyrev et al. 1983), and part may be degraded in the litter structure. There are four principal groups of soluble organic material in litter: sugars, phenolics, hydrocarbons, and glycerides. The soluble sugars are predominantly mono- and oligosaccharides that were involved in metabolic processes of the plant. The soluble phenolics are low-molecular-weight compounds that either serve as defensive agents against herbivory, are lignin precursors, or are waste products; partly hydrolyzed tannins are a common example of soluble phenolics. Phenolics are highly variable in their solubility, and many have a tendency to condense into less soluble forms, or to react with larger molecules. Not all nutrients bound to organic molecules form soluble compounds, and many are insolubly bound into organic complexes.

2.3.2 Patterns of Degradation of the Main Organic Compounds in Litter

Decomposition generally follows a sequential pattern with different classes of organic compounds dominating the decay process as it proceeds, and it appears that this may be related to the fiber structure and the relative composition of compounds. Based on new information, we may distinguish two kinds of pattern.

A First, Established Pattern. In a first established pattern (Fig. 2.2A), the degradation of soluble and low-molecular-weight compounds dominates the first stage of litter decay. Next, hemicelluloses, especially those that are arabinan-based, begin to disappear. Somewhat later, cellulose degradation is the dominant activity, and finally lignin degradation becomes dominant. Although individual processes may dominate a particular stage of decomposition, any or all the processes may occur to some extent throughout the decay continuum (Figs. 2.2A, 2.3; Table 2.1). This general pattern has been observed in numerous studies. Aber et al. (1984) described the patterns for 12 types of forest litter. One early interpretation was that there are different decomposition rates for different chemical components (Mindermann 1968), an opinion that provides a reasonable first approximation but is not quite correct.

In a study on Scots pine needle litter the degradation of single components was followed by Berg et al. (1982a; Fig. 2.3). The onset of mass loss due to polymer carbohydrate degradation, namely, cellulose and single hemicelluloses, began after different periods of incubation. The degradation of arabinan and galactan begins almost immediately after litter fall (Table 2.1). Degradation of cellulose and mannan starts later, with the first measurable loss of these components being observed after ca. 1 year. Figure 2.4 shows that the amount of cellulose increases before a decrease starts, and a net decrease does not start until after about 1 year. For xylan, the degradation started about half a year later, while with lignin, the first net loss was not noted until after 2 years (Figs. 2.3, 2.5).

The degradation pattern probably is related to the arrangement of the components in the fiber (cf. Fig. 4.1). Microorganisms may first attack and degrade those

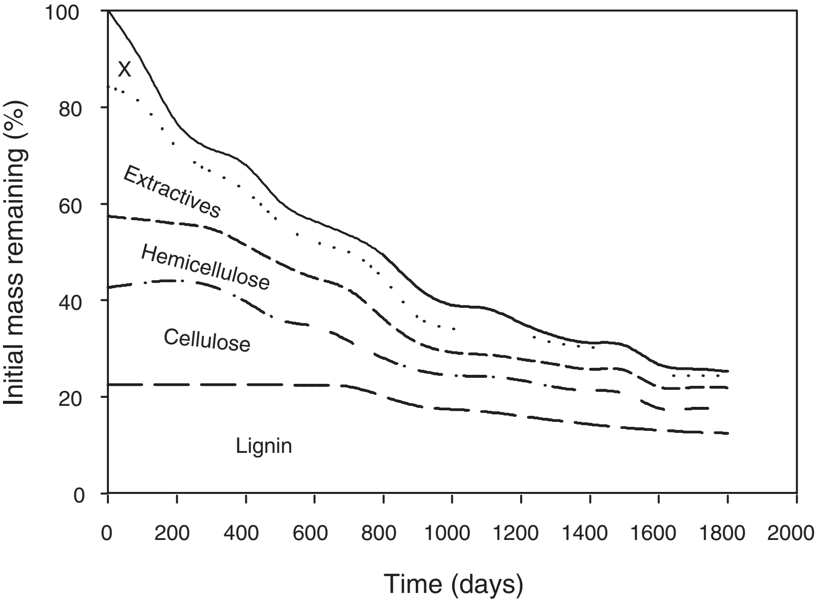

Fig. 2.3 Disappearance of the main organic-chemical components in Scots pine needle litter decomposing in a boreal Scots pine forest. *X* denotes unidentified compounds (from Berg et al. 1982a)

Table 2.1 The time for onset of net mass loss of different organic-chemical components and their relative degradation rates in decomposing Scots pine needle litter (cf. Fig. 2.5; data from Berg et al. 1982a)[a]

	Lignin	Cellulose	Mannans	Xylans	Galactans	Arabinans
Onset (days)	726	376	376	545	Immediate	Immediate
Rate (% day^{-1}) 0–726 days	-	0.1041	0.0647	0.1077	0.0633	0.1461
Rate (% day^{-1}) >726 days	0.0418	0.0393	0.0526	0.0461	0.0375	0.0449

[a] The rates given refer to two stages of decomposition, namely, the early stage when the unshielded polymer carbohydrate components and solubles are degraded independently of lignin, and the late stage when the degradation of carbohydrate components is regulated by the degradation of lignin and all components have similar rates

carbohydrates that are located on the more available outer structures. A practical consequence of this is that after the onset of decomposition, the relative degradation rates of the different components are initially different (Table 2.1; Fig. 2.5). Figure 2.5 illustrates the typical pattern. When degradation of lignin begins, there may be little or no easily available carbohydrate, and the microbial community must change to one that degrades lignin. In this environment, namely, in Scots pine needle litter with an N concentration above the initial level of 4 mg g^{-1}, there may

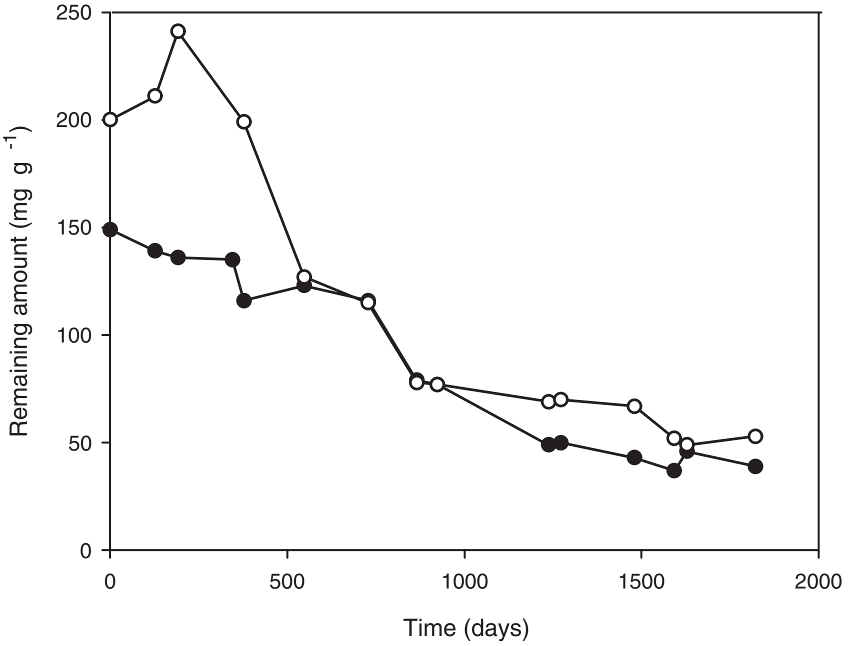

Fig. 2.4 Disappearance of cellulose (○) and hemicelluloses (●) in Scots pine needle litter decomposing in a boreal Scots pine forest (Berg et al. 1982a)

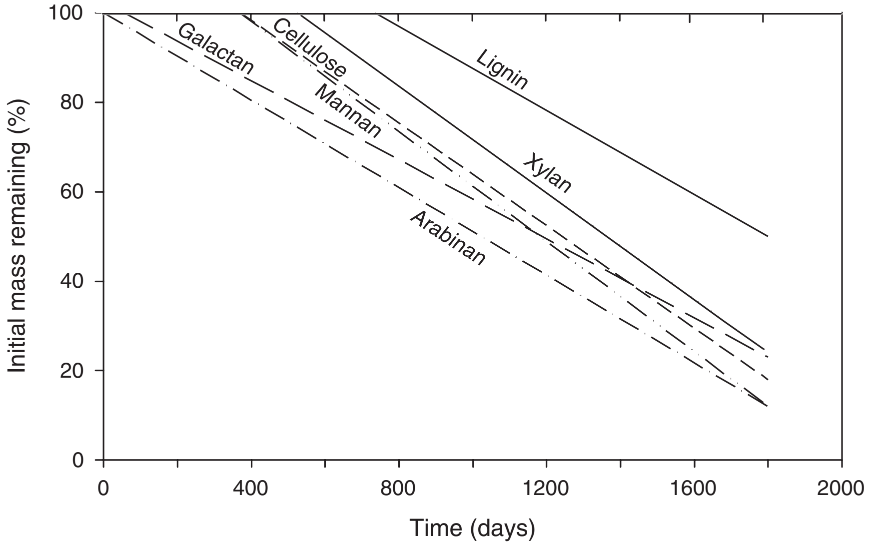

Fig. 2.5 Onset of decomposition of different polymer carbohydrates and lignin, showing the different rates of decomposition in the initial and the late phase. Decomposition rates are given in Table 2.1 (data from Berg et al. 1982a)

be a suppression of lignin degradation (cf. Sect. 6.2.2); in this study, its rate was less than half of the initial rate of carbohydrate degradation. The rate of lignin degradation from the start of year 2 until the end of year 5 was about 0.04% day^{-1}. When we compare the degradation rates of the carbohydrates during the same period, they were similar in magnitude to that of lignin.

This suggests that once lignin degradation has started, these components are degraded at the same rates because they are so well mixed in the fiber structure that they cannot be degraded separately. It thus appears that we may see at least two different groups of carbohydrates: those for which degradation starts immediately after litter fall (hemicelluloses dominated by arabinans and galactans), and those made up of mannans, cellulose, and xylan for which degradation starts later. This could mean that the latter group of components is less available as a result of being more lignified. In addition, a hemicellulose such as arabinan is easily hydrolyzed at a lower pH (O. Theander, pers. comm.).

Few attempts have been made to follow the degradation of simple soluble components in litter, and it should be pointed out that most studies describe net disappearance only. The soluble fraction is challenging to study, due to the complexities of tracing the formation of new solubles during decomposition, and the disappearance of the same solubles due to leaching or metabolism. For example, glucose, which is present initially in newly shed litter, is also produced from decomposing cellulose and thus is found even in the later stages of decomposition. The same applies to the simple sugars of hemicelluloses. Similarly, several phenolic substances are found in newly shed litter, but are also produced during the degradation of lignin.

Berg et al. (1982a) found that compounds such as triglycerides and hydrocarbons that are soluble in light petroleum disappeared quickly, whereas fatty acids and diterpene acids remained. Compounds such as simple sugars – for example, glucose and fructose – or ones related to simple sugars, such as glycosides and pinitol, were also degraded very early and at a high rate (Fig. 2.6).

A New, Additional Pattern. Recent findings suggest that we can distinguish a pattern that deviates from the traditional one to some extent. It is possible that the degradation of lignin, for reasons not yet known, assumes a greater importance immediately after litter fall. At the same time, in this pattern the role of manganese concentration in the litter is important for the degradation of lignin (Sect. 2.4.4) from the onset of decomposition, rather than emerging as a factor later during the process.

2.4 A Model for Decomposition from Newly Shed Litter to Humus-Near Stages

In the section above, we demonstrated that the decomposition patterns for non-lignified organic-chemical components differed from those of these same components in lignified tissue. This may be a general basis for considering rate-regulating factors, but the fraction of lignified tissue may vary among litter species, and possibly among stands and locations. A given litter may have only a certain fraction

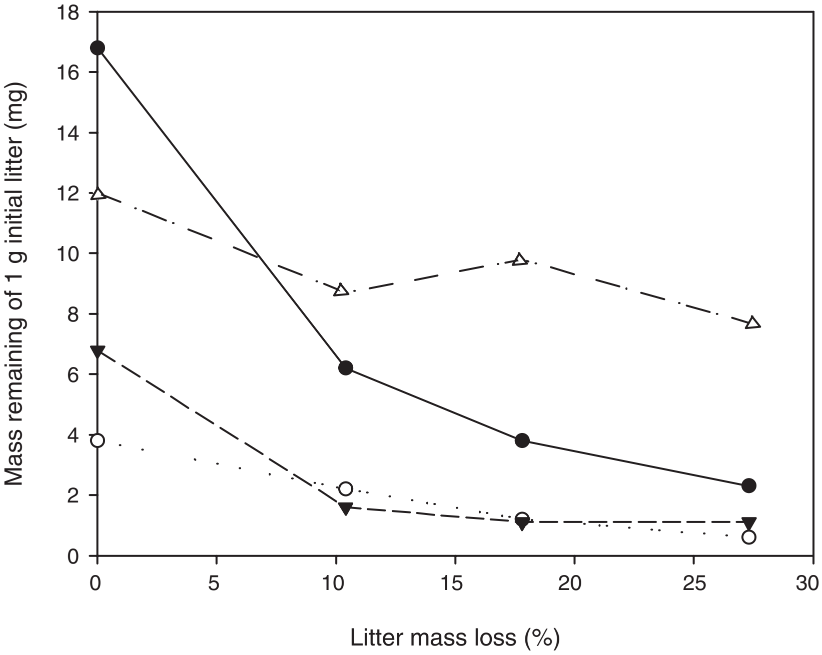

Fig. 2.6 Disappearance of some groups of solubles in the very early decomposition phase (Berg et al. 1982a): combined simple sugars (●), hydrocarbons (○), triglycerides (▼), and acidic compounds (△)

of its holocellulose lignified, while another litter may have its holocellulose completely embedded in lignin, a fact that may change its decomposition pattern and rate-regulating factors. We can use information obtained from pure-culture and physiological studies on microorganisms, compare this to the degradation of different components, and organize a three-stage conceptual model (Fig. 2.2A). It has been recently shown that as additional litter species are investigated, the original three-stage model (Berg and Matzner 1997) can be further developed and modified, and we can now see differences in the initial stage (Fig. 2.2B), possibly due to the level of lignification of the holocellulose. Thus, when we describe the different stages, we include the range in behaviors observed within the various steps. In the two cases, explanations are given for the different steps, which are connected to in situ decomposition experiments for litter and humus. Although each stage can be described separately, the process is more accurately assessed as a continuum in which transition points cannot be defined precisely.

In the three-phase model describing the decomposition of litter into humus, the process may be subdivided into functionally defined stages: (1) newly shed litter – early decomposition stages; (2) late stages for partly decomposed litter; and (3) humus-near stages, or limit-value stages where litter is close to becoming stable humus. These are the main stages that we intend to interconnect. The model is focused toward the effects of climate, the effects and roles of nutrients in the early phase, and of lignin and N in the late phase, but also accounts for theories of humus formation (humus-near stage, cf. above). As an introduction, we briefly explain the essential contrasts between the effects of N in newly shed litter and in litter that approaches humus. Information so far available has indicated that the early phase may encompass different fractions of litter mass, apparently ranging from almost no mass to possibly 30–40% percent. Thus, the decomposition of some litter species may start with the degradation of lignin. In these extreme cases, it may simply be that the early decomposition stage is missing, possibly due to a complete lignification of the holocellulose in the litter that is shed.

The reasons for subdividing the decomposition process into different stages are rather straightforward. The substrates – for example, needles or leaves – that microorganisms decompose are far from homogeneous. On the level of plant cells, the polymers lignin, cellulose, and hemicelluloses are structurally organized (see Figs. 4.1, 4.2), and the main parts of the cellulose and hemicelluloses are found in the primary cell wall, whereas lignin is distributed in the secondary wall and in the middle lamella (Eriksson et al. 1990). One result of the distribution in the cell wall is that there is a separation of carbohydrates into those that are not lignified and those that are encrusted into lignin. Microorganisms that are not lignolytic may degrade only the former. We discuss the possibility (Chap. 4) that foliar litter of some litter species may have a structure with a much higher level of lignified tissue (Fig. 4.1), which may explain the very short early phase, and the fact that the litter can not decay to a significant extent until the onset of lignin degradation. In the following sections, we describe these different phases or stages. Still today it is not clear if this lignification is due to species-related differences, or properties related to, amongst others, the balance of nutrients in the soil that may influence, e.g., the formation rate of lignin. An example of this may be boron (see Sect. 4.3.5).

2.4.1 Degradation of Solubles and Non-Lignified Carbohydrates

The ingrowth of microorganisms, mainly fungi, into the litter may begin prior to litter fall, but most of the ingrowth of decomposers takes place when the litter has reached the ground. The more fast-growing microorganisms start invading the litter, with part of the litter C becoming microbial biomass and part CO_2. Although the microorganisms degrading the polymer carbohydrates and lignin may be partly the same, the physiology of the degradation of celluloses and lignin is different, as are the induced enzyme systems (Chap. 3). It would therefore be reasonable to use this physiological background for a definition of different steps in the decomposition process, based on substrate and nutrient availability.

The degradation of solubles, and the early degradation of hemicelluloses and cellulose are rather rapid processes, and raised nutrient levels, in particular N, P, and S that are normally the main limiting nutrients for microbial growth, stimulate microbial degradation of cellulose, hemicelluloses, and many solubles.

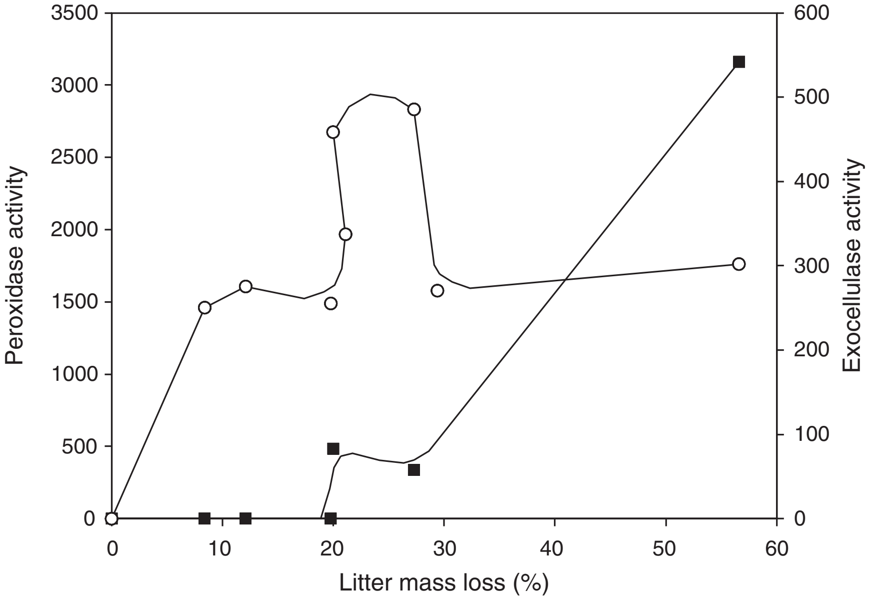

Fig. 2.7 Development of enzyme activity was followed during the decomposition of Scots pine needle litter. Cellulases (○) appear when the decomposition has proceeded for some time, and a peroxidase (■) appears later, indicating the onset of lignin degradation (C. McClaugherty, unpubl. data)

In a field experiment, the measured early-stage rates were at least twice as high as in the late stage. The relative degradation rates of the polymer carbohydrates are relatively high, ranging from 0.063 to 0.146% day^{-1} (Table 2.1). In the late stage, the rate of decomposition of these same components can range between 0.038 and 0.053% day^{-1}. The higher rate of disappearance of arabinan may be due to this hemicellulose being more easily hydrolyzed and/or less protected. Thus, the cellulose and hemicelluloses were degraded rather quickly until the unshielded portions were consumed. Investigations of the changing patterns of enzyme activities in decomposing litter also support this subdivision into different phases (Fig. 2.7). The cellulolytic enzymes appear relatively early, reach a maximum, and decrease before peroxidase (part of the lignolytic system) appears.

The majority of studies on litter decomposition present results from the stage when the litter is recently shed, where normally positive relationships are seen between litter concentrations of N, P, or S and factors such as the mass-loss rate or litter CO_2 release (Taylor et al. 1989; Berg et al. 1997). Also climatic factors have a strong influence on the turnover rate in newly shed litter (Jansson and Berg 1985; Berg et al. 1993a). This description of decomposition in an early stage thus applies to a three-phase model. For fresh litter with only lignified tissue, this phase should not really be distinguishable.

The simplified, albeit incorrect picture is that climate regulates the rate of decay in early stages on a regional scale, and substrate quality on a local one. This picture holds in a few cases, but is far from general. We discuss the basic model with this reservation, while recognizing that local climate and nutrient availability appear to dominate the early stage of decomposition.

2.4.2 Degradation of Lignin, Modified Lignin, and Lignified Holocellulose Tissue

In decomposing foliar litter, there is an increase in concentration of the relatively resistant compound lignin, and its recombination products that, from the point of view of degradation, resemble lignin (Fig. 2.2A, B). This may be explained by the fact that the lignin-degrading microorganisms, under the nutrient conditions that exist in most foliar litter types, grow more slowly than those degrading the polymer carbohydrates, and that lignin as a chemical compound in foliar litter normally is degraded more slowly than many other components (cf. below, Table 2.1). A basic condition appears to be that the fiber structure enables the holocellulose to be degraded to a higher extent than lignin. Eventually decomposition will reach a condition in which the litter contains primarily material that is rich in lignin, and any remaining cellulose and hemicelluloses are enclosed and protected by lignin and newly formed humic compounds. The point at which this occurs varies among litter types, and with environmental conditions. For Scots pine needle litter, Berg and Staaf (1980a) estimated this to be at about 30% mass loss.

Under the conditions present in many partly decomposed foliar litters (viz. low levels of available carbohydrate, and relatively high N levels; see below), lignin is degraded slowly.

When it was found that a lignolytic fungus had an improved degradation of lignin in the presence of a more easily metabolized C source (e.g., cellulose), several attempts were made to explain differing lignin degradation rates using different indices. These indices were all based on relative amounts of cellulose, hemicellulose, and lignin. Some investigators have used the lignin concentration itself (Fig. 2.8); others have proposed quotients between the lignin in litter and the holocellulose plus lignin parts (HLQ; Berg et al. 1984b; McClaugherty and Berg 1987), or between lignin and lignocellulose (LCI; Aber et al. 1990). These developments have not improved our understanding of the degradation rates of either lignin itself, or of litter in the late stage of decomposition where the lignin degradation rate regulates the decomposition of the whole litter (Berg and Staaf 1980a; Berg et al. 1987).

The effect of lignin as a rate-retarding agent may be illustrated by a relationship between increasing lignin levels in litter and the decomposition rate of litter (Fig. 2.8A). Several scientists have observed this kind of relationship (Fogel and Cromack 1977; Meentemeyer 1978). A notable phenomenon (Meentemeyer 1978; Berg et al. 1993e) is that the influence of lignin on the decomposition rate is so strong that the effect of climate is not only suppressed, but appears to disappear completely when lignin

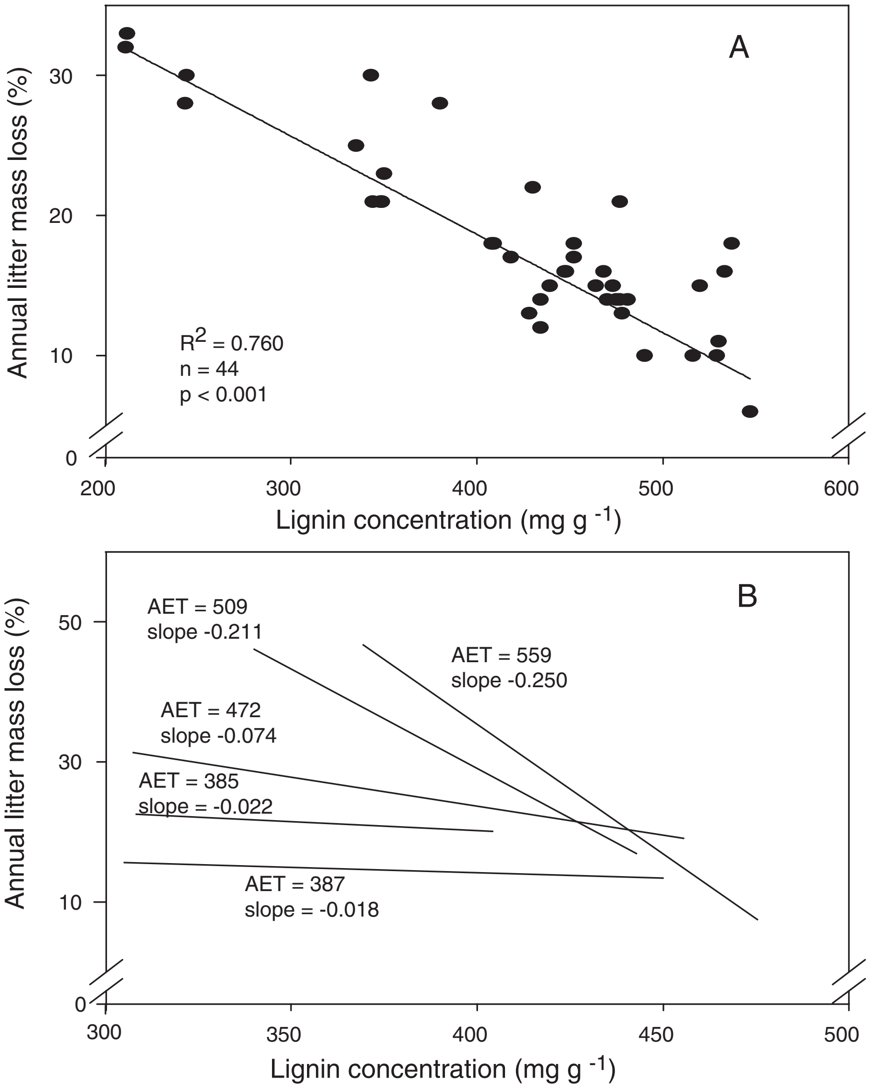

Fig. 2.8 Annual litter mass loss (%) as a function of initial lignin concentration at the start of each 1-year period. Lignin in foliar litter is normally resistant to degradation, and an increasing lignin concentration suppresses the decomposition rate of the litter. The basic condition is that litter N levels be high enough to suppress the degradation of lignin. **A** The relationship indicated here, namely, a decreasing rate with increasing lignin concentrations for one type of litter incubated at its own forest stand, has been observed by several scientists. **B** Corresponding relationships under different climate conditions indicate that the rate-retarding effect of lignin is stronger in warmer and wetter climates (redrawn from Berg et al. 1993e)

concentrations become high enough. This phenomenon has been studied further along a climatic transect with a range in annual average temperatures from ca. 0 to 8 °C, extending from northern Scandinavia to northern Germany. In that study, using Scots pine needle litter incubated in litterbags in the field, it was found that in a warmer and wetter climate the lignin-related effect on litter mass-loss rate was stronger than under colder and drier conditions (Johansson et al. 1995; Berg and Meentemeyer 2002; Fig. 2.8B, see also Chap. 7). This kind of comparison of lignin concentration to, e.g., annual mass loss (see Glossary) has given us new information on the effects of "ageing" litter. Still, considering the findings commented on below, we should be aware that although we may see relationships in some cases or for some litter types, we can not generalize from the findings based on only one, or even a few litter species.

Respiration rates from decomposing litter (and humus) often are used directly as measured, and in short-term experiments this means that the total respiration rates from litter are determined by those components that decompose the fastest. In an attempt to overcome this, Couteaux et al. (1998), using Scots pine needle litter, subdivided the litter into three compartments with components of different degradability, i.e., "labile", "intermediate", and "recalcitrant". Using different approaches, they determined the sizes of these pools, and the rate constants for decomposition. The dominant pool was the recalcitrant one, making up between 79 and 85% of litter samples. The respiration rate for the recalcitrant fraction was lower than 0.0001% day^{-1} (<3.6% in 100 years), and for the labile one about 0.124% day^{-1} (Table 2.2). They found support for an early and a late decomposition phase, with a transition at about 25% mass loss, but concluded that decomposition rates measured under laboratory conditions should be interpreted with care.

Degradation of Humification Products. It has been shown recently that humification products may be degraded by, e.g., white-rot fungi (Steffen et al. 2002). We still do not know whether this degradation proceeds at the same rate as that for lignin, if the degradation of these products requires other sets of enzymes, or whether the lignin-degrading enzyme system can degrade these humified components. It is likely that the degradation of gravimetric lignin includes the formation and degradation of polymerized humification products. The measured "lignin" degradation thus is a net process in terms of native lignin, but encompasses other components as well.

Table 2.2 Compartments of different stability in decomposing Scots pine needle litter and humus in a Scots pine forest. The sizes of the compartments were estimated, and the rate constants were based on respiration measurements. Standard deviation in parentheses (Couteaux et al. 1998)

Labile comp. (%)	K_L (% day^{-1})	Intermediate comp. (%)	K_{IN} (% day^{-1})	Recalcitrant comp. (%)	K_R (% day^{-1})
Needle litter incubated in litter layer for 16 months					
4.09 (0.39)	0.124	17.01 (2.41)	0.0087	78.52	<0.0001
Brown needle litter from forest floor					
4.67 (0.61)	0.124	21.91 (1.54)	0.0087	74.93	<0.0001
H-layer particles <2 mm					
0.00	0.124	9.80 (1.32)	0.0087	91.20	<0.0001

2.4.3 Effect of N on Lignin Degradation

As litter decomposes and the lignin level increases, the concentration of N also increases (Fig. 2.2A, B, and also see Figs. 5.2 and 5.4). This is a well-known and general phenomenon in decomposing litter. We emphasize this because N has an important role in the degradation of lignin, and in the formation of humus. This is discussed by Stevenson (1982) and described by, among others, Nömmik and Vahtras (1982), and Eriksson et al. (1990).

There is no really clear border between the late stage and the one that we call the humus-near, or the limit-value stage of decomposition. Several functional properties, such as the effect(s) caused by N, appear to be common to both stages. This is an important observation that helps us to interpret and predict properties in humus.

The rate-retarding effect normally ascribed to increasing lignin concentrations (Fogel and Cromack 1977; Berg and Lundmark 1987) is probably due more to the associated high concentration of N that has a suppressing effect on the formation of ligninase, and thus on lignin mass loss. Evidently, it is not the lignin concentration per se that is rate retarding, but rather the lignin in combination with N concentrations above a certain level. We may, as an extreme case, imagine that with sufficiently low N levels, and thus no suppressing effect, a higher degradation rate for lignin may result, and probably no raised lignin concentration. In fact, there is evidence for this in wood decay, because wood is extremely low in N. Based on litterbag studies on Black Hawk Island (Appendix III), wood chips of red maple and white pine lost more mass (88%) than any of ten other litter types including leaves, needles, bark, and fine roots after 10 years of incubation. The initial N concentration in these wood samples was 0.09% for red maple, and 0.04% for white pine (Aber et al. 1990; McClaugherty, unpubl. data).

Much remains unknown about the roles of lignin and N during this middle stage of decomposition. We do not know whether the rate-retarding effect ascribed to lignin, or the combination of lignin and N, in ageing litter is due to the level of N initially present in litter, or if the availability of N from the outside is more important. The transport of N through fungal mycelia into the litter is one available source of N from outside the decomposing substrate (Berg 1988), but inputs from atmospheric deposition may be becoming increasingly important in some systems. Possibly both internal and external sources are influential, but this requires further investigation.

The question that arises is whether the declining rate of decomposition observed in the late stage of decay is due to lignin, N, or a combination of both. The suppressing effect of N on the degradation of lignin, as well as on the decomposition of whole litter, has been observed in studies with different levels of resolution, and is based on both organic-chemical observations (Nömmik and Vahtras 1982) and evidence at a microbiological-physiological level (cf. reviews by Eriksson et al. 1990; Hatakka 2001). The effect of N has also been observed directly, producing different lignin degradation rates in decomposition experiments (Berg and Ekbohm 1991).

There are two main paths recognized today that can influence degradation of lignin and its modified forms, one biological and the other chemical.

Table 2.3 Relative effects of N levels in liquid pure cultures on the wood degradation activity of some N-sensitive white-rot fungi. A comparison is made to the natural concentrations of N in Scots pine needle litter

Substrate	N addition	Effect
Wood[a]	None	No inhibition
Wood[a]	0.0036% (2.6 mM)	20–70% inhibition
Wood[a]	0.0109% (7.6 mM)	40–95% inhibition
Scots pine needles – natural levels[b] degradation	0.4–1.2%	Delayed

[a]Eriksson et al. (1990)
[b]Berg and Ekbohm (1991)

***Biological Mechanisms*.** Raised N levels may suppress the degradation of lignin (Keyser et al. 1978; Eriksson et al. 1990; Hatakka 2001), and consequently also the decomposition rate of litter (Berg et al. 1987; Berg and Ekbohm 1991; Berg and Matzner 1997). This simply means that the higher the level of available N, the stronger the repression of the formation of lignolytic enzymes in the population of lignin-degrading organisms (see also Chap. 3). The ability of several fungal species to degrade lignin was heavily suppressed when N was added to the culture medium at concentrations of 2.6–7.8 mM, corresponding to 0.0036–0.0109%. The level of N in solution in a pure fungal culture is not directly comparable to that in litter, where the N will be bound in different compounds and will be much less mobile than in solution. However, trends apparent in culture may stimulate speculation as to possible mechanisms in litter (Table 2.3). With an N concentration of 0.4% in our case study litter, N concentration is 100-fold greater than in the fungal culture system. In both cases, the status of the N changes over the course of the experiment. In liquid pure culture, the N becomes bound in microbial biomass, and thus less available. In the litter substrate, there may be mineralization and degradation of proteins, thus converting a fraction of the bound N into more available N.

***Chemical Mechanisms*.** After litter has started to decompose, the lignin begins to incorporate N, and condensation reactions take place that mark a first step in humification (Stevenson 1982; Nömmik and Vahtras 1982). These chemical transformations may result in structures that are not easily degradable by the soil microorganisms. These recalcitrant compounds – for example, humins (Nömmik and Vahtras 1982; Bollag et al. 1983; Liu et al. 1985) – may act as chemical barriers to the decomposing microorganisms, limiting their access to the more readily degradable hemicelluloses and cellulose. This concept was suggested by Mindermann (1968), and may explain why Staaf and Berg (1977) and others have found cellulose and hemicelluloses in well-developed A_{01} and A_{02} horizons.

The nature of the fixation of NH_3 to organic matter, both humus and decomposing litter, is unknown, although several mechanisms are plausible. One such mechanism involves phenolic groups that are formed during lignin degradation (Nömmik and Vahtras 1982). Methoxyl groups are removed from the lignin aromatic ring, forming phenolic groups that then may react with, and bind NH_3. Fixation of NH_3 may also

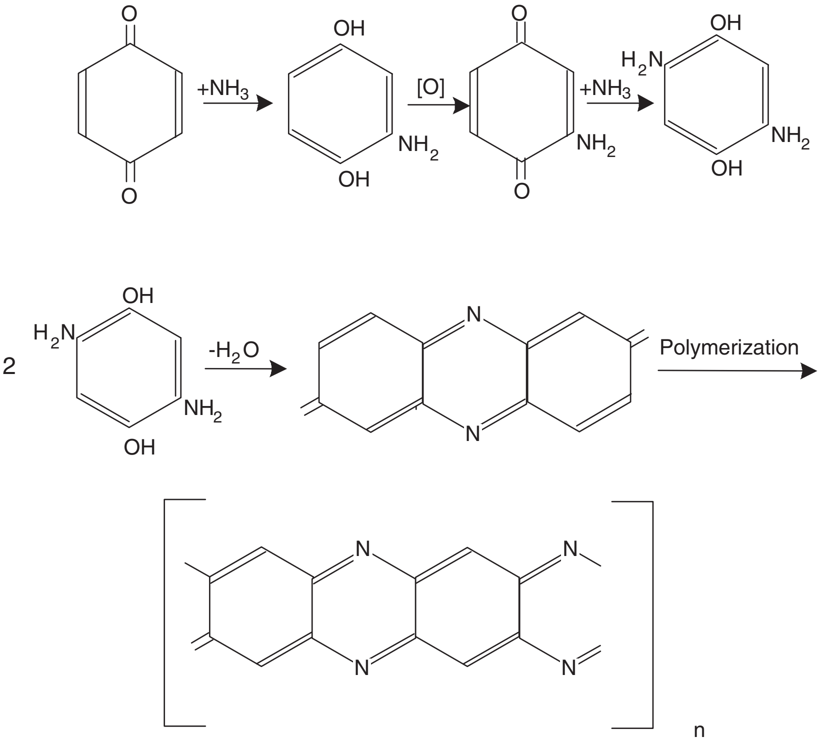

Fig. 2.9 A suggested mechanism for the reaction between NH_3 and a *para*-quinone, resulting in a polymer heterocyclic ring (originally proposed by Lindbeck and Young 1965)

occur during degradation of both cellulose and hemicelluloses, where reducing ends are formed on the chains of carbohydrates (see above; Chap. 3), which can react with NH_3. A fixation mechanism has been suggested involving quinones that are formed during lignin degradation as side products from laccase or peroxidase acting on di-phenol rings (Nömmik and Vahtras 1982). These quinones, by reacting with ammonia via di-phenols, could be transferred to heterocyclic polymeric compounds (Fig. 2.9).

Thus, phenolic groups, quinones, and also carbohydrates may react with NH_3, producing fixed N. In their review, Nömmik and Vahtras (1982) define the term "fixed NH_3" as the NH_3 that is retained by soil organic matter after intensive extraction and leaching with either diluted mineral acid or neutral salt solutions.

The fixation process involves ammonia, not the ammonium ion, and therefore the reaction is faster at higher pH values. Also, amino acids react at higher rates at higher pH values for the same reason. Broadbent and Stevenson (1966) demonstrated that close to pH 9, the reaction was 10–20 times as fast as at pH 6 and below. The higher the level of N in litter (or the higher the degree of humification), the lower was the NH_3-fixing capacity of the organic matter studied. For Scots pine needle litter, Axelsson and Berg (1988) largely confirmed these findings, and

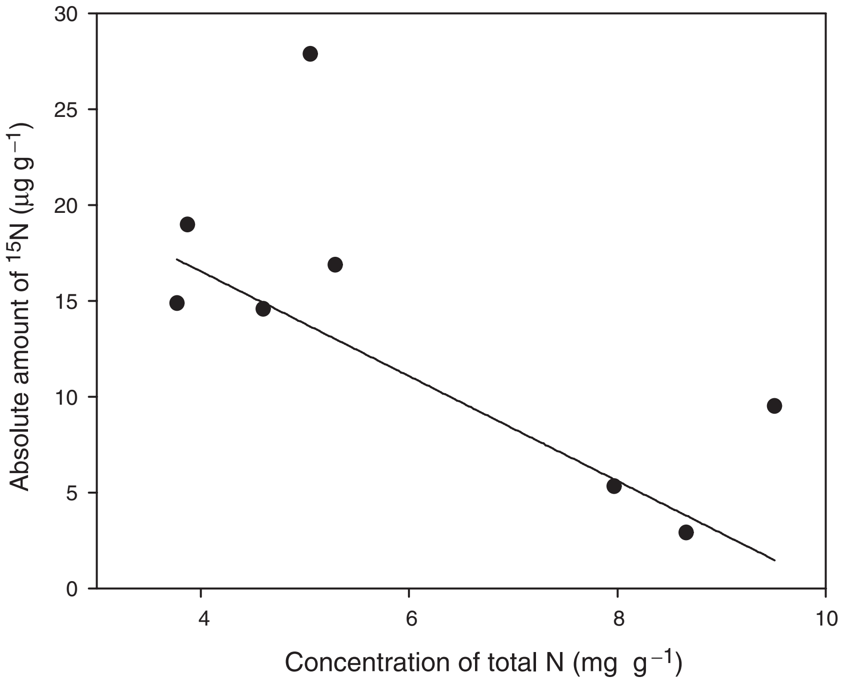

Fig. 2.10 Linear relationship between concentration of total N in Scots pine needle litter decomposed to different extents, and absolute amount of ^{15}N (as NH_3) adsorbed g^{-1} litter (Axelsson and Berg 1988)

estimated a fixation rate three times higher at pH 9 than at pH 5. They also found that Scots pine needle litter that had reached a higher accumulated mass loss, and thus higher N concentrations, adsorbed/fixed less ^{15}N (Fig. 2.10).

The "chemical" mechanisms for slower decomposition that are suggested here are not yet confirmed experimentally. In their review, Nömmik and Vahtras (1982) point out that prolonged exposure of organic matter to NH_3 under aerobic conditions leads to degradation of humic acid polymers by hydrolytic and oxidative processes, which results in the formation of low-molecular-weight soluble compounds (cf. Sect. 11.3.2).

2.4.4 Effects of Litter Mn Concentration on Lignin Degradation and Litter Mass Loss

Evidence of the suppressing effect of N on the formation of the ligninase system in several fungal species was followed by the discovery of the enzyme manganese peroxidase (MnP), produced by the majority of wood-degrading basidiomycetes that cause white-rot, as well as by various soil litter-colonizing saprotrophic fungi.

Mn is essential for the activity of MnP, a lignin-degrading enzyme, and enhances its production (Perez and Jeffries 1992). Mn is also involved in the regulation of other lignolytic enzymes, including laccase (Archibald and Roy 1992) and lignin peroxidase (Perez and Jeffries 1992). In a large number of laboratory studies, it has been shown that this nutrient is essential for the formation and activity of lignin-degrading enzymes, and thus for the degradation of lignin.

Among the ligninolytic enzymes, MnP is probably the most widely spread peroxidase produced by these fungi (Hofrichter 2002). Manganese peroxidase is a glycosylated heme protein that is secreted by the fungi into their environment. It oxidizes Mn^{2+} ions, which are found in plant residues, wood and soil, to highly reactive Mn^{3+} ions. These ions in turn are stabilized by organic acids also produced by these fungi. Organic acids, such as oxalic or malic acid, chelate Mn^{3+} ions and prolong their lifetime until they attack the phenolic structure of lignin or humic acids.

How we should measure the effect of Mn on lignin degradation as part of litter decomposition is still not clear. There may be a relationship between lignin degradation and litter Mn concentration, but the variation in concentration both during decomposition and among litter species has so far prevented drawing of any general conclusions.

2.4.5 Humus-Near Stage in Litter Decomposition – Limit Values

Literature that describes the functional transfer from partially decomposed litter to humus is rare. Nonetheless, moderately decomposed litter, the humus-near stages, and humus have properties in common, an example being concentrations of N and the rate retardation that may be related to N concentration. Also analyses of decomposition rates (Couteaux et al. 1998; Table 2.2) show similar values in the labile, intermediate, and recalcitrant fractions, both for litter close to the limit value and in humus.

It has been possible to adapt mathematical functions to the accumulated mass loss in litter, and with good statistical precision to estimate how far the decomposition process should continue. A number of such investigations have been carried out on our case-study litter. Within a given forest plot, there is a certain repeatability of limit values. For example, Berg and Ekbohm (1993) found some homogeneity among limit values within groups of studies on decomposing litter of Scots pine and lodgepole pine. They also stated that the limit values of the two groups were significantly different. Berg et al. (1999b) published data for 11 studies on Scots pine litter decomposition in one forest system, and found that the limit values ranged between 76.0 and 93.2%, giving an average of 84.7%. In other words, on average 15.3% of the initial litter became stabilized as essentially non-decomposing remains (cf. Fig. 11.3). The SE of this estimate was 1.57.

The variation in concentrations of N and lignin in the needle litter collected in different years (Johansson et al. 1995) may explain part of the variation in limit values (Table 2.4). For the same litter type, Couteaux et al. (1998) calculated a limit

Table 2.4 Initial concentrations of N, Mn, water solubles, and lignin in annually collected Scots pine needle litter. The Scots pine needle litter was incubated in the forest floor in its own system (SWECON site, Jädraås, Appendix III), and limit values for accumulated mass losses were calculated

Initial concentrations (mg g^{-1})				Limit value	
N	Mn	Wsol[a]	Lignin	(%)	SE
4.0	n.d.	n.d.	267	93.2	11.70
3.8	1.55	92	223	86.6	3.02
4.0	n.d.	151	255	92.2	8.51
4.4	n.d.	n.d.	256	78.2	4.03
4.8	0.79	164	231	89.0	7.00
3.8	1.00	165	257	89.4	17.04
3.9	1.17	214	231	83.2	9.23
3.8	0.77	180	231	84.3	5.21
3.7	1.12	82	288	76.0	5.80
3.8	1.08	178	229	82.5	3.10
3.8	1.18	162	250	85.3	8.19
Averages					
3.9	1.08	154	226.5	84.7	1.57

[a] *Wsol* Water-soluble substances, *n.d.* not determined

value of 96%, and a mass loss rate measured as release of carbon dioxide that was less than 10^{-4}% day^{-1} for the recalcitrant fraction (see above; Table 2.2).

It should be emphasized that the limit-value pattern is not inconsistent with those studies that describe two- or three-factorial models for decomposition, in which the different linear factors give different rates at different decomposition stages (see Chap. 10). Early work with such two-factorial models included that by Lousier and Parkinson (1976), and Berg et al. (1982b). Subsequently, Couteaux et al. (1998) developed a three-factorial model that was used to estimate the decomposition rate at stages close to the limit value.

Bosatta and Ågren (1985) proposed a conceptual mathematical model of decomposition. Their model was based on a continuous decline in substrate quality during decomposition. Depending on the relative rates of mass loss and quality decline, the model predicts different final outcomes for litter decay. One possible outcome is that all litter will disappear completely in a finite time; another outcome is that mass loss will eventually cease, leaving a residue for an indefinite time.

The role of animals in the decomposition of litter toward a limit value is unclear. Most of the studies that are used to estimate limit values have been carried out in forest soils containing relatively small numbers of animals that would attack litter. The existence of limit values, and their levels in these studies may in part be ascribed to the absence of soil animals. However, other studies have indicated that decomposition may also have a limit-value pattern in systems in which soil animals are found in higher numbers.

Although it is possible to estimate significant limit values for litter decomposition, we do not conclude that such limit values necessarily indicate completely recalcitrant remains in the humus-near litter. The estimated values may illustrate a fraction that is stabilized, and thus is decomposed at a very low rate, or not at all. Even if this were the case, the phenomenon is no less interesting or useful, especially if we can connect this resistance or recalcitrance in litter to its properties – for example, to the concentration of lignin or some nutrient, or to climate. Alone the fact that allophanic humus (see Glossary) exists shows that an "eternal" storage is possible. Although allophanic organic material may be regarded as an extreme case, the level of stabilizing components (for example, aluminum and iron ions) necessary to stop the decomposition process is not known (Paul 1984). The fact that the use of limit values allows us to reconstruct a humus buildup over a period of 3,000 years also indicates that the sources of error in undisturbed systems are probably minimal (Chap. 11).

What May Cause the Decomposition to Cease?

Nitrogen. The influence of N on the lignin-degrading microbial population was discussed above. We described the rate-suppressing effect of N during the late and humus-near stages of decomposition. With N concentration increasing linearly with mass loss until the limit value is reached (Berg et al. 1999b), it would be reasonable to expect an increased effect of N at least until then. Although the chemical reaction between N compounds and lignin degradation products appears to be a slow process, the time required for our case-study litter to reach a mass-loss level within 5% of the limit value is of the magnitude of 8–10 years. Thus, even though the process of NH_3 fixation is very slow, especially at low pH values, it can become of significance over time. In a laboratory study, Axelsson and Berg (1988) found that newly shed Scots pine needle litter binds mineralized N in a pH-dependent fashion, with 10 μg N g^{-1} litter bound in 24 h at pH 9.0, while at pH 5.0 the rate was about a third of that. The rate was probably dependent on the concentration of N, and apparently the number of reactive sites, as well as the litter pH (Fig. 2.10, Table 2.5).

Table 2.5 The capacity of milled Scots pine needle litter to bind NH_3 in a solution of about pH 9.0. The incubation time was 24 h and the milled needle litter was extracted with 1 M KCl. The rate at pH 5.0 was about a third of that at pH 9.0 (Axelsson and Berg 1988)

Mass loss (%)	Lignin conc. (mg g^{-1})	Total N conc. (mg g^{-1})	Excess of ^{15}N (10^3)	Bound ^{15}N (μg g^{-1})
0	300	3.9	516	20.1
10.6	332	3.75	449	16.8
26.3	374	4.6	362	16.6
35.9	381	5.05	542	27.4
41.8	402	5.3	345	18.3
58.7	433	8.0	115	9.2
62.1	426	8.65	84	7.3
68.7	444	9.5	132	12.5

Manganese. Although the causal relationships remain uncertain, the concentration of Mn appears to influence the limit values of the litter (see Chap. 6). When discussing the possible relationship of nutrients or heavy metals to limit values, their initial concentrations may be used as indices, because they are relatively conserved during decomposition. For N, the concentration increases linearly with accumulated mass loss (Chap. 7; Berg et al. 1999b), and the use of initial concentrations as an index should thus not cause any problem. For Mn, such an increase does not normally take place, and it remains to be determined how Mn levels could be used as an index to predict decomposition processes. The concentration of Mn may decrease or increase during decay, depending on the litter species. As seen from Fig. 5.8, there seems not to be any simple relationship between, e.g., accumulated mass loss and the Mn concentration. As its solubility increases at decreasing pH, we expect that acid litter species or acid environments may cause concentration decreases in decomposing litter simply because of increased solubility. Compared to other main nutrients, concentration appears difficult to predict in this case (Berg and Cortina 1995).

Chapter 3
Decomposer Organisms

3.1 Introduction

The dominant primary decomposers in boreal and temperate forest soil systems are the microorganisms, encompassing both fungi and bacteria. Both these main groups of microorganisms can degrade cellulose, hemicellulose, and the different lignins. This chapter will emphasize the functional roles of organisms (e.g., cellulolytic and lignolytic), rather than their taxonomy. The concepts white-rot, brown-rot, and soft-rot, and what they stand for functionally in terms of degradation processes will be presented.

Many microorganisms degrade cellulose and hemicellulose in nature. These organisms have in common the production of extracellular hydrolytic enzymes that are either bound onto the outside of the cell or released into the surrounding environment. Polymer carbohydrates may be degraded both aerobically and anaerobically, but a complete degradation of lignin (white-rot type) requires the action of aerobic organisms (fungi and/or aerobic bacteria). Partial lignin degradation (brown-rot type) may also be carried out by anaerobic bacteria, but is found mainly among fungi and aerobic bacteria.

We have used the functional concepts white-rot, brown-rot, and soft-rot as a basis for the discussion of degradation of litter. Although the terms originally seem to refer to visually different types of lignin degradation, it now appears that the degradation of cellulose and hemicellulose is also different among the groups (Worrall et al. 1997). The terms refer to the type of rot, rather than to a group of organisms, but we have adopted the common use of the terms and refer to fungi when using the terms white-rot, brown-rot, and soft-rot. As regards degradation by bacteria, it is described and discussed as such.

The composition of the microbial population (e.g., cellulolytic vs. lignolytic) may vary with general properties of the soil/litter ecosystem, such as nutrient status and pH. A specific functional property that may discriminate among systems and populations is their sensitivity to N concentrations in litter and humus, which may be either stimulating or suppressing. Such sensitivity is not universal, but common in species of both white-rot and brown-rot organisms.

B. Berg and C. McClaugherty, *Plant Litter*,

By tradition, soil animals such as collembola, mites, and earthworms have been considered important for litter decomposition. Such groups have been ascribed different roles in decomposition, although those roles are not always clear. The decomposition by free-living microorganisms has also been considered important, but the relative influences of soil animals and soil microorganisms have not been apparent, thereby indirectly supporting studies of the more easily studied visible component, namely, soil animals.

In recent decades, it has become increasingly clear that for some systems, at least boreal and temperate coniferous ones, the microbial component is of absolute dominance. For example, Persson et al. (1980) estimated that at least 95% of energy flow is channeled through the microbial population. The implications of this proportion are considerable, and we could express this in a somewhat simplified way by stating that the decomposition of litter in a given system is determined by conditions and limitations that are valid for the microbial community of that system, which may be quite different from those of the soil faunal community.

Considering that the focus of this book is directed toward boreal systems, which have a decomposition process dominated by microorganisms, we have described both the microbial population (Sect. 3.2) and the microbial enzymatic degradation mechanisms (Sect. 3.3). This chapter will describe those properties of the organisms that are important in the degradation of cellulose, hemicellulose, and lignin. The main combined effects on the decomposition of whole litter are given in Chapters 2, 6, and 11.

Mycorrhizae have been found to turn into aggressive decomposers under certain circumstances, and may decompose humus that has been considered as stabilized. Such a degradation can take place at a high rate. This phenomenon may be related to nutrient stress in growing trees. The role of mycorrhizae in decomposition in general is still under dispute, and we present observations here without taking part in that dispute (Sect. 3.5).

The ecology of decomposer communities can influence the pattern of decay. The changes in the community and its function during the decay process, and the cyclic nature of the successional process in the soil will be addressed. The effects of moisture and temperature on the activity of the microbiological decomposition process are presented later, in Chapter 7.

3.2 General Properties of a Given Microbial Population

The two main groups of litter decomposers are bacteria (including the filamentous bacteria that earlier were called actinomycetes), and fungi – two groups that appear to include some of the same basic physiological properties in terms of degradation of fresh litter polymers. Still, the fungi are generally considered the most important group, and we know more about their litter-degrading properties and enzyme systems. Each of these two groups may be subdivided into functional subgroups with different properties, degrading different groups of chemical components.

Table 3.1 Some general properties of the main groups bacteria and fungi

Property	Bacteria	Fungi
Mobility	+	+
Spore-forming ability	+	+
Can degrade cellulose/hemicellulose	+	+
Can degrade lignin completely	+	+
Can degrade lignin anaerobically[a]	+	−
Can degrade intact fiber walls	+	+
Species with N repression of the ligninase system	?[b]	+
Species without N repression of the ligninase system	?[b]	+

[a] Incomplete degradation to be compared to the brown-rot type

[b] Not known

The taxonomy of both fungi and bacteria is complex, and is beyond the scope of this book.

The bacteria include both aerobic and anaerobic organisms, which distinguishes them from the exclusively aerobic fungi. Both groups have organisms able to degrade all the main polymers: lignin, cellulose, and the hemicelluloses. There are also organisms able to degrade woody tissue where all these components are combined into fibers. Complete degradation of lignin appears to be carried out by a small number of the fungi and aerobic bacteria. Some of the general properties of main groups of bacteria and fungi are collected in Table 3.1.

The biological diversity in the soil microbial community is high. The potential species diversity is strikingly evident simply by comparing crude numbers of identifiable species. For only 1 m^2 of a given soil system, we may estimate that for bacteria there may be 1,000–5,000 species, and for fungi perhaps 100 dominant species.

The high density of bacteria in, for example, an organic soil creates a high potential for invading a new substrate, such as newly shed litter. Estimates of 10^9 bacteria g^{-1} organic soil either active or in a resting stage are common when made by direct light microscopy counting. This value is conservative, since there are numerous bacteria that are simply too thin to be detected with light microscopy and would need to be counted using electron microscopy. In the same soil, total mycelial lengths have been estimated to reach ca. 2,000 km L^{-1} of humus, of which perhaps 10% would be live mycelium.

Microorganisms will be actively dividing and growing only when environmental conditions are favorable. When the conditions cannot support growth, the microorganisms will be in some kind of resistant, resting stage, or spore form. Wind and animals easily transport fungal and bacterial spores. This means that spores may be transplanted among ecosystems, and that a given ecosystem may have a passive gene bank, able to quickly produce active microorganisms that can attack a particular litter type, possibly with new chemical components that are novel in a given environment.

The size of most microorganisms gives them access to different parts of the fiber and tissues that make up litter (cf. Fig. 4.1). For many bacteria, the diameters range largely from 0.1 to 2 µm, and for filamentous fungi from ca. 1 to less than 20 µm. The lengths of rod-shaped bacteria vary mainly from ca. 1 to 10 µm, while those of the fungal mycelia are more undetermined.

Bacteria may be either immobile, or mobile, with one or more flagella, a whip-like structure. Fungal mycelia demonstrate mobility in another way, in that they simply grow in one direction and thus move their protoplasm, leaving an empty cell-wall structure behind.

The term "decomposer" microorganism is sometimes used for those microbes that decompose plant litter structures, sometimes for the larger group that decomposes organic matter, thus including the whole group of free-living heterotrophic microorganisms. Free-living in this context simply means those microorganisms that do not live in obligate symbiosis. Here, we will focus on what may be called primary litter decomposers, namely, those that attack and degrade (at least in part) the polymer structures to carbon dioxide and/or small, partly degraded molecules. We discuss below the hypothesis that not only free-living microorganisms play a role in the turnover of organic matter, but that mycorrhizal fungi may also be important.

3.3 The Degradation of the Main Polymers in Litter

3.3.1 Degradation of Cellulose

Cellulose is degraded by numerous species of both bacteria and fungi. These organisms rely on extracellular enzymes that either are secreted into their immediate surroundings or are located on the cell surface. It is necessary that cellulose be degraded outside the microbial cell (Fig. 3.1), and that the insoluble macromolecules be degraded to monomers, or oligomers of a few glucose units (Fig. 3.1), such as cellobiose, which can be taken into the cell and metabolized.

A common feature among all cellulose-degrading organisms is that they produce hydrolytic, extracellular enzymes that attack the cellulose polymer. Part of the cellulose in the plant fiber is arranged in a crystalline form that makes it harder to attack (see Chap. 4), and relatively few cellulolytic organisms have the necessary complete set of enzymes to degrade this structure. Many organisms are able to degrade the more amorphous kind of cellulose (see Eriksson et al. 1990).

The most studied group of cellulose-degrading organisms are the fungi, and no less than 74 species (Eriksson et al. 1990) have been investigated in some detail. The traditional division of wood-degrading fungi into three main groups, i.e., white-rot, brown-rot, and soft-rot fungi, relates primarily to their mode of lignin degradation, but these groups also differ in the way they degrade polymer carbohydrates.

Perhaps the most studied wood-decay fungus is the white-rot basidiomycete *Phanerochaete chrysosporium* Burdsall (also known as *Sporotrichum pruniosum*

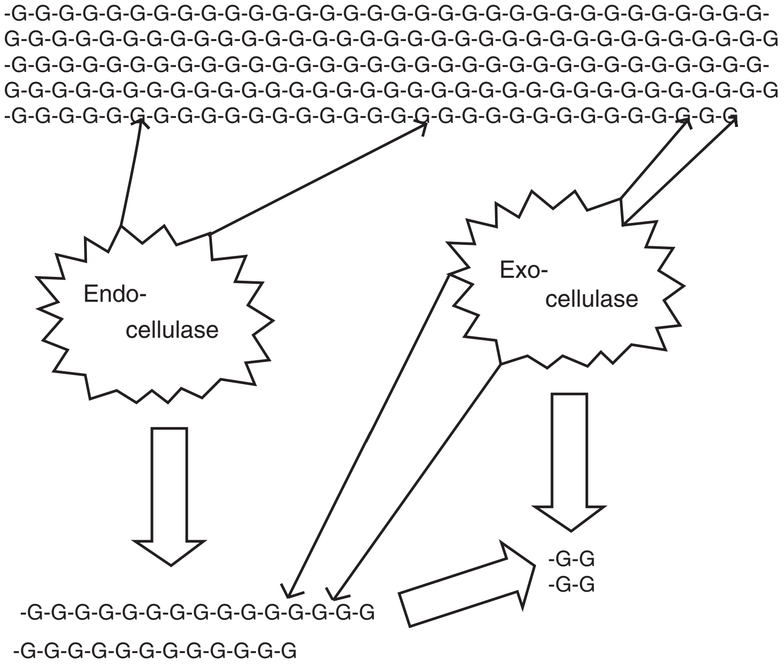

Fig. 3.1 Part of the cellulose fiber is attacked by an endo-1, 4-β-glucanase (endocellulase) breaking the chains and splitting off oligosaccharides in a random manner, including soluble shorter chains with, for example, 3 to 5 glucose units. An exo-1, 4-β-glucanase (exocellulase) splits off cellobiose units from the non-reducing end of the carbohydrate chains. *G* Glucose unit

and previously called *Sporotrichum pulverulentum* Novabranova). Much of what is known about the decay of lignocellulosic materials in nature is based on studies of this fungus (Ander and Eriksson 1977; Tien and Kirk 1984; Higuchi 1993). Three main hydrolytic enzymes are involved in cellulose degradation; one type of enzyme (endo-1, 4-β-glucanase) covers the cellulose chain, and splits the glucosidic linkages in a random fashion (Fig. 3.1), producing oligosaccharide units of different lengths that may still be attached to the microfibril structure. Another enzyme, an exo-1, 4-β-glucanase, splits off either cellobiose or glucose from the non-reducing end of the cellulose chain. Finally, 1,4-β-glucosidase hydrolyzes cellobiose and other water-soluble oligosaccharides, such as triose and tetraose, to glucose. One important aspect of this enzyme system is that the different enzymes with different specificities (the endo- and exoglucanases) exert a synergistic action that enables them to degrade both crystalline and amorphous cellulose.

In addition to hydrolytic enzymes, some cellulolytic organisms produce cellobiose dehydrogenase. This enzyme is found in a variety of fungi, and appears to have roles in both lignin and cellulose degradation. There was much confusion in the early literature about this enzyme, but recent work has resulted in a renaming of both cellobiose oxidase and cellobiose:quinone oxidoreductase to cellobiose dehydrogenase (Cameron and Aust 2001).

The soft-rot fungi as a group appear to have a cellulose-degrading system similar to that of the white-rots. However, brown-rots have not been found to have the synergistic enzymes that are found in white-rots, and they appear not to have the exoglucanase mentioned above. However, Highley (1988) found several species of brown-rotters that were able to solubilize microcrystalline cellulose. Thus, the generally held conclusion that these fungi merely seem to depolymerize cellulose without producing soluble monomers or dimers may not be entirely correct. Still, no other enzyme has been found to substitute for the missing exoglucanase that splits off soluble units. This has led Eriksson et al. (1990) to conclude that there may be a non-enzymatic mechanism involved. An observation that hemicellulose is virtually absent in wood decayed by brown-rots suggests that brown-rot fungi may degrade hemicelluloses. Although the mechanisms for degradation of cellulose are far from clear, work on a basidiomycete (Wolter et al. 1980) suggested that, at least for some species, a less specific or multifunctional enzyme that could degrade several different polysaccharides was active, an observation that suggests that this enzyme also has an effect on cellulose.

The ability to degrade crystalline cellulose is also found in many bacteria. Detailed studies on *Clostridium cellulolyticum* show that the organism produces at least six different cellulases, each with slightly different structural and catalytic properties. The cellulases, along with xylanases, are held together in a large structure, the cellulosome, by a scaffolding protein (Bélaich et al. 1997), much as was envisioned by Eriksson et al. (1990). In the anaerobic bacterium *Clostridium thermocellum*, a multi-component complex of cellulolytic enzymes was named “cellulosome” in the very early work of Viljoen et al. (1926). A close contact between the cellulose substrate and the organism often appears to be necessary.

The degradation of cellulose by bacteria has been suggested to be hydrolytic, although the mechanisms seem to be different from those found in fungi. For bacteria, the cellulolytic enzymes are arranged in clusters, and act in a combined way as described above. There are a few other groups of cellulolytic bacteria that have been studied, including *Cytophaga*, *Cellulomonas*, *Pseudomonas*, and *Cellvibrio*. It appears that these have their cellulolytic enzymes bound to the cell wall, and therefore a close contact is needed between the cell and the substrate (Berg et al. 1972; Eriksson et al. 1990). This property seems today to be widely recognized (Wiegel and Dykstra 1984).

Actinomycetes, in contrast to some other bacterial groups, appear to degrade cellulose in a manner similar to that of the fungi, and can also degrade the crystalline form. Several strains have the ability to degrade the lignocellulose complex. The fungal model for enzymatic attack on the cellulose molecule, namely, that an endo- and an exocellulase act synergistically, appears to be valid for actinomycetes, supporting their similarity to white-rot and soft-rot fungi. The synthesis of cellulases is induced by cellulose, cellobiose, sophorose, and lactose. The presence of cellulose appears to be the best induction agent. On the other hand, the presence of glucose seems to repress the synthesis of the cellulase system. As cellulose is a large and non-soluble molecule, it cannot be absorbed into the microbial cells and exert an inducing effect. Today, the accepted theory is that the organisms have a constant, basic level of cellulase on their surface. Upon contact with cellulose, low amounts of inducing substances are released from the cellulose, enter the microbial cell, and induce cellulase formation. It is likely that both the type of compound – for example, cellobiose, or cellotriose – and a low intracellular concentration of these compounds influence the synthesis of cellulase. There are also theories that metabolic transfer products of glucosyl are active as inducing agents, one of these being sophorose (Eriksson et al. 1990).

3.3.2 Degradation of Hemicelluloses

In wood, the total concentration of hemicelluloses usually ranges from 20 to 30% (cf. Chap. 4). There are distinct differences in the composition and structure of hemicelluloses in softwood as compared to hardwood litters. The composition of hemicelluloses is clearly different between hardwoods and softwoods (cf. Table 4.1). The hemicelluloses are composed of both linear and branched heteropolymers of D-xylose, L-arabinose, D-mannose, D-glucose, D-galactose, and D-glucuronic acid. These individual sugars may be methylated or acetylated, and most hemicellulose chains contain between two and six different kinds of sugars. Hemicelluloses from hardwoods have average degrees of polymerization in the range of 150–200 units, and most hemicelluloses are based on the 1,4-β-linkage of their main sugars.

Degradation of hemicelluloses requires more complex enzyme systems than are needed for the hydrolysis of cellulose. For example, xylan-based hemicellulose contains both 1,4-β-linkages and branched heteropolysaccharides, each of which requires a complex set of enzymes for degradation (Dekker 1985). Figure 3.2 shows the possible structure of a xylan-dominated molecule. The xylan backbone is made up of both acetylated and nonacetylated sugar units. On the branches, there are units of glucose and arabinose. The degradation of such a molecule requires the concerted action of several different hydrolytic enzymes (Eriksson et al. 1990).

3.3.3 Degradation of Lignin

Lignin degradation is regarded as a process that differs among the three general groups of decomposers: white-rot, soft-rot, and brown-rot fungi. Although the names are old and refer to characteristics easily seen by the eye, there are also functional differences in the degradation mechanisms, motivating the continued use of the terminology. The names are often used in connection with fungi, although bacteria are also lignin degraders.

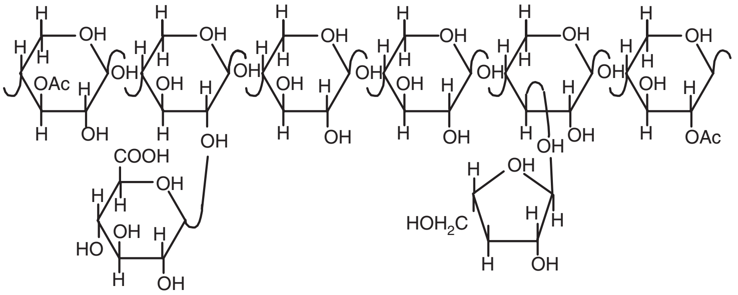

Fig. 3.2 Example of a fragment of a xylan molecule. The backbone of the molecule is constituted by xylan units of which part are acetylated (*Ac*). The branches in this case are composed of glucose (*left*) and arabinose (*right*) units. The main enzyme attacking the unbranched part of the chain would be an endo-1, 4-β-xylanase, producing oligomers of different lengths. β-xylosidases split the oligomers into simple xylose units. Other enzymes are necessary to split off the side chains as well as, for example, the acetyl substituent (Eriksson et al. 1990)

The number of different enzymatic mechanisms of lignin degradation with which organisms operate appears to be large, and only a few are well described. In fact, today it appears that only one mechanism of lignin degradation is well described, namely, that for *Phanerochaete chrysosporium*, a white-rot fungus. Some characteristics for each of the groups are given below, starting with white-rots since these are not only the most studied ones, but also probably the strongest lignin degraders known.

Lignin Degradation by White-Rot Fungi

White-rot fungi possess the ability to completely mineralize lignin to CO_2 and H_2O. The result, for wood, is that the entire lignocellulosic complex is degraded more or less simultaneously. A large group of the white-rots may even degrade lignin preferentially to cellulose (Hatakka 2001).

The attack on lignin structure has long been considered to start with a removal of the methoxyl group (Figs. 3.3 and 3.4). Newer research has shown that a combination of hydroxylation and demethylation is followed by an oxidative attack on the aromatic ring (Eriksson et al. 1990). The cleavage of the aromatic ring (Fig. 3.4) is an oxygen-demanding step, and the data in Table 3.2 illustrate the importance of the presence of O_2.

The lignolytic enzyme system of our example fungus (*P. chrysosporium*) is synthesized as part of several physiological events that appear to be triggered by N starvation. As described by Kirk (1980), a whole set of enzymes are synthesized under conditions of N starvation (see below). Almost all white-rot fungi produce Mn-peroxidase, a fact that may create an ecological niche, based on Mn as a limiting nutrient.

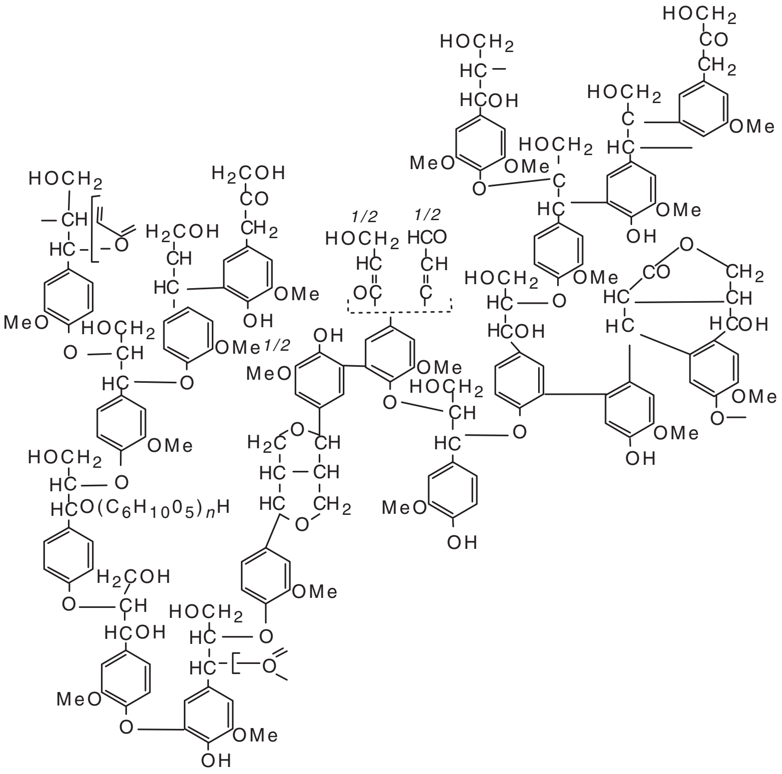

Fig. 3.3 Part of a lignin molecule from spruce

Table 3.2 Degradation of aspen wood lignin by different white-rot fungi in the presence of air or pure oxygen. Determinations were made as $^{14}CO_2$ evolution, and as Klason lignin (Reid and Seifert 1982). Nomenclature updated according to Cline et al. (2007)

	$^{14}CO_2$ evolution (%)		Klason lignin loss (%)	
Fungal species	Air	O_2	Air	O_2
Phanerochaete chrysosporium	10.8	35.2	13	40
Trametes versicolor	14.6	35.5	24	46
Gloeoporus dichrous	9.7	18.1	22	24
Polyporus brumalis	16.6	33.0	19	33
Phlebia tremellosus	14.0	22.3	30	40
Pycnoporus cinnabarinus	13.6	22.6	18	37
Lentinula edodes	9.7	18.0	18	41
Bondarzewia berkeleyi	9.0	13.8	25	27
Pleurotus ostreatus	11.7	11.6	17	17
Grifola frondosa	9.2	10.6	8	15

Although we may know more about the lignolytic system of *P. chrysosporium* than those of other white-rots, it appears that the lignolytic systems are species-specific, and it has been suggested that they depend on the ecological niche of the fungus in question (Hatakka 2001). For example, the white-rot *Ganoderma lucidum* produces Mn-peroxidase in a medium with poplar wood, but not in one with pine wood (D'Souza et al. 1999). Such observations may support the finding that white-rot fungi are more commonly found on angiosperm than on gymnosperm wood (Gilbertson 1980).

Lignin Degradation by Brown-Rot Fungi

Brown-rot fungi decompose mainly the cellulose and hemicellulose components in wood, and have the ability to significantly modify the lignin molecule, but are not able to completely mineralize the compound (Eriksson et al. 1990). They allow for the degradation of cellulose with a relatively small loss of lignin mass.

Brown-rot and white-rot fungi are considered to have similarities in degradation mechanisms. In both cases, the formation of hydroxyl radicals that attack wood components is important, and high oxygen tensions support the degradation (Hatakka 2001). It has been assumed that all brown-rot fungi use the same mechanism for wood decay. However, newer research has indicated that, in a parallel with white-rots, brown-rot fungi appear to have different mechanisms. The initiation of the degradation of both lignin and cellulose appears to be by diffusible small molecules that can penetrate the cell wall. In contrast to white-rots, only one brown-rot has been found to produce Mn-peroxidase.

The radicals formed by brown-rot fungi can remove methoxyl groups from lignin and produce methanol, leaving residues of mainly modified lignin (Eriksson et al. 1990). Relative to native lignin, brown-rotted lignins are structurally modified, and have a decreased number of methoxyl groups (Fig. 3.4) and an increase in phenolic hydroxyl groups (Crawford 1981). Brown-rotted lignin is more reactive than native lignin due to the increased content of phenolic hydroxyl groups. Carbonyl and carboxyl groups are also formed (Jin et al. 1990).

Lignin Degradation by Soft-Rot Fungi

The traditional view has been that soft-rot fungi do not degrade lignin, but rather act to soften wood by breaking down the middle lamella of the cell wall (cf. Fig. 4.1). Most soft-rot fungi are ascomycetes and deuteromycetes, and are most active in moist wood. Crawford (1981) reviews a number of studies in which purported soft-rot fungi were able to decrease the lignin content of decaying wood.

Today, it has been well confirmed that soft-rot fungi do degrade lignin: in laboratory experiments, up to 44% was degraded at a wood mass loss of 77% (Nilsson et al. 1989). In general, they are considered to degrade lignin to some extent.

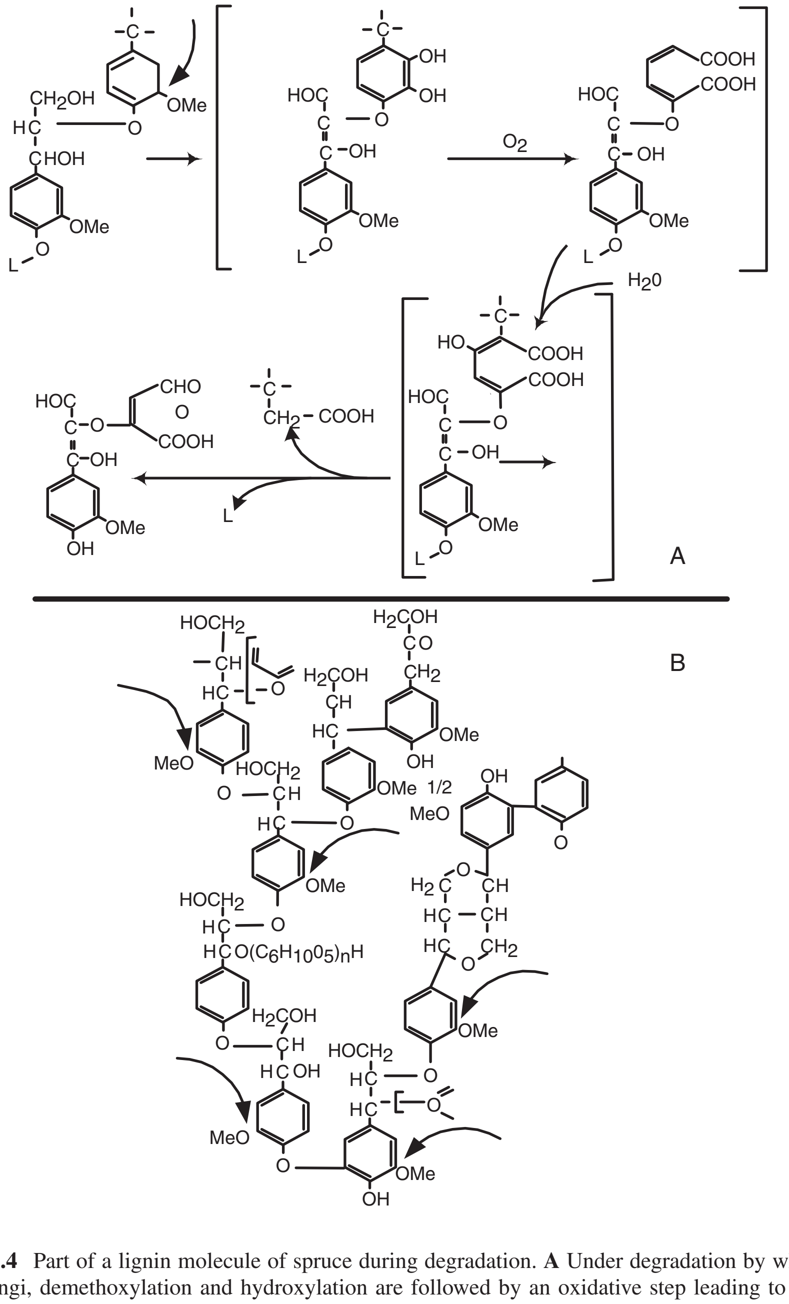

Fig. 3.4 Part of a lignin molecule of spruce during degradation. **A** Under degradation by white-rot fungi, demethoxylation and hydroxylation are followed by an oxidative step leading to ring cleavage (from Kirk 1984). **B** The same molecule under attack by brown-rot fungi, resulting only in demethylation in which the methoxy groups (MeO) are replaced by an OH group

Evidence from a study on the fungus *Daldinia concentrica* may explain why these fungi preferentially degrade hardwoods. This fungus degraded birch wood efficiently, but not that of pine (Nilsson et al. 1989). The lignolytic peroxdidases of soft-rot fungi do not have the potential to oxidize the softwood lignin,which has a high level of guaiacyl units (Fig. 3.5). In contrast, soft-rot fungi readily oxidize the syringyl lignin in hardwoods (Nilsson et al. 1989).

Enzymes Directly Affected by Mn Concentration in the Substrate

Manganese-peroxidase belongs to a group of enzymes that are classified as phenoloxidases. Manganese is essential for the activity of the lignin-degrading Mn-peroxidase (Perez and Jeffries 1992). Although not much was published on this enzyme before 1983, Lindeberg (1944) discovered in the 1930s that *Marasmius* spp. were dependent on Mn for their growth, and that a low level of Mn in a substrate hampered the degradation of lignin. This finding was not pursued, and it was not until the 1980s that additional detailed studies followed.

Manganese is also involved in the regulation of other lignolytic enzymes, including laccase (Archibald and Roy 1992) and lignin peroxidase (Perez and Jeffries 1992). The role of Mn-peroxidase in lignin degradation is not clear, although this may involve the formation of H_2O_2. The enzyme itself shows no affinity for non-phenolic compounds, which on the other hand are readily attacked by ligninase. Blanchette (1984) found that Mn often accumulates as MnO_2 in wood attacked by white-rots, which suggests that Mn-peroxidases are important for the degradation of lignin. It has also been found that MnO_2 stabilizes lignin peroxidase.

Effect of N Starvation on Lignin Metabolism

Lignin degradation may be repressed by high N levels in the substrate, an effect seen mainly in white-rot fungi, but also in brown-rots and soft-rots. As mentioned above, Kirk (1980) described a set of effects for *P. chrysosporium* that were

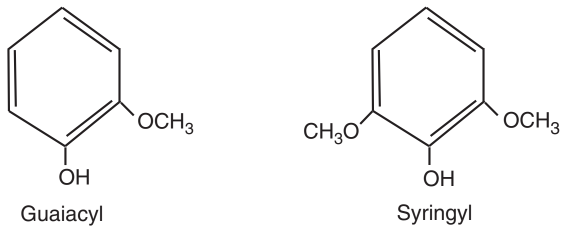

Fig. 3.5 Structures of guaiacyl and syringyl components of lignin

regulated by N starvation. A dramatic effect on lignin degradation was seen when the N concentration in the culture medium was increased from 2.6 to 5.6 mM (Keyser et al. 1978), namely, the lignolytic activity (measured as transformation of ^{14}C-lignin to $^{14}CO_2$) was repressed by 83%. The same property has since been described for several fungal species in laboratory experiments with pure cultures, although the levels of N and the magnitude of the effect vary. For three species (*Phlebia brevispora*, *Trametes versicolor*, and *Kuehneromyces mutabilis*), there were effects at 7.8 and 34 mM N in the culture, but not at 2.6 mM N. The magnitude of the effect varied from an almost complete repression in *P. chrysosporium*, to approximately a 50% repression in *K. mutabilis*. When using ^{14}C-labeled lignin from red maple wood, there was a clear effect of 20 mM N. There are also several fungi that are not sensitive to N. For example, a white-rot strain isolated from an N-rich environment (cattle dung) showed no sensitivity to raised N concentrations. Table 3.3 lists a number of species investigated for this property.

The results suggest that repression of lignin degradation by N is common, but not always the rule. The addition of N to fungal cultures may in certain cases even increase their ability to utilize lignin. We would expect that such fungi, and tolerant fungi in general, would be found in environments with high N concentrations, as in the example given above with cattle dung, whereas most white-rot fungi that grow in and on wood are adapted to low N concentrations. Many of the fungi that have been studied were isolated from wood, and the low N content in wood (with C-to-N ratios in the range of 350 to 500) may explain the generally strong influence of increased N levels.

Effect of the C Source on Lignin Degradation

It appears that the presence of a carbon source other than lignin stimulates lignin degradation in several white-rot species, including *P. chrysosporium*, *T. versicolor*,

Table 3.3 Some fungal species for which raised N concentrations have, or alternatively, have not elicited a repressing effect on lignin degradation

Species	Comments	Reference
Sensitive to N		
Phanerochaete chrysosporium	Isolated from wood	Keyser et al. (1978); Eriksson et al. (1990)
Phlebia brevispora		Leatham and Kirk (1983)
Trametes versicolor		Leatham and Kirk (1983)
Heterobasidion annosum	Some repression	Bono et al. (1984)
Not sensitive to N		
Pleurotus ostreatus		Freer and Detroy (1982)
Lentinula edodes		Leatham and Kirk (1983)
NRRL 6464 not identified	Isolated from cattle dung	Freer and Detroy (1982)

Trametes hirsutus, *Polyporus* spp., and *Lentinula edodes*. One observation was that cellulose had a stronger stimulating effect on lignin degradation than glucose, an observation that was ascribed to its *lower* availability; thus, an influence of catabolite repression could be expected (cf. Sect. 3.3.1). The major organic components in litter are usually the insoluble ones such as lignin, cellulose, and hemicelluloses. The latter two normally supply the lignin-degrading organisms with alternative carbon sources.

3.4 Degradation of Fibers

3.4.1 Bacteria

Though bacteria have long been known to be involved in litter decomposition, they have received far less study than have fungi. In most cases, bacteria coexist with fungi, particularly basidiomycetes and yeasts, and their presence has been shown to double the rate of fungal growth on wood and to increase the overall rate of decay (Blanchette and Shaw 1978). Although it was once thought that bacteria were not capable of degrading lignified cell walls without some type of pretreatment, a variety of fiber-degrading bacteria have now been identified. Three types of bacterial degradation are recognized, based on the manner in which they degrade the cell walls of the substrate: tunneling, erosion, and cavitation (Blanchette 1995). Bacterial decomposition seems to be more common in situations where fungi are under stress. Bacteria have also been found to degrade substrates that are resistant to fungal decay, especially wood (Singh et al. 1987).

3.4.2 Soft-Rot

Soft-rots commonly occur under conditions that are not favorable for basidiomycetes. However, a key for good growth of soft-rots is a high availability of nutrients. It is also generally held that soft-rots require moist conditions, though this requirement may not be different from that of basidiomycetes (Worrall et al. 1991). Two forms of soft-rots are identified based on the morphology of the degradation they cause (Blanchette 1995). Type I causes the formation of cavities in the secondary wall, and is most commonly found in conifers, where lignin-like materials accumulate on the edge of the cavities. Type II causes cell-wall erosion, but unlike white-rot, it does not degrade the middle lamella (cf. Fig. 4.1). It is possible that the middle lamella is resistant because it contains more guaiacyl–propane units. Type II is more common in angiosperms.

3.4.3 Brown-Rot

Brown-rot fungi have the ability to degrade holocellulose in plant cell walls without first removing lignin. Brown-rots apparently begin their attack on fibers by degrading the hemicellulose matrix, because xylans begin disappearing before cellulose (Highley 1987). They do this by initially causing a rapid decrease in the degree of polymerization of the holocellulose polymers. The decomposition occurs in a diffuse manner, and in wood, with a rapid loss of strength. These two factors suggest that agents smaller than enzymes are involved (Green and Highley 1997). This initial degradation is generally accompanied by relatively little mass loss.

When attacking fibers, brown-rot fungi appear to attack the S2 layer first, leaving the S3 layer until later (cf. Fig. 4.1; Highley et al. 1985). The reason for this is not known, but Hirano et al. (1997) propose a mechanism that agrees with the observations. They suggest that the brown-rot fungus grows into the cell lumen, and releases a low-molecular-weight substance (1 to 5 kDa) that diffuses into the S2 layer. Fe (III) is then reduced to Fe (II), and chelates it. The newly formed complex with the Fe (II) catalyzes a redox reaction that produces hydroxyl radicals. These hydroxyl radicals are able to cut canals through the S3 layer large enough for cellulases to penetrate. Clearly, more work is needed to validate this mechanism, and to identify the unknown substances required for its operation.

3.4.4 White-Rot

White-rot fungi carry out two different types of fiber degradation: simultaneous rot, and selective lignin degradation. Some species are capable of both (Blanchette 1991). In simultaneous rot, the fungi are able to either erode the cell wall adjacent to the hyphae, creating erosion channels, or they generally erode the lumen surface, resulting in an overall thinning of the cell wall. In addition, the hyphae move from cell to cell through pits, or by boring through the wall. The other type, selective delignification, often results in cell separation as well as overall thinning of the cell walls. Anagnost (1998) provides numerous photomicrographs that illustrate the various types of decay.

White-rots sometimes seem to have a delay, or a lag time of relatively slow mass loss before a period of more rapid mass loss (cf. Fig. 9.1). Blanchette et al. (1997) used a novel biotechnological approach to demonstrate why this might occur. They incubated loblolly pine wood with a white-rot fungus, *Ceriporiopsis subvermispora*. They then placed the wood, in various stages of decay, in solutions containing proteins of known size. Using immunocytochemical techniques, they were able to show that proteins of the size of cellulases and lignin-degrading enzymes could not freely pass through the wood until later stages of decay. After cell walls had been thinned enough to increase their porosity, it was possible for extracellular enzymes to move freely from lumen to lumen, thus initiating the stage characterized by a higher rate of mass loss.

3.5 Mycorrhizae

In undisturbed soil systems, there also appear to be mechanisms that can change the composition of the microflora in ways that enhance its ability to degrade the otherwise stable humus. Hintikka and Näykki (1967) gave a good description of the mycorrhizal basidiomycete *Hydnellum ferrugineum*, and its effects on the humus layer. The development of thick mycelial mats under the mor layers was described, as well as bursts of soil respiratory activity, followed by a large decrease in the amount of humus in the FH layer. The effect was observed on dry, sandy, nutrient-poor sediment and till soils, and could be attributed to plant growth. This appears to be a powerful mechanism driving humus decomposition. Unestam (1991) discussed this effect for certain other mycorrhizal fungi. Furthermore, Griffiths et al. (1990) studied the effects of the ectomycorrhizal fungus *Hysterangium setchellii* on respiration in humus under Douglas-fir, and identified patches with very high respiratory activity.

3.6 Ecological Aspects

The composition of the microbial community that invades litter depends on the properties of the litter that falls onto the soil system, and the changes in those properties over time. The community of decomposers undergoes many of the same ecological processes that act on communities of primary producers. These processes include succession and competition, while the pathway of decay may be influenced by modifications in these processes.

Microbial succession, the change in community composition over time, occurs as the quality of the decomposing substrate changes, but it also occurs because different organisms invade substrates at different rates. Griffith and Boddy (1990) followed the development of the fungal community on common ash, common oak, and European beech twigs. The primary colonizers included endophytes that were present on the twigs while they were still alive. Secondary invaders were not endophytic, and did not appear in appreciable numbers until about 11 months after twig death. They identified a third type of colonizer, the superficial, which appeared on the surface rather early into decay, but was not present on the living twig. This pattern is probably similar for all litter types, though of course the species and timing may differ. For example, spruce needles can persist on the twigs for some time after death, and decomposition can begin then. However, when the needles ultimately fall to the forest floor, the changing environmental conditions and the availability of a rich variety of inocula result in a change in the microbial community.

In addition to the change in microbial community that occurs along with decay, there are seasonal changes in the microbial community reflecting temperature and moisture. For example, Kayang (2001) followed fungi, bacteria, and selected enzyme activities in freshly fallen leaves of Nepalese alder in India. The climate was described as subtropical monsoon. The dry season occurred from November through March, with frosts during December and January. The fungal and bacterial propagule numbers varied by a factor of nearly five between winter and summer. Enzyme activities (invertase, cellulase, and amylase) reached their peaks before the peak of microbial numbers, between April and June, and then fell slowly. The sequence of peaks suggests a succession of enzyme activities, with invertase, an enzyme involved in sucrose metabolism, peaking first. Amylase, which catalyzes the hydrolysis of starch, and cellulase appeared later.

Examining activities of cellulases and cellobiose dehydrogenase on leaf litter in laboratory microcosms, Linkins et al. (1990) observed similar patterns for three different litter species. The species, flowering dogwood, red maple, and chestnut oak, differed in lignin contents and decay rates. However, all three species exhibited an increase in cellulase activity that peaked when cellulose disappearance rate was at its maximum. Cellulase activity then began to decline, and cellobiose dehydrogenase activity to increase (Fig. 3.6).

As enzyme activities are changing, so are the fungal communities. Osono and Takeda (2001) studied the fungal populations on Japanese beech leaves as they decomposed in a cool temperate deciduous forest. Total and living fungal biomass,

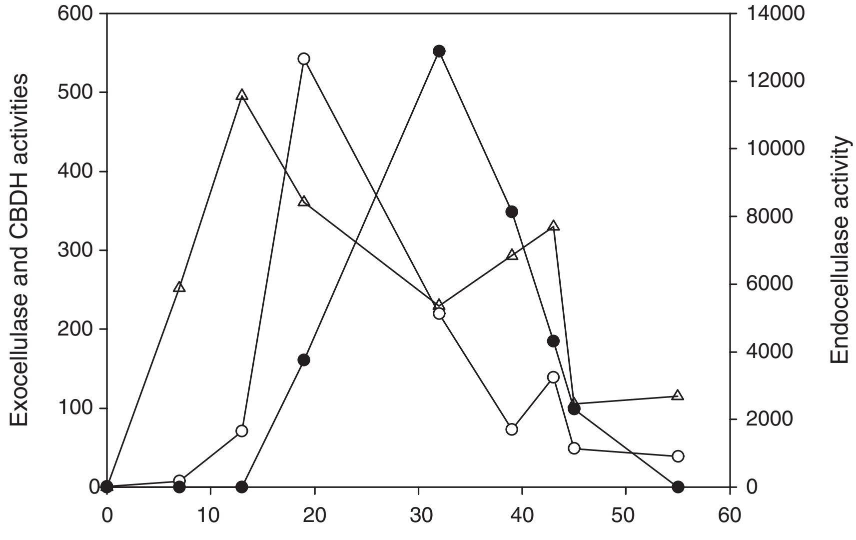

Fig. 3.6 Activities of exocellulase (▲), endocellulase (○), and cellobiose dehydrogenase (*CBDH*, ●) during chestnut oak leaf litter decay in microcosms (Linkins et al. 1990)

estimated using a modified Jones and Mollison (1948) technique (Ono 1998), increased during the first year of decay, and then fluctuated for the remainder of the study period. In the fungal community, the proportion of basidiomycetes increased for the first 21 months of the study, reaching a maximum of 25 to 35% of the total living fungal biomass. They noted that the relative abundance of basidiomycetes was linearly and negatively related to the lignocellulose index (cf. Chap. 2), an index of litter quality equal to the fraction of holocellulose in the lignocellulose. They identified over 100 fungal taxa on the beech leaves during their study, and distinguished three groups: an early-appearing group, a late-appearing group, and a constantly appearing group. The early-appearing fungi were present during the period of net nutrient immobilization, and the late-appearing fungi increased in number as the litter moved into the phase of net mineralization.

Decomposer populations may work synergistically, or in competition. Competition is visible in decaying logs where discrete zones of decay caused by different organisms can be easily discerned. In some cases, the organisms define their boundaries with black zone-lines. Interspecies dynamics can change as decomposition proceeds. For example, Bengtsson (1992) found a synergism, with no evidence of competition between fungi and bacteria on European beech leaves during their first year of decay in stream microcosms. In comparison, Møller at al. (1999) found clear evidence of competition between fungi and bacteria on 1-year-old beech leaf litter, also in a microcosm study. This difference probably relates to the age, and hence the state of decomposition and the quality of the litter. Though there are not many studies on this phenomenon, it is possible that as litter quality decreases, the competition for the remaining resource becomes more intense.

As decomposition proceeds, the microorganisms themselves can become important substrates for the microbial community. Some fungi, including wood-decay fungi, are able to use the cell walls of other fungi or bacteria, presumably as an N source. Some bacteria are able to degrade hyphal walls (Tsuneda and Thorn 1995).

There are many interactions among the organisms involved in decomposition, and these interactions change over time. These complex, dynamic systems are not easily described. However, this natural complexity does have implications for the interpretation of pure-culture and microcosm studies. Such studies are often the only way to control variability enough so as to ask a precise question. On the other hand, the behavior of a single, isolated species, or of a simple community in a mesocosm may not reflect its behavior in the more complex natural environment.

Molecular microbial ecology promises to be a powerful tool for the study of decomposition and nutrient cycling (Zak et al. 2006). As molecular analytical tools become more available, molecular databases more accessible, and computer systems to analyze these more powerful, molecular tools will be able to provide information on microbial community structure and function at a level previously not possible. For example, Blackwood and Buyer (2007) have demonstrated the potential of terminal restriction fragment length polymorphism (T-RFLP) to identify microorganisms from a variety of soils.

Chapter 4

Initial Litter Chemical Composition

4.1 Introduction

In forested ecosystems, litter fall is the largest source of organic material and nutrients for the humus layer. The quality and quantity of litter fall influences the nature of the microbial community, including its size, composition, function, and physiological properties. The composition of the microbial community may, in turn, influence the course of decomposition, and the chemical changes in the litter during decomposition. With knowledge about the initial chemical composition of litter and the chemical changes during decomposition, it is possible to predict how mass-loss rates will change even in late decomposition stages. With a close connection between the chemical composition of newly shed litter and the relative amount of recalcitrant residual litter (cf. Chap. 11), we see a direct connection between litter chemical composition and rate of humus (soil organic matter) buildup.

Plants shed not only foliar litter, but with trees as an example, also twigs, branches, bark, roots, flowers, and occasionally cones. Structures such as cones are often quantitatively important, and may sometimes exceed foliar litter as the largest component. Several litter types are not "recently dead", but are recognized as litter after they have been shed and have started to decompose, and their chemical composition to change. This applies, for example, to twigs, branches, and boles that remain standing after their death, and often start decomposing before they fall to the ground and are easily recognized as litter. Roots die and are "shed" differentially based on their size and function, and dead roots may remain attached to their parent tree for extended periods.

The combinations of main chemical components in live vascular plants have general similarities among species and genera. Quantitatively dominant groups of polymer carbohydrates and lignin are ubiquitous. However, their proportions vary, and minor structural differences occur among species.

Similarly, the same plant nutrients are found in the different plant materials and in the litter, though in very different proportions. All plant litter contains essential nutrients such as N, P, S, K, Ca, Mg, Mn, and Fe, but the concentrations vary with the litter species. For example, leaf litter of the N_2-fixing genus alder (*Alnus*) has very high levels of N (often above 3%); in contrast, pine needle litter is more N-poor

B. Berg and C. McClaugherty, *Plant Litter*,

(often below 0.4%). Species is thus one dominant factor in determining the nutrient levels in litter, but climate and the composition of the mineral soil, parent material, and the humus are also of importance. In undisturbed Scots pine systems, for example, it appears that the concentration of N may be related to both climate (Berg et al. 1995a; Liu et al. 2006) and N concentration in the humus (Berg et al. 1999b).

This chapter focuses on the litter fall from trees, and aims to give an insight into the present knowledge on the chemical composition of needle litter fall, principally in pine stands, though other conifers and deciduous species are also examined. Though the emphasis is on foliar litter, we will include some discussion on wood. We introduce the characteristics of the main insoluble chemical constituents of plant litter. We also identify factors that may influence litter chemical composition, with an emphasis on climate and soils. As data are limited, case studies have been used. The purpose of this chapter is not to explain the chemical composition of litter as based on the physiology of living plants, but rather to take into account the effect of general environmental conditions. As such, we focus on environmental components that appear to have a significant influence on the chemical composition of the litter.

4.2 Organic-Chemical Components of Plant Litter and Fiber Structure

4.2.1 Organic-Chemical Components

The plant fiber structures are composed principally of lignin, a complex aromatic, polymer compound formed mainly by esterification of phenylpropanoid structures (cf. Fig. 3.3), and polymer carbohydrates. The quantitatively most common components in plant litter are the different polymer carbohydrates such as cellulose and the main hemicelluloses. Of these, cellulose is the most common compound, and is made up of glucose units connected with β-1-4 bonds forming long chains of molecules organized into fibers. Cellulose may constitute between 10 and 50% of the litter mass (Table 4.1).

Hemicelluloses are polymers of sugars other than β-1-4-bound glucose that form long and somewhat random chains of monosaccharides (cf. Fig. 3.2) that are incorporated into the fiber. However, they do not provide structural strength in the same way as cellulose. Hemicelluloses are named based on the simple sugars from which they are synthesized, such as mannan, galactan, arabinan, and xylan. Also starch, viz. glucose bound by α-1-4 bonds, is sometimes considered a hemicellulose. The proportions of hemicelluloses vary among litter species (Table 4.1). Differences in the major hemicelluloses are reflected primarily in the concentrations of xylose and mannose (Eriksson et al. 1990). Deciduous leaves are lower in mannans, whereas Norway spruce needles have higher levels, and birch leaves are richer in xylans. The ratio of hemicelluloses to cellulose ranges from about 0.7 to 1.2 (Table 4.1),

Table 4.1 Comparison of the major organic-chemical compounds in several boreal litter types. Foliar litter data from Berg and Ekbohm (1991) and Berg and Tamm (1991), wood data from Eriksson et al. (1990)

	Concentration of compound (mg g^{-1})									
Litter type	Wsol[a]	Esol	Lig.	Glu	Man	Xyl	Gal	Ara	Rha	H:C
Coniferous needles										
S. pine (br)	164	113	231	245	75	23	32	36	3	0.69
S. pine (gr)	180	90	220	217	75	19	30	23	2	-
LP. pine (br)	103	42	381	254	90	34	46	48	6	0.88
LP. pine (gr)	147	36	346	239	81	29	37	40	33	-
N. spruce (br)	32	48	318	288	105	33	28	40	7	0.74
N. spruce (gr)	358	43	208	-	-	-	-	-	-	-
Deciduous leaf litter										
S. birch (br)	241	57	330	166	14	77	44	49	16	1.2
S. birch (gr)	222	57	322	168	9	54	51	36	12	-
G. alder	254	39	264	116	10	30	32	44	9	1.08
Deciduous wood										
S. birch	-	-	217	351	9	207	-	-	-	-
Aspen	-	-	220	462	16	189	-	-	-	-
R. alder	-	-	246	470	4	176	-	-	-	-
Coniferous wood										
S. pine	-	300	383	111	65	-	-	-	-	-
R. pine	-	279	449	123	84	-	-	-	-	-
N. spruce	-	271	416	136	52	-	-	-	-	-

[a] *Wsol* Water-soluble, *Esol* ethanol-soluble, *Lig.* lignin, *Glu* glucans (cellulose), *Man* mannans, *Xyl* xylans, *Gal* galactans, *Ara* arabinans, *Rha* rhamnans, *S. pine* Scots pine, *LP. pine* lodgepole pine, *R. pine* red pine, *N. spruce* Norway spruce, *S. birch* silver birch, *G. alder* grey alder, *R. alder* red alder, *H:C* hemicellulose:cellulose ratio, *br* brown litter, *gr* green litter

with higher ratios often seen in deciduous litter than in coniferous litter. Hemicelluloses may together make up as much as 30–40% of the fiber, and are normally present at between 1 and 10% each (Table 4.1). In contrast to cellulose, hemicelluloses are often branched (Fig. 3.2).

Lignin often makes up between 15 and 40% of the litter mass. In some extreme cases, litter can have lignin contents as low as 4%, or as high as 50%. Lignin, in contrast to cellulose, is a highly variable molecule. The initial composition of lignin varies with the plant species, and this variation is enough to make the lignin of each species unique. This also rules the terminology. Thus, the native lignin of different species may be specified by the name of the species – for example, Norway spruce lignin, and aspen lignin. A generalized structure of Norway spruce lignin has been illustrated in Fig. 3.3. The terminology pertaining to lignin and its transformation products is, however, not always clear, especially after some degradation has taken place (Dean 1997; see Chap. 2 and Glossary).

The lignin content of deciduous species is generally lower than that of the coniferous ones, although the variation is large in both groups. Furthermore, the types of lignin formed in gymnosperms and angiosperms are different. Whereas angiosperms (deciduous species) contain varying ratios of syringyl and guaiacyl types of lignin, gymnosperms (conifers) have mainly guaiacyl lignin (Fengel and Wegener 1983). While some basic structural elements are common over a wide range of species, individual species show variation among a variety of groups, such as methoxyl groups and other substituents located at different sites in the molecule.

Litter also contains large quantities of low-molecular-weight substances, such as amino acids, simple sugars, short-chain fatty acids, and lower-molecular-weight phenolic substances. Complex compounds such as high-molecular-weight fatty acids and complex phenolic compounds are also found. We may be able to identify some hundred different molecules from these two groups. Often they are analyzed simply as water solubles for the former group, and ethanol- or acetone solubles for the latter.

Cutin and suberin are resistant molecules that can influence decomposition, and they can increase in concentration during decay (Kolattukudy 1980, 1981, 1984). Although present in rather small amounts and seldom identified in litter decomposition studies, these polyesters act as barriers to protect living plants and to delay invasion by microorganisms. Cutin is found on and in leaves, and suberin in bark and roots. Both are polymers composed of hydroxy- and epoxy-alkonic acids. Kögel-Knabner et al. (1989) extracted these acids from the L layers of European beech and Norway spruce forests. They found that cutin and suberin contributed 12 to 24 mg g^{-1} organic matter. The presence of suberin in root tissues may retard their decay.

4.2.2 Fiber Structure

Fiber structure appears to be a critical concept for the pattern of decomposition. The fiber's main organic-chemical components may be arranged in different ways, and in terms of decomposition, the arrangements may be of importance for the properties of the fiber. Thus, a fiber may have holocellulose and lignin separated to a high degree, or the holocellulose and the lignin may be well integrated; the cellulose has a high degree of lignification. We may even expect that cases occur in which all cellulose is integrated in, or covered by lignin.

Description of One Type of Fiber

The insoluble components of plant litter are concentrated in the cell wall, a multilayered structure. The wood cell wall is composed of various layers (Fig. 4.1), and is made up of a primary wall (P) and the secondary wall (S), which has three layers designated S1, S2, and S3. The middle lamella and the primary wall make up the compound middle lamella that is located between the secondary wall layers of adjacent cells (Core et al. 1979). The S3 layer is located closest to the lumen (L). The normally thickest layer (S2) is the middle layer, and S1 is the outermost layer of the secondary wall. These layers are distinct from each other because the cellulose is arranged in different microfibril orientations. A model describing the

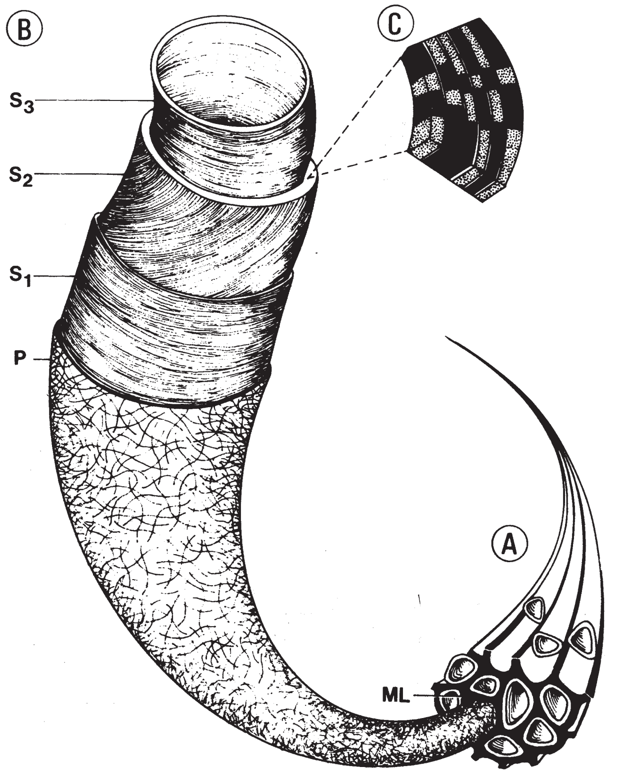

Fig. 4.1 Overview of a plant fiber. *A* Tracheids. *B* Cell-wall layers. *C* Arrangements of polymer carbohydrates and lignin in the secondary wall. Shown are the middle lamella (*ML*), primary wall (*P*), and layers of the secondary wall (*S1*, *S2*, and *S3*). The microfibril orientation and the thickness are different among the layers, and some species have an additional warty layer over the inner (*S3*) layer. The schematic representation of the secondary wall in *C* demonstrates the distribution of the lignin–hemicellulose matrix (*black*), hemicellulose (*white*), and cellulose fibrils (*dotted*; from Eriksson et al. 1990)

arrangement of lignin, hemicellulose, and cellulose within the cell wall was proposed by Kerr and Goring (1975; Fig. 4.1). The model shows how a matrix of lignin and hemicellulose encrusts the cellulose fibrils. There is a tremendous diversity in wood structure among the hundreds of hardwood species that grow throughout the world (Panshin and de Zeeuw 1980). Still, the drawing in Fig. 4.1 may serve as a model for our discussion.

In plant fibers the cellulose, the hemicelluloses, and the lignin molecules are not only combined physically, but the celluloses are normally more or less encrusted with lignin. Within the cell wall, cellulose forms microfibrils composed of individual strands of cellulose that are often about 10–25 nm in diameter (Fig. 4.1). Microfibrils group together into larger strands called macrofibrils. These are visible with a light microscope, and are about 0.5 µm in thickness.

Of the several cell-wall layers, the thickest (S2) normally has a width of 0.5–4.0 µm. The walls are constructed of a matrix of cellulose, hemicellulose, and in many plant tissues, lignin. The thickness of the entire primary and secondary wall complex is highly variable.

The formation of lignin in the fibers (lignification) of the live plant is a slower process than that of cellulose. As a result, the last parts of the cell wall to be formed may be very low in lignin, and the older parts richer. Thus, in wood, lignin is distributed throughout the secondary (S) wall and compound middle lamella, but the greatest concentration is in the middle lamella. The secondary wall makes up a large part of the total cell wall, and most of the cell-wall lignin (60–80%) is located in this region (Musha and Goring 1975; Saka and Thomas 1982a, b). The distribution of hemicellulose parallels that of lignin within the wall (Parameswaran and Liese 1982). The hemicellulose surrounds the cellulose microfibrils, and occupies the spaces between the fibrils.

The pattern and extent of lignification of fibers are probably different among tree species, and thus also among litter species. This appears to be an area in which we lack good information, although it has a potential importance for the decomposition process. For a fiber in which the lignification is complete, or close to complete, the cellulose and hemicelluloses may be completely encrusted in lignin, and the structure of the fiber may be very different to that of fibers that are less lignified. Such differences may give rise to different properties, e.g., in terms of rate limitation. Thus, fibers with a complete lignification may decay differently than those in which this is incomplete, or in which the fiber tissue is without lignin (cf. Fig. 2.2, and the discussion in Sect. 2.4). The lignin concentration in litter as such seems not to give enough information to be really useful (Fig. 4.2) as regards the level of lignification, although we may expect that fibers with a high lignin concentration would have a more complete lignification.

4.3 Nutrient Concentrations in Newly Shed Litter

4.3.1 General Features

Many of the nutrients found in newly shed plant litter have their origins in strictly controlled structures in the live plant parts, and a nutrient such as N can be found in membranes, cytoplasmic enzymes, structural proteins, or nucleic acids. In green foliage, ribulose bisphosphate carboxylase/oxygenase (rubisco) may account for most of the N. When a leaf dies and foliar litter is being formed, these cellular constituents disintegrate, at least in part. Before a leaf dies, a proportion of the nutrients is translocated into the perennial portion of the plant, leaving the remainder in the dead material, a process that may take place over several weeks. This process is called retranslocation.

Nutrients, as usually measured by ecologists, are expressed in their elemental or ionic form, generally making no distinction as to the origin of the nutrient within

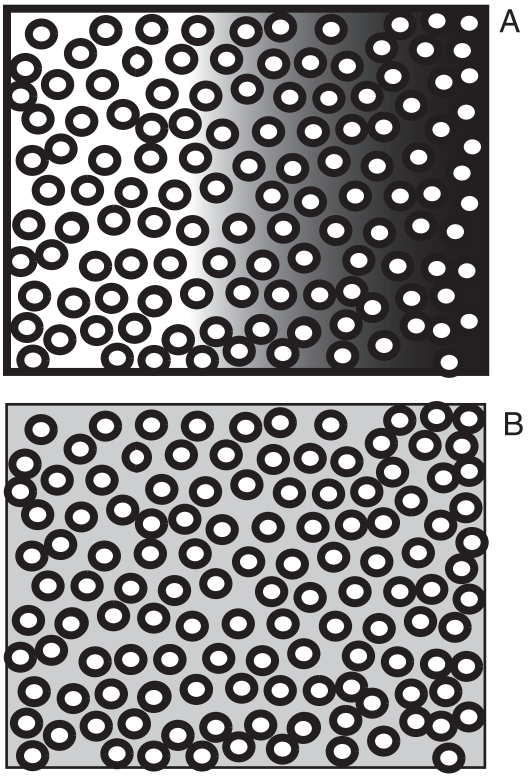

Fig. 4.2 Schematic cross section of a fiber. The white dots surrounded by a black circle indicate polymer carbohydrates. The surrounding field indicates the degree of lignification of the carbohydrates with a clear field indicating unlignified and dark grey indicating heavy lignified. **A** Lignification is not complete. **B** All carbohydrates are covered by, or encrusted in lignin

the plant's structure. What is often measured as simply a "mineral nutrient" – for example, N – can thus originate from a number of different components in the litter, such as proteins or nucleic acids.

Nitrogen is found in concentrations normally ranging between 0.2 and 3.0% in foliar litters. In woody structures, such as branches, the concentration may be as low as 0.02%. We cannot assume that, e.g., the total N in different litter species, or in different parts of the same species is chemically bound in the same molecules across species, plant parts, and concentration ranges. Phosphorus is bound in nucleic acids, and S is found in proteins, too, among other molecules.

When decomposition and microbial ingrowth have started, further changes occur and the distribution of nutrients in compounds, as well as concentrations of nutrients, will be very different from those of both the living and the freshly senescent material. In this book, we will not generally discuss the nutrients in terms of the macromolecules they are part of, but rather simply as nutrients.

4.3.2 Nutrient Resorption and Withdrawal Efficiency

The chemical composition of the living plant is reflected in its litter. This applies particularly to structural components such as lignin, the relative composition of hemicelluloses, and to a smaller extent, nutrients.

Many genera, such as pine, growing on relatively nutrient-poor soils retrieve the main part of their nutrients before shedding their foliar litter. This "inner circulation" is a conserving mechanism that has been suggested to be in effect mainly in nutrient-poor soils (Gosz 1981; Staaf and Berg 1981). An example at the opposite extreme is the N_2-fixing genus alder, which produces leaf litter that has as high a concentration of N as the live leaves, ca. 2–3%.

Trees also withdraw substances other than nutrients before shedding their leaves and needles. Thus, at senescence, different soluble C components, such as sugars and phenolics, are withdrawn, resulting in mass loss from the living tissue; 15 to 35% loss of mass have been measured (Table 4.2). This may result in an increase in concentration of those nutrients that are withdrawn or leached to a smaller extent, and a decrease only for those that have been withdrawn or leached to a greater extent. Thus, nutrients that have an increase in concentration during senescence may not represent a real increase in amount, but rather an increase in proportion as total organic compounds are depleted.

A study on green and senesced leaves from four deciduous tree species (Hagen-Thorn et al. 2006) quantifies both the changes in carbon compounds and the nutrients (Table 4.2), as the measurements were related to unit leaf surface. We may see that of the main nutrients N, P, K, and S, varying fractions remained in the shed litter, ranging from ca. 30 to 60% depending on the species and element.

Calcium, on the other hand, was resorbed to a much smaller degree, and has even shown a 7% higher amount in birch foliar litter as compared to the green leaves. Resorption efficiency as well as nutrient loss from the foliage due to leaching may vary among species and elements (Hagen-Thorn et al. 2006).

A thorough study on leaves of European beech (Staaf 1982) indicates that there was a positive correlation between the withdrawal of nutrients and the concentration of nutrients in green leaves. This relationship was especially steep for N (Fig. 4.3), showing that a higher initial concentration led to a relatively higher withdrawal. In contrast, the relationship was rather flat for Ca, indicating a lower effect of initial concentration on the withdrawal (Fig. 4.3). Soil pH had an effect on the withdrawal of Ca (Staaf 1982), and at sites with a lower soil pH, there was a lower withdrawal. This effect was seen only for Ca.

4.3.3 Nutrient Concentration Change, Green vs. Brown Foliage

A comparison was made between concentrations of the main nutrients in green leaves collected in July and those of newly shed ones (Table 4.3). Concentrations of N, P, S, and K were considerably lower in newly shed litter, whereas Ca, Mg, and Mn had

Table 4.2 Concentrations of some main nutrients in green and senesced (brown) leaves as calculated on an area basis, and concentrations of nutrient or mass in brown litter as a percent of that in green litter. All concentrations are given in micrograms per cm^2 leaf area (from Hagen-Thorn et al. 2006)

	Ash	Birch	Lime	Oak
N green	173.8	170.4	135.4	185.2
N brown	103.1	49.6	55.8	72.1
N % in litter	59.3	29.1	41.2	38.9
P green	13.5	23.6	12.5	16.3
P brown	7.17	12.6	4.71	8.92
P % in litter	53.1	53.3	37.7	54.7
S green	35.5	11.2	14.2	12.3
S brown	17.65	5.52	7.45	6.23
S % in litter	49.7	49.3	52.5	50.6
K green	72	65	95.9	82.1
K brown	23.6	31.9	36.5	44.2
K % in litter	32.8	49.1	38.1	53.8
Ca green	152.4	69.7	95.7	68.5
Ca brown	108.1	74.7	90.8	63.9
Ca % in litter	70.9	107.2	94.8	93.3
Mg green	37.5	22.9	10.3	13.1
Mg brown	22.3	21.4	9.5	10.9
Mg % in litter	59.5	93.4	92.3	83.2
Mn green	0.37	15.5	5.94	5.89
Mn brown	0.28	13.2	5.64	5.28
Mn % in litter	75.7	85.2	94.9	89.6
Fe green	0.66	0.66	0.58	0.79
Fe brown	0.47	0.41	0.53	0.55
Fe % in litter	71.2	62.1	91.4	69.6
Cu green	0.08	0.04	0.05	0.05
Cu brown	0.05	0.03	0.04	0.03
Cu % in litter	62.5	75	80	60
Mass green	8,757.9	7,239.9	5,377.8	7,222.4
Mass brown	5,903.2	5,821.6	4,600.2	5,347.2
Mass % in litter	67.4	80.4	85.5	74

increased concentrations in the shed litter. For the heavy metals, the concentrations were the same, or higher than the initial values (albeit based on a limited amount of data).

In the case of Scots pine, lodgepole pine, silver birch, and trembling aspen, the concentrations of N may decrease to about 1/3 of that in green leaves before the leaves and needles are shed in autumn. For example, in pines the concentration may decrease from about 12–14 to about 3–4 mg g^{-1} (Table 4.3). This retrieval process may of course be disturbed, occasionally leading to extreme levels of N (Table 4.4). For Norway spruce, the N concentration decreased to about 50% of the level in green needles (Table 4.3). When comparing only changes in concentrations of remaining P to those in green leaves, the values were of the same magnitude as for N, ranging from 15 to 50%. For S, less of the nutrient was retrieved, and in general more S remains, with concentrations ranging from 38 to 103% of those in green leaves. For K, there was a difference between coniferous and deciduous trees, with deciduous

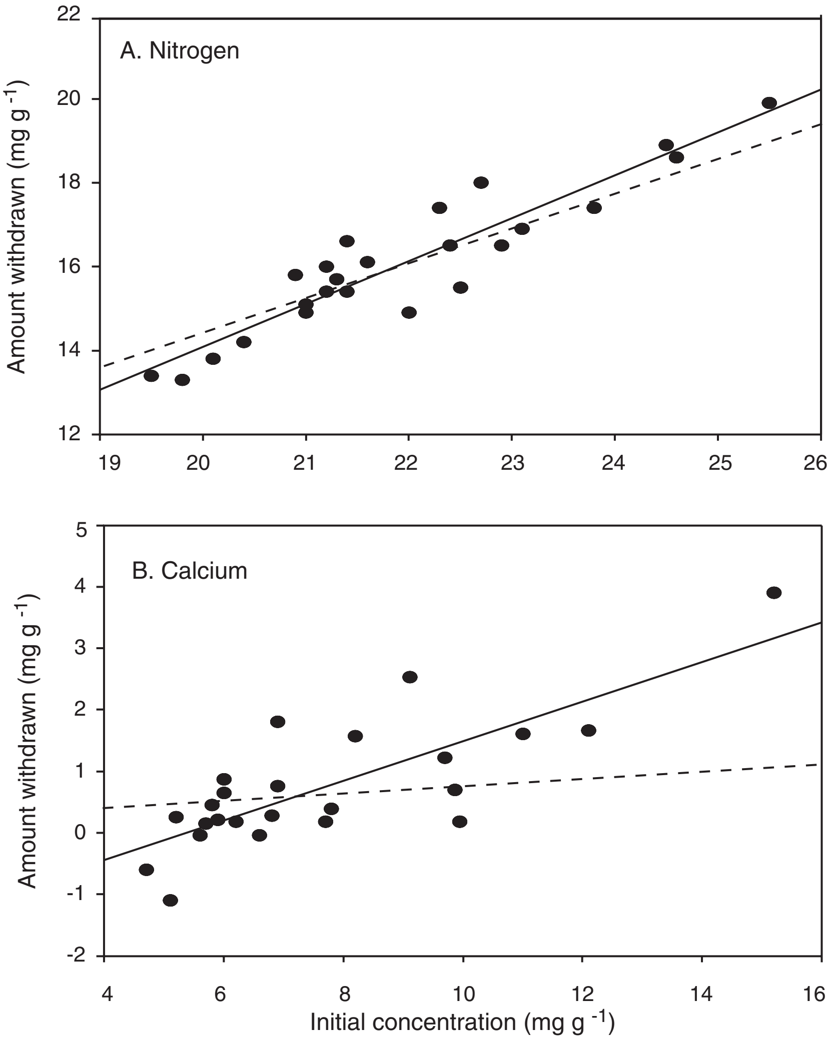

Fig. 4.3 Linear relationships between concentrations of N (**A**) and Ca (**B**) in green leaves of European beech, and the amount of the nutrient that has been withdrawn before senescence. The amount withdrawn is expressed per unit leaf mass before senescence. The *continuous line* shows that the amount withdrawn increases with the initial concentration in the green leaves. The *dashed line* shows a theoretical relationship for a constant fraction having been withdrawn (redrawn from Staaf 1982)

trees having clearly higher concentrations when shed, in the range of 40–50% of the concentrations in green foliage. The newly shed conifer needles had less than 25% of their summer K concentrations, while pines as a group had even lower levels.

Calcium was retrieved to a small extent, resulting in an increase in its concentration to 115–220% (see below). This may be explained by the decrease in leaf mass from green to senesced leaves (see Sect. 4.3.2). The remaining Mg ranged from 43 to 113%

Table 4.3 Comparison of concentrations of some common nutrients in green leaves collected in July, and in the corresponding foliar litter collected at litter fall (B. Berg, unpubl. data). N.B. The table compares only concentrations, and does not consider retention or withdrawal of nutrients (Sect. 4.3.2). Data for European beech are from Staaf (1982)

	Concentration of nutrient (mg g^{-1})						
Litter type	N	P	S	K	Ca	Mg	Mn
S. pine (br)[a]	3.6	0.20	0.44	0.5	5.6	0.34	1.19
S. pine (gr)	12.1	1.36	0.81	5.9	3.9	0.79	0.53
% conc. change[b]	30	15	55	8	143	43	224
LP. pine (br)	3.1	0.29	0.44	0.5	8.7	1.06	2.03
LP. pine (gr)	10.5	0.82	1.17	3.8	4.0	0.93	0.82
% conc. change	30	35	38	13	220	113	250
N. spruce (br)	4.2	0.41	-	1.0	13.1	0.89	1.32
N. spruce (gr)	8.5	1.32	-	4.0	11.3	1.22	1.07
% conc. change	49.0	31	-	24	115	73	123
S. birch (br)	7.7	1.05	0.80	4.7	11.8	3.30	1.23
S. birch (gr)	24.3	1.96	1.54	9.0	9.5	3.37	0.76
% conc. change	32	53	52	52	124	98	158
T. aspen (br)	6.8	0.63	1.37	6.3	17.1	2.13	0.15
T. aspen (gr)	24.2	2.12	1.87	14.2	8.4	2.29	0.10
% conc. change	28	30	73	44	204	92	150
E. beech (br)	9.1	0.63	1.21	2.7	10.0	1.70	-
E. beech (gr)	22.6	1.44	1.18	5.4	7.7	1.67	-
% conc. change	40	44	103	50	130	102	-

[a] *S. pine* Scots pine, *LP. pine* lodgepole pine, *N. spruce* Norway spruce, *S. birch* silver birch, *T. aspen* trembling aspen, *E. beech* European beech, *br* brown, *gr* green

[b] Concentration change is here expressed simply as the concentration in brown litter as percentage of that in green litter

of the initial concentration. Manganese contrasted with the other nutrients by having increased concentrations in all cases, ranging from 123 to 250%.

4.3.4 Nutrients in Needle Litter of Pine spp. – a Case Study

Extensive data are available on the initial organic-chemical and nutrient composition of Scots pine needle litter over extended periods of time and a wide geographical area, as well as for some other pine species. Using these data, we can examine the variability in chemical composition within a single stand over time, among stands in a small geographical area, and among stands across a climatic gradient.

Annual Variation at One Site – Scots Pine

In a single stand, there is a clear variation in the chemical composition of the newly shed needle litter over different years. This is illustrated (Table 4.4) with an investigation in which some nutrients in freshly fallen needle litter were measured in 17

Table 4.4 Annual variation in concentration of solubles, lignin, and nutrients of Scots pine (*P. silvestris*) needle litter collected in a nutrient-poor forest at Jädraås (SWECON site, cf. Appendix III; Johansson et al. 1995)

	Concentration (mg g^{-1})									
Year	Wsol[a]	Esol	Lig.	N	P	S	Ca	K	Mg	Mn
1973	92	120	223	3.8	0.19	0.42	6.5	0.73	0.38	1.55
1974	145	84	276	4.2	0.22	0.29	5.4	0.71	0.49	n.d.
1975	172	107	238	3.4	0.20	0.32	4.7	0.61	0.39	n.d.
1976	151	89	255	4.0	0.21	0.36	4.9	0.53	0.42	n.d.
1977	202	102	224	4.1	0.19	0.38	6.0	0.87	0.42	1.02
1978	164	96	257	3.8	0.21	0.33	5.5	0.62	0.55	1.00
1979	129	95	288	10.4	0.29	0.78	2.3	0.97	0.39	0.31
1980	180	102	246	3.8	0.18	0.50	6.1	1.72	0.53	0.77
1981	213	94	231	3.9	0.28	0.61	7.1	1.02	0.58	1.17
1982	164	113	231	4.8	0.33	0.55	4.4	1.07	0.49	0.79
1983	178	112	229	3.8	0.30	0.45	5.9	0.9	0.39	1.08
1984	82	116	288	3.7	0.21	0.47	6.3	0.82	0.44	1.12
1985	182	94	241	3.0	0.19	0.45	4.8	0.52	0.38	1.24
1986	170	89	257	4.0	0.23	0.44	5.6	0.58	0.57	1.13
1987	162	100	250	3.8	0.21	0.42	4.9	0.55	0.41	1.18
1988	165	94	247	3.8	0.21	0.39	5.0	0.67	0.38	1.18
1989	n.d.	n.d.	n.d.	3.6	0.17	0.38	4.0	0.59	0.42	0.92
Avg.	159	100	249	4.2	0.23	0.44	5.3	0.79	0.45	1.03
SD	35	11	21	1.6	0.05	0.12	1.1	0.29	0.07	0.27

[a] *Wsol* Water solubles, *Esol* ethanol solubles, *Lig.* lignin, *n.d.* not determined, *Avg.* average value, *SD* standard deviation

consecutive years. Also, the levels of water solubles and lignin were followed, with some constituents being much more variable than others.

Concentrations of N varied from 3.0 up to a high value of 10.4 mg g^{-1}. Compared with other years, the latter value is exceptionally high relative to concentrations of elements such as P and S in the same year. The frequency of occurrence of such a high value has not been established, and may be regarded as a consequence of an unknown extreme event. However, in another study on litter chemical composition along a transect, a similarly high value was found (Johansson et al. 1995). With the next highest value being 4.8 mg g^{-1} (Table 4.4), N concentration still shows considerable variation (1.6-fold) compared to the lowest value. The average concentration for N at this site was 4.2 mg g^{-1}. The concentration of P varied between 0.17 and 0.33 mg g^{-1}, showing a range factor of 1.9. For S, the range was from 0.29 to 0.78 mg g^{-1}, corresponding to a factor of 2.7.

Within the same stand, Ca concentrations varied with a factor of 3.1 from 2.3 to 7.1 mg g^{-1}, a relatively large variation considering that earlier analyses indicate a strong dependence of soil type for this nutrient. For K, the mean value was 0.79 mg g^{-1} and the range from 0.52 to 1.72 mg g^{-1}, corresponding to a factor of 3.3. The mean for Mg was 0.45 mg g^{-1}, and the range was from 0.38 to 0.58 mg g^{-1}, a range with a factor of 1.5. Manganese was the most variable nutrient; the mean value was 1.03 mg g^{-1} and the range from 0.31 to 1.55 mg g^{-1}, corresponding to a range factor of 5.

The concentrations of the main nutrients N, P, and S were in the average proportions of 1:0.055:0.105. As we will discuss later, both N and P each have been ascribed the role of being rate-limiting for decomposition. When we relate both P and S to N, the relative proportions of P are seen to vary considerably, from 0.028 to 0.079, and for S from 0.069 to 0.156. There evidently was a variation in proportions between years that may influence which nutrient was rate-limiting (see Chaps. 2 and 6). Even disregarding the few extreme values, there is still clear variation between years. A trend analysis did not reveal any significant change in nutrient concentrations over time. The variation in concentrations of water-soluble substances ranged from 82 to 213 mg g^{-1}, with an average value of 159 mg g^{-1}. For lignin concentrations, the range was from 223 to 288 mg g^{-1} with an average value of 249 mg g^{-1}.

No strong correlation existed among the constituents, and using the Spearman rank correlation, only three correlations were significant: water solubles and lignin ($R=-0.535$, $p=0.033$), N and P ($R=0.546$, $p=0.029$), and S and K ($R=0.599$, $p=0.014$). Ash concentrations in the collections of Scots pine needle litter were relatively low (average value = 20 mg g^{-1}), compared with those of some other tree species (Bogatyrev et al. 1983).

Variation Among Scots Pine Sites, and Along a Transect of Scots Pine and Other Pine Species

In Europe, Scots pine grows mainly from the Barents Sea in the north to the Pyrenees and northern Greece in the south, although it forms forests to about the latitude of the Alps and the Carpathians. Scots pine may grow on both nutrient-poor granite sand and on clayey soils. On a European scale, the magnitude and pattern of litter fall varies with the geographical position and climate.

Litter fall begins relatively early in the north, close to the Barents Sea (ca. 70°N) normally in the first week of August. In south Poland (ca. 50°N), it may start as late as November. A strong drought may change this pattern, and induce an earlier litter fall. That drought does influence the onset of litter fall is seen in the Mediterranean climate zone where native pine species shed their needles in July. Scots pine, when growing in a Mediterranean climate, has adopted the litter-fall pattern of the Mediterranean pine species, and has its main foliar litter fall in summer during the dry period.

Litter chemical composition varies with the site's geographical position and climate (Berg et al. 1995a). A study along a transect ranging from the Barents Sea in the north to about the Carpathian Mountains in the south, and thus encompassing half the length of Europe, shows a clear trend in chemical composition with climate. Concentrations of N, P, S, and K are positively related to AET; for example, N levels range from about 3 mg g^{-1} in the north to about 9 mg g^{-1} at the more southern locations (Fig. 4.4).

For Mn, a significant but negative relationship indicated that the highest Mn concentrations were found in the north at lower AET, and the lowest at the southern

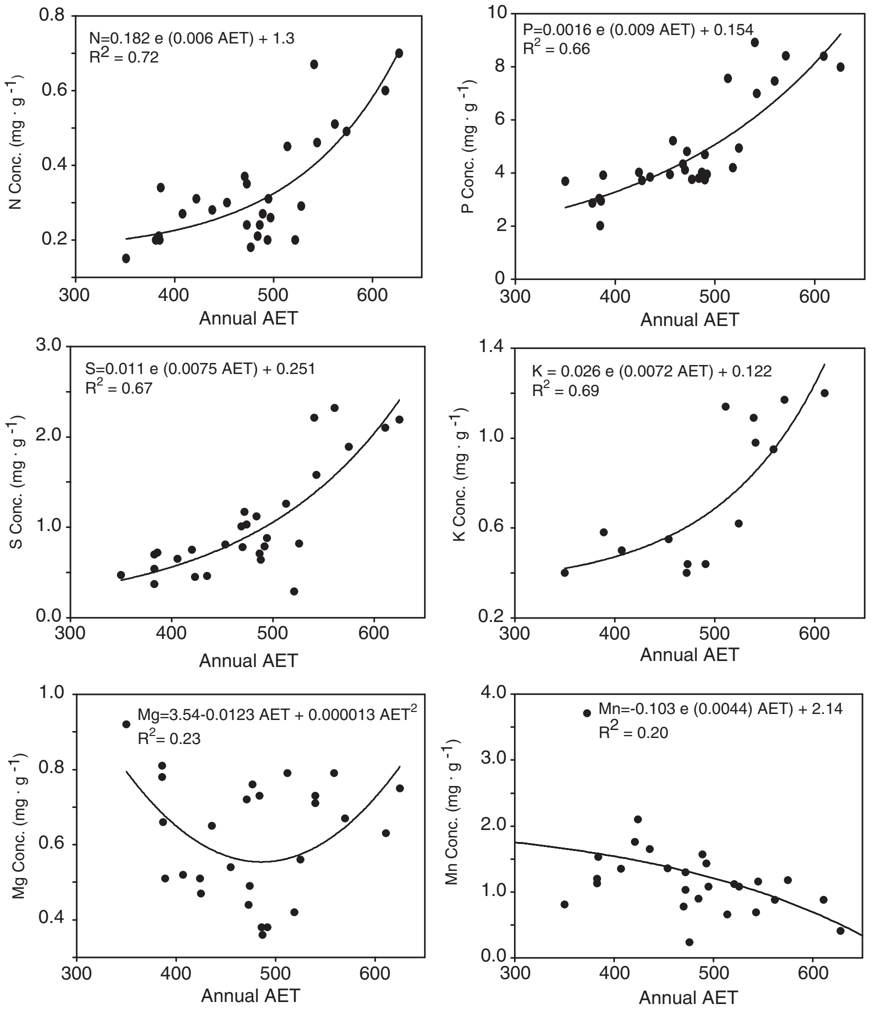

Fig. 4.4 Relationships between the climatic index actual evapotranspiration (AET) and concentrations of nutrients in newly shed Scots pine needle litter: N, P, S, K, Mg, and Mn. The litter was collected along a climatic transect of Scots pine forests ranging from the Barents Sea in the north to central Europe (Berg et al. 1995a)

sites with a higher AET. This was subsequently confirmed by a study on different pine species over Europe, using simple linear regression analysis ($R^2=0.253$, $n=40$, $p<0.001$).

These findings of Berg et al. (1995a) were followed by those of Oleksyn et al. (2003) who used mainly the same climatic transect with Scots pine, investigating the N concentrations in green Scots pine needles and comparing these levels to those recorded in brown needles. They suggested a retrieval mechanism with a stronger retrieval of N under colder and drier climate conditions. Also other studies have shown that the resorption of N in trees is related to climatic factors (Killingbeck 1996). Their suggested mechanism is not contradictory to that proposed for common beech by Staaf (1982; Fig. 4.3). Here, we have included both, as they seem to complement each other. However, we cannot exclude that for different species such mechanisms may be different.

Within Scots pine, the variation in litter N concentration is weakly but positively correlated to the concentration of N in the organic matter in the humus layers ($R^2=0.121$, $n=36$, $p<0.05$). This ties to climate, and illustrates the triangular relationship between soil, climate, and litter discussed by Aerts (1997). Thus, a climate favorable for the growing plant gives a higher N concentration in the needle litter, which thus leads to humus with a high N level.

In a continental-scale investigation over Eurasia, Liu et al. (2006) used data from eight species of pine (Fig. 4.5), i.e., Scots pine, lodgepole pine, stone pine, maritime pine, Khesi pine, Chinese pine, Chir pine, and Korean pine. Liu et al. (2006) distinguished between climatic factors with annual average temperature ranging from ca. −1.7 to about 30 °C, and annual precipitation from ca. 500 to 3,000 mm. Along this transect with 56 samples, they found highly significant relationships – a positive relationship to annual average temperature, and a negative one to annual precipitation (Table 4.5). They also used "standardized" (see legends to Table 4.6) temperature and precipitation in a linear regression, and found a significant difference in response for pine species in terms of these two climate factors. They found a highly significant multiple linear relationship (Table 4.6) between N concentration in pine needle litter, and temperature and precipitation. The coefficient for temperature was positive, and that for precipitation negative (both highly significant). This pattern distinguished *Pinus* needles from the rest of their material. The difference in effect of relative temperature and precipitation was highly significant ($R^2_{adj}=0.435$, $p<0.001$; Table 4.6). We may comment that such effects possibly can

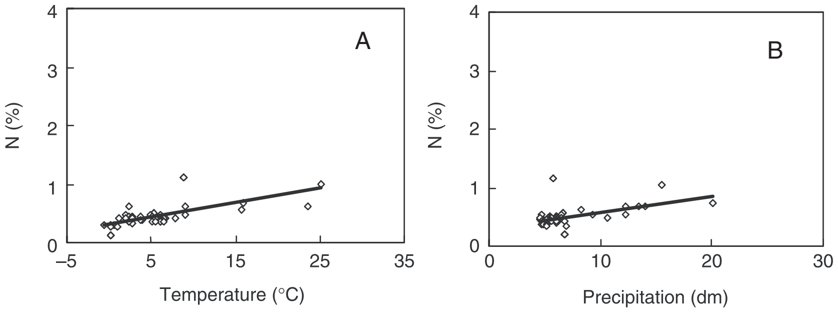

Fig. 4.5 Variation in needle litter N concentration for different pine species along a climatic transect across Europe and Asia in relation to **A** annual average temperature (°C), and **B** annual precipitation (dm). The linear relationships are both significant at $p<0.001$ (from Liu et al. 2006)

Table 4.5 Simple and multiple linear relationships over Eurasia for nitrogen concentration (%) in leaf litter regressed against annual average temperature (°C) and annual precipitation (dm) for the groups of (1) coniferous plus broadleaf litter, (2) coniferous litter, (3) broadleaf litter, (4) deciduous litter, and (5) evergreen litter, as well as for the genus *Pinus* (data from Liu et al. 2006)

	Intercept			Temperature			Precipitation					
Forests	Coeff.	SE	*p*	Coeff.	SE	*p*	Coeff.	SE	*p*	*n*	R^2_{adj}	*p*
ln(N) = c+a×Temp.												
Conif.+broadleaf	–0.907	0.054	<0.001	0.046	0.004	<0.001				204	0.454	<0.001
Coniferous	-1.054^{a}	0.064	<0.001	0.052^{b}	0.009	<0.001				81	0.307	<0.001
Broadleaf	-0.576^{a}	0.100	<0.001	0.031^{b}	0.005	<0.001				123	0.215	<0.001
Deciduous	-0.647^{a}	0.134	<0.001	0.037	0.009	<0.001				52	0.229	<0.001
Evergreen	-0.425^{a}	0.182	0.023	0.024^{b}	0.008	0.007				71	0.089	0.007
Pinus	-1.189^{a}	0.060	<0.001	0.051^{b}	0.008	<0.001				56	0.421	<0.001
ln(N) = c+b×Precip.												
Conif.+broadleaf	–0.925	0.064	<0.001				0.050	0.005	<0.001	204	0.369^{c}	<0.001
Coniferous	-1.142^{c}	0.077	<0.001				0.048	0.008	<0.001	81	0.298	<0.001
Broadleaf	-0.515^{c}	0.092	<0.001				0.033	0.006	<0.001	123	0.209	<0.001
Deciduous	-0.613^{c}	0.153	<0.001				0.037	0.012	0.003	52	0.150	0.003
Evergreen	-0.379^{c}	0.118	<0.001				0.027	0.007	0.002	71	0.184	<0.001
Pinus	-1.242^{c}	0.133	<0.001				0.049	0.018	0.012	56	0.104	0.009
ln(N) = c+a×Temp.+b×Precip.												
Conif.+broadleaf	–1.063	0.058	<0.001	0.033	0.004	<0.001	0.027	0.005	<0.001	204	0.522	<0.001
Coniferous	–1.193	0.074	<0.001	0.034	0.010	<0.001	0.030	0.009	0.002	81	0.384	<0.001
Broadleaf	–0.756	0.105	<0.001	0.022	0.005	<0.001	0.023	0.006	<0.001	123	0.298	<0.001
Deciduous	–0.815	0.157	<0.001	0.029^{d}	0.010	0.004	0.023^{e}	0.012	0.060	52	0.268	<0.001
Evergreen	–0.689	0.183	<0.001	0.017^{d}	0.008	<0.033	0.024	0.007	<0.001	71	0.226	<0.001
Pinus	–1.045	0.111	<0.001	0.063^{d}	0.011	<0.001	-0.031^{e}	0.020	0.131	56	0.435	<0.001

[a] Significant difference between the intercepts for coniferous vs. broadleaf, and for the *Pinus* model and those for deciduous and evergreen models (t-test, $p < 0.001$)

[b] Significant difference between temperature (temp.) coefficients for coniferous vs. broadleaf, and for evergreen and *Pinus* models (t-test, $p = 0.02$)

[c] Significant difference between the intercepts for coniferous vs. broadleaf, and for the *Pinus* model and those for deciduous and evergreen models (t-test, $p = 0.002$)

[d] Significant difference between temperature (temp.) coefficients for the *Pinus* and deciduous models (t-test, $p < 0.001$), and between the intercepts of the *Pinus* and evergreen models (t-test, $p = 0.025$)

[e] Significant difference between precipitation (precip.) coefficients for the *Pinus* and deciduous models (t-test, $p = 0.025$), and between the precipitation coefficients for the *Pinus* and evergreen models (t-test, $p = 0.005$). Note that precipitation is given in dm simply for practical reasons, as the traditional mm would give too many zeros in the coefficients. The authors used logarithmic transformation of data

Table 4.6 Multiple linear relationships for leaf litter N concentration regressed against annual average temperature (°C) and annual precipitation (in dm) for a dataset of 204 values for N concentrations in litter collected over Asia and Europe. The data were also subdivided into the subgroups "coniferous" and "broadleaf", as well as the subgroup of pine spp. (from Liu et al. 2006)[a]

	Intercept		Standard temp.		Standard precip.				
Forest/litter type	Coeff.	*p*<	Coeff.	*p*<	Coeff.	*p*<	*n*	R^2_{adj}	*p*<
BrdCon	0	1	0.486	0.001	0.326	0.001	204	0.522	0.001
Broadleaf	0	1	0.336	0.001	0.327	0.001	123	0.298	0.001
Coniferous	0	1	0.367	0.001	0.349	0.001	81	0.384	0.001
Pine spp.	0	1	0.808^*	0.001	-0.217^*	0.131	56	0.435	0.001

[a] The data were standardized to allow a direct comparison of coefficients. *Coeff.* thus represents the slope of the regression equation, and can be used as an index within each row to indicate the relative importance of temperature versus precipitation for the litter N concentration. Standardized temperature and moisture data were generated using the program Standardize Transform (SPSS Inc., Chicago, IL, 1997), which means that the effects of temperature and precipitation can be directly compared. *BrdCon* Broadleaf plus coniferous, * significant difference between coefficient for standardized temperature and standardized precipitation

be distinguished only on species or genus level. Indeed, for the broader groups, encompassing several genera, they found positive relationships for both temperature and precipitation (Sect. 4.3.5).

We may conclude that this gradient in litter N levels appears to be normal in pines as a genus. On the level of species, the progressive increase in concentrations of P, S, and K in litter with increasing AET remains to be shown for species other than Scots pine. For *Pinus*, it seems to reflect a direct effect of climate on the N retrieval mechanism, and thus on litter quality.

4.3.5 Several Deciduous and Coniferous Leaf Litters

Coniferous vs. Deciduous Genera, and Influence of Species

To expand this review of litter chemical composition from Scots pine and the genus *Pinus* to even the most common litter types in a given ecosystem is today not possible, due to a lack of basic information. We can, however, distinguish some of the main patterns that relate to tree genera or species, and their nutritional patterns. Litter chemical composition may be related to a few factors such as soil nutrient supply, climate (see Figs. 4.5 and 4.6), and species.

As regards organic-chemical components, one general difference between deciduous and coniferous trees involves the relative concentrations of hemicelluloses and cellulose (Table 4.1). Thus, as far as we know today, the ratio of hemicellulose to cellulose appears to be above 1.0 for deciduous, and below this value for coniferous trees.

As regards nutrients, Liu et al. (2006) showed on a large geographic scale, for more than 90 species and for N on a continental level, and using 204 litter samples from the Equator to north of the Arctic Circle, that foliar litters of broadleaf trees generally have higher N concentrations and a larger variation under given climatic conditions than was the case for coniferous trees. For instance, at an annual average temperature of 10 °C, the average N concentration was about 1.0% for broadleaf foliar litter and only about 0.5% for that of coniferous trees (Fig. 4.6, Table 4.5; Liu et al. 2006).

A set of data including average values for some principal northern European tree species will indicate clear patterns in nutrient richness among genera and species.

One general difference between deciduous and coniferous trees lies in nutrient richness encompassing more than only nitrogen (Table 4.7). There are also clear differences among species. The coniferous foliar litter overall appears less rich in nutrients such as N, P, Ca, and K (Table 4.7). The 13 coniferous litter species largely had N levels under 7 mg g^{-1}, whereas most of the deciduous species were above this value. Likewise, there were large differences in P levels, with deciduous litters averaging three times as much P as did coniferous litters. For Ca, the pines were generally low, with Aleppo pine being an exception. Norway spruce had a

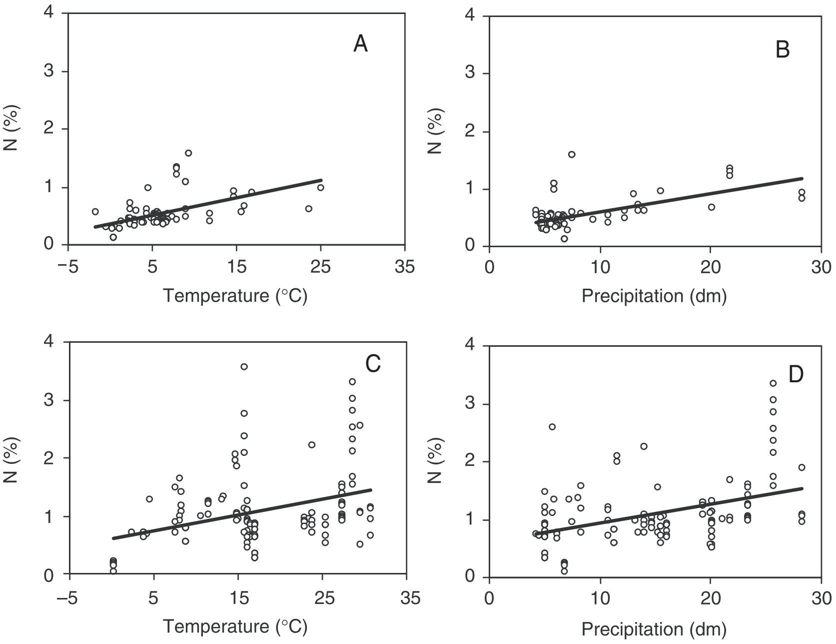

Fig. 4.6 Variation in litter N concentration along a climatic transect covering Europe and Asia. N concentration in newly shed litter is related to annual average temperature (°C) and annual precipitation (dm) for coniferous (**A**, **B**) and broadleaf trees (**C**, **D**). The linear relationships are all significant at $p < 0.001$ (from Liu et al. 2006)

Table 4.7 Major nutrients in some boreal and temperate litter species

	Concentration of nutrient (mg g^{-1})						
Litter	N	P	S	K	Ca	Mg	Mn
Coniferous needles							
Scots pine[a]	4.8	0.33	0.55	1.07	4.4	0.49	0.79
Lodgepole pine[b]	3.9	0.34	0.62	0.56	6.4	0.95	1.79
Maritime pine[c]	6.8	0.54	1.01	1.95	3.1	1.90	0.59
Red pine[c]	6.0	0.36	0.73	1.40	8.9	2.00	0.73
White pine[c]	5.9	0.21	0.68	0.70	7.2	1.10	0.80
Jack pine[c]	7.8	0.64	0.77	2.30	4.0	2.10	0.25
Limber pine[c]	4.3	0.43	0.52	1.10	5.3	1.10	0.21
Norway spruce[d]	4.9	0.45	0.73	0.72	17.9	0.65	-
Stone pine[e]	3.0	0.57	1.36	5.9	7.1	2.4	0.19
Corsican pine[f]	4.7	0.54	0.71	3.5	7.8	1.3	0.5
Monterey pine[f]	5.6	0.22	0.7	1.3	1.9	0.93	0.47
Aleppo pine[g]	4.3	0.38	1.3	1.73	25.2	2.33	0.03
Average	5.2	0.42	0.81	1.85	8.3	1.43	0.58
Deciduous leaves							
Grey alder[h]	30.7	1.37	6.12	15.6	12.3	2.32	0.10
Silver birch[h]	7.7	1.05	0.80	4.7	11.8	3.30	1.23
Ash[i]	8.6	1.96	-	15.3	33.2	2.28	0.03
Mountain ash[i]	7.1	0.31	-	10.8	12.4	2.86	0.30
Trembling aspen[i]	8.2	0.93	-	5.1	29.9	4.69	0.53
European maple[i]	5.1	3.15	-	13.1	20.4	1.46	0.12
European beech[d]	9.5	1.40	1.30	2.3	7.4	1.20	1.90
Common oak[f]	15.9	0.73	-	0.75	7.2	0.68	0.89
Average	10.9	1.45	2.74	9.6	18.2	2.59	0.60

[a] Johansson et al. (1995)
[b] Berg and Lundmark (1987)
[c] C. McClaugherty and B. Berg (unpubl. data)
[d] Berg et al. (2000)
[e] Berg et al. (2003)
[f] DELILA database (cf. Appendix IV)
[g] Faituri (2002)
[h] Berg and Ekbohm (1991)
[i] Bogatyrev et al. (1983)

higher value, and deciduous trees had Ca concentrations that were at least 2–10 times higher than those of coniferous litters, the average value being about 2.5 times higher. Mg and Mn were more similar among species, but there may be a tendency for concentrations of Mn to be lower in deciduous leaves.

To resolve differences among species, comparisons may be made between paired stands, thereby eliminating differences caused by climate and soil properties. For Scots pine vs. Norway spruce, there were significant differences between water solubles, lignin, N, Mg, and K (Table 4.8).

In another comparison between paired stands of Scots pine and lodgepole pine, the differences had a different pattern. Lodgepole pine had higher levels of P, Mg, Mn, and lignin, whereas Scots pine was richer in ethanol-soluble substances.

Table 4.8 Average values for some chemical components in Scots pine and Norway spruce needle litter collected in eight paired stands in boreal and temperate forests. Paired stands imply that mineral soil and climate were identical. Significant differences are indicated (Reurslag and Berg 1993)

	Components (mg g^{-1})								
	Wsol[a]	Esol	Lig.	N	P	Ca	Mg	K	Mn
Scots pine									
Avg.	132	97.4	261	4.1	0.25	6.0	0.53	0.81	1.20
SD	43	12.0	40	0.2	0.06	1.6	0.16	0.25	0.48
n	8	8	8	8	8	8	8	8	8
Norway spruce									
Avg.	153	48.9	305	5.2	0.75	15.2	1.06	1.90	2.45
SD	36	8.2	23	0.4	0.27	9.2	0.28	0.65	1.02
n	8	8	8	8	8	8	8	8	8
Sign. (p<)	0.001	n.s.	0.05	0.01	n.s.	n.s.	0.001	0.01	n.s.

[a] *Wsol* Water solubles, *Esol* ethanol solubles, *Lig.* lignin, *Avg.* average value, *SD* standard deviation, *Sign.* (*p*) significant differences tested by t-test, *n* number of samplings, *n.s.* not significant

Nitrogen, K, and Ca were not significantly different. Generally, the most nutrient-poor foliar litters are those of pines – for example, Scots pine, lodgepole pine, red pine, and white pine. This general picture applies to most nutrients.

A study on concentrations of K in needle litter (Laskowski et al. 1995) encompassed more than 25 boreal and temperate tree species. The full range for K concentrations in the whole dataset was 0.31–15.64 mg g^{-1}. Laskowski et al. (1995) found a large and statistically significant ($p < 0.0001$) difference in average initial K concentrations between coniferous and deciduous litters (1.03 vs. 4.52 mg g^{-1}, respectively). In terms of individual species, lodgepole pine needle litter had the lowest initial concentrations among the litter types studied, followed by Scots pine. Both these litter types had lower initial K concentrations than were found in the leaf litter of Norway spruce, mixed oak–hornbeam, and silver birch. The highest average K value was that for grey alder leaves (8.26 mg g^{-1}), followed by silver birch leaves (5.01 mg g^{-1}). In contrast, leaves of European beech, with 1.67 mg g^{-1}, were in the same range as the coniferous litter. Their investigation also covered temperate forests, and both the most common litter species found in forests of north-central Europe, as well as some major North American species.

Influence of Soils, Within Species

Soil chemical composition, including the availability of nutrients, has an influence on the chemical composition of the live leaves, and thus also on the chemical composition of foliar litter. The chemical composition of the soil, and the availability of the nutrients would be two main factors acting either directly or indirectly on the composition of foliar litter. That nutrient availability has an influence is evident from, for example, N fertilizer experiments (Sect. 4.5.1) in which different dosages of ammonium nitrate resulted in increased N concentration in the needle litter. Nitrogen availability in undisturbed or unmanaged forests may vary greatly among sites dominated by different species (Pastor et al. 1984). However, variations in N availability among natural, undisturbed sites dominated by the same species appear to be much smaller. For a given group of species, the variation in, for example, litter N concentration can be related to the concentration of N in the organic matter in the humus layers ($R^2 = 0.668$, $n = 61$; Berg et al. 1999b). Still, the reason for this good correlation may be that the humus is created from litter species with different N levels. In another study, Johansson et al. (1995) compared N levels of needle litter among three neighboring stands of Scots pine with the same climate, but with different soils: a dry sandy sediment soil, a richer till soil and a moist mull soil on clay. The N concentrations increased in the order 2.9, 3.0, and 3.2 mg g^{-1}, respectively, soil type evidently having only a minor effect on needle litter N content.

Although the levels of N available to plants in natural soils often are low enough not to influence the litter chemical composition, the levels of other nutrients in litter appear to be more directly dependent on their occurrence in soil. Thus, the concentrations of Ca and Mg in litter appear to increase as their availability in soil increases. These, and other nutrients such as Mn are dependent on pH for their mobility. At lower pH values, a better supply of mobile Mn will lead to higher levels in the leaves and needles.

The influence of soil pH is also well illustrated by a study on leaf litter of European beech in 24 stands in a climatically homogeneous area (Table 4.9). Compared with the plots with a mor soil, ten plots with mull soils had significantly higher average humus pH, and the litter had higher concentrations of Ca (12.0 vs. 8.5 mg g^{-1}, $p < 0.002$) and Mg (1.97 vs. 1.56 mg g^{-1}, $p < 0.0001$), whereas the concentrations of N, P, S, and K were not affected. In the same study on Ca in beech leaves, Staaf (1982) found a clear relationship between the humus (A_0) pH and Ca concentrations in the leaf litter (Fig. 4.7).

Table 4.9 Concentrations of nutrients in leaf litter of European beech on two different types of forest floor. The litters were sampled from stands within a region limited to about 100×100 km (Staaf 1982)[a]

	Concentration (mg g^{-1})						
	N	P	S	Ca	Mg	K	N:P:S
Mor humus n = 14							
Mean	9.06	0.66	1.18	8.54	1.50	2.59	1:0.07:0.13
SD	0.43	0.10	0.02	0.85	0.07	0.49	
Mull humus n = 10							
Mean	9.04	0.58	1.26	11.97	1.97	2.84	1:0.06:0.14
SD	0.33	0.04	0.05	6.3	0.04	0.31	
t-Test							
t-Value	0.07	0.50	−1.12	−4.73	−4.82	−0.93	
Significance (*p*)	n.s.	n.s	n.s.	<0.001	<0.0001	n.s.	

[a] *n* number of sites sampled, *n.s.* not significant

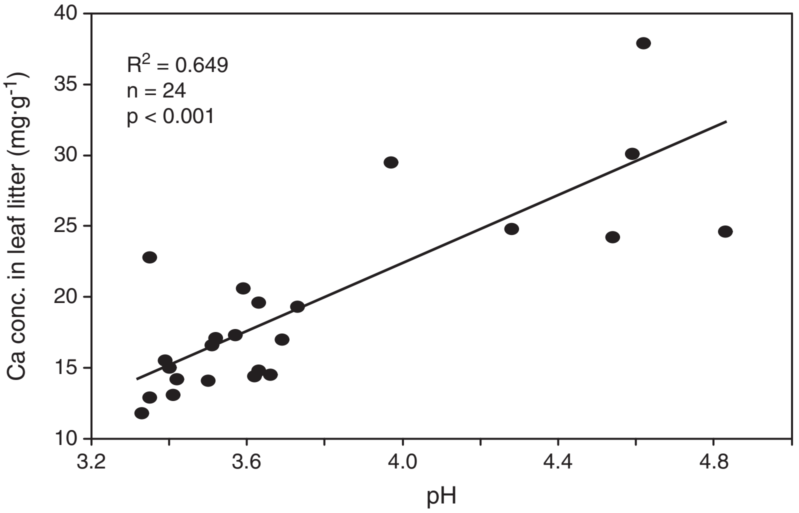

Fig. 4.7 Example of relationship between pH in the humus (A_0 to A_{01}–A_{02}) layers and Ca concentration in the shed leaf litter of European beech (from Staaf 1982)

Another group of nutrients has an indirect effect on the chemical composition of litter. For example, a lack of boron will not only be reflected in a lower B concentration in the litter, but will also have an indirect effect by influencing the litter lignin level. Boron has an important role for the formation of an enzyme transporting phenols out from the needles. A lack of B results in an accumulation of phenolics in the needles, which causes increased lignin synthesis (Lewis 1980; Dugger 1983; see also Chap. 12). Excessively high levels of available Cu have been suggested to have a similar effect.

Variation in Litter N Concentrations Along Climatic Transects on a Continental Scale

Litter from tree species other than Scots pine also appear to show variation in chemical composition with climate. Available data for various pine species follow the same pattern as for Scots pine. Different approaches have been taken to describe this relationship. Thus, Berg and Meentemeyer (2002) related available data for foliar litter N concentrations for Europe to AET. All available data for N concentration in foliar litter on a European basis have been related to AET, indicating a more general relationship. Considering this wider range of species, the relationships are weaker than with Scots pine alone, but the trends remain the same for both N and S. For Mn, there was a similar, general negative relationship to AET as that recorded for Scots pine, and no general relationship was found for other nutrients including P, Ca, Mg, and K.

In a large study covering Europe and Asia, Liu et al. (2006) distinguished between temperature and precipitation as influencing factors. Their study encompassed 204 datasets with ca. 92 species, and the transect ranged from an annual average temperature of −1.7 to 30 °C, an annual precipitation of 500 to 3,000 mm. Overall, the zone they used extended from north of the Arctic Circle to the Equator. The litter N concentrations ranged from ca. 0.1 to ca. 3.6% (in that comparison, N_2-fixing species were excluded). They related N concentrations to annual average temperature and annual precipitation, and obtained a highly significant relationship when all species were combined ($R^2_{adj}=0.522$, $n=204$, $p<0.001$; Table 4.5). For both coniferous and broadleaf trees investigated separately, the overall concentration of leaf litter N over Eurasia appeared to increase with temperature and precipitation (Table 4.5, Fig. 4.6). They investigated coniferous and broadleaf trees both separately and combined, and found clear relationships between leaf litter N concentration and annual average temperature, as well as between N concentration and annual precipitation (Table 4.5, Fig. 4.6).

Liu et al. (2006) evaluated the relative influences of temperature and precipitation on leaf litter N concentration, using "standardized" data after transformation by means of the program Standardize Transform (SPSS Inc., Chicago, IL, 1997). The standardized temperature (STemp) and precipitation (SPrecip) are dimensionless, with a mean of zero and a standard deviation of 1.0. Thus, in a multiple regression equation, the values of the intercept coefficients are forced to zero, and the slope coefficients for STemp and SPrecip indicate their relative contributions to variations in leaf litter N concentration. For a general relationship, they compared the two factors temperature and precipitation by using STemp and Sprecip, and found that for all data combined, temperature appeared to have a stronger effect than precipitation (cf. coefficient of 0.486 for the former, and 0.326 for the latter; Table 4.6).

For all three models tested, i.e., (1) broadleaf and coniferous litter combined, as well as (2) coniferous, and (3) broadleaf separately, coefficients for STemp (range 0.336 to 0.486) were larger (albeit not significantly) than those of standardized SPrecip (range 0.326 to 0.349). This suggests the possibility of a stronger effect of a change in temperature than of precipitation on leaf litter N, on a relative basis and within their present ranges (Table 4.6).

Along their transect, Liu et al. (2006) had enough pine data to allow an investigation of *Pinus* as a genus, and we may note that for pine spp. the coefficient for SPrecip was negative (Table 4.6, Sect. 4.3.4). Liu et al. (2006) also made a separate study of the genus *Quercus*, and could subdivide that into a deciduous group and an evergreen group. The deciduous group had a tendency of increasing leaf litter N with increasing temperature, the evergreen group did not indicate such a tendency with temperature, but the two groups had a similar pattern of leaf litter N along the precipitation gradient. We may note that compared to the larger groups comprising different species, the single genera that were investigated by Liu et al. (2006) behaved in different ways, and we cannot exclude that single species and genera with their defined ecological niches have different behavioral patterns, e.g., as regards response to temperature, in contrast to continuously changing species along a continental transect.

4.3.6 Variation in N and Lignin Concentrations

In a study on needle litters in three adjacent stands, Berg (2000b) found that when plotting N against lignin concentrations, the pairs clustered by species. Thus, Scots pine, lodgepole pine, and Norway spruce showed consistent patterns over a 4-year period. Extending the study, Berg (2000b) showed that these different litter types may be arranged into different, fingerprint-like groups even for a larger region (Fig. 4.8). Needle litter of Scots pine, lodgepole pine, Norway spruce, silver birch, and European beech were investigated. The litter and data on chemical analyses were collected for the region of Scandinavia, and for beech this was expanded to encompass Western Europe.

Scots pine needle litter formed a homogeneous group that did not overlap with the lodgepole pine or Norway spruce groups (Fig. 4.8). In this comparison, Scots pine needle litter was characterized as having simultaneously low concentrations of both N and lignin, whereas lodgepole pine litter formed another homogeneous group, with low N and high lignin concentrations. Norway spruce needles formed a group that had higher N concentrations than those of the two pine species, and lignin concentrations that were in between. The birch leaves had lignin concentrations similar to those of the spruce needles, and generally higher N concentrations. The leaves of European beech formed an extreme group with very high concentrations of both N and lignin.

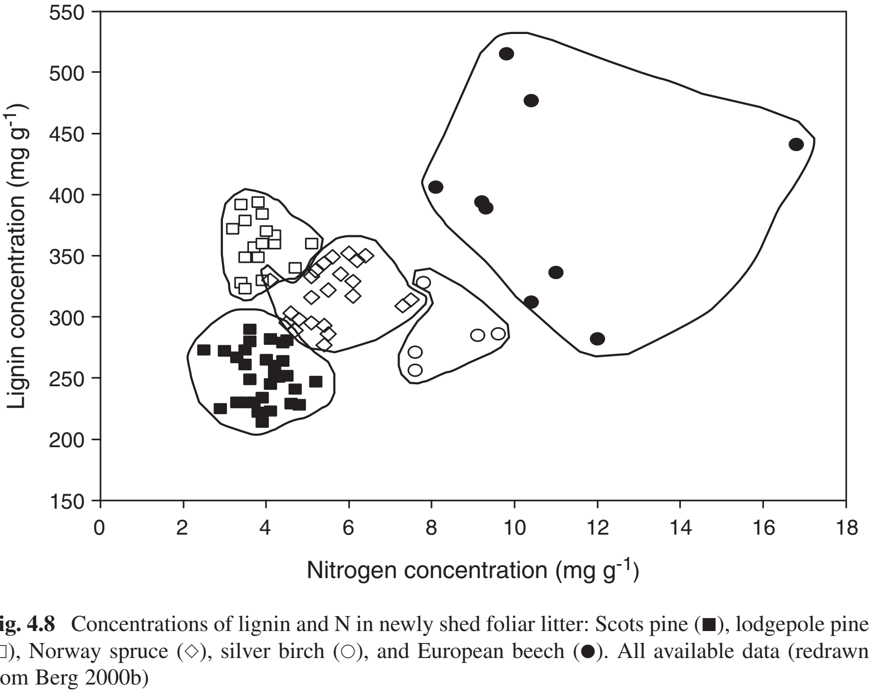

Fig. 4.8 Concentrations of lignin and N in newly shed foliar litter: Scots pine (■), lodgepole pine (□), Norway spruce (◇), silver birch (○), and European beech (●). All available data (redrawn from Berg 2000b)

4.4 Wood and Fine Root Litter

Nutrient concentrations in woody litter are dramatically different from those of foliage. Fine root litters, in contrast, are often rather similar to foliage in initial nutrient concentrations, but have different decay patterns. Because of the unique nature of wood and fine roots, discussion of their decay will be treated separately in Chapter 9. Here, we will briefly review the range of values observed for nutrient and organic-chemical composition of wood and fine roots (Tables 4.1 and 4.10).

Nutrient concentrations are much lower in wood than in foliage litter. We may see that, for example, N concentrations may be a factor of 10 lower for the species Norway spruce, trembling aspen, silver birch, and European beech (Tables 4.1 and 4.9). Wood is composed largely of cellulose, lignin, and hemicelluloses in different proportions. As a whole, the woody parts of the tree are poorer in nutrients than the photosynthesizing or actively growing parts. It also appears that the levels of water solubles are lower in wood than in the corresponding foliar litters (Tables 4.1 and 4.10).

4.5 Anthropogenic Influences on Initial Litter Composition

Human activities can dramatically influence the chemical composition of newly formed litter. These effects may be either direct or indirect. Clearly, fertilization with nutrients can have an effect on the nutrient composition of litter. This is true

Table 4.10 Concentrations of N, water-soluble compounds, and lignin in wood and fine roots from some boreal and temperate tree species (*n.d.* not determined)

Species	N (mg g^{-1})	Water-soluble	Lignin
Coniferous wood			
Norway spruce[a]	0.39	37	271
White pine[b]	0.40	15	221
Coniferous fine roots			
Norway spruce[c]	3.5	210	330
Scots pine[c]	2.5	134	273
White pine[b]	9.3	135	253
Deciduous wood			
European beech[a]	0.92	35	228
Red maple[b]	0.90	22	125
Trembling aspen[a]	0.55	39	197
Silver birch[a]	0.64	26	195
Deciduous fine roots			
Black alder[d]	12.8	n.d.	254
Hybrid poplar[d]	9.4	n.d.	262
Sugar maple[b]	16.7	196	338

[a] Staaf and Berg (1989)
[b] Aber et al. (1984)
[c] Berg et al. (1998)
[d] Camiré et al. (1991)

whether the nutrients (usually including some form of N) have been added as part of forest practice, or because of atmospheric N deposition. Here, we examine only the effects of selected human activities on initial litter composition, specifically the effects on litter chemical composition of artificial N enrichment and heavy metal deposition. The anthropogenic influences on decomposition will be discussed in Chapter 12 (see also Chap. 6).

4.5.1 N-fertilized Scots Pine and Norway Spruce Monocultures

Additions of N to soils have been performed to simulate N deposition. Such experiments may be done by small daily additions, but also by larger annual additions in direct experiments with N fertilization. The latter may be useful to interpret these effects, keeping in mind that such heavy additions should be interpreted with care. With experimental dosages as high as 100–500 kg N ha^{-1} year^{-1}, it appears that most of the supplied N exits the system relatively quickly, with only a low percentage (9–30%) being recovered from the topsoil (Miller 1979; Nömmik and Möller 1981; Tamm 1999). This strong outflow of N can be attributed in part to the fact that the fertilization technique added the full annual dosage of N fertilizer in a period of only hours. As discussed by Tamm (1999), the percentage of added N that is retained in soil depends on the magnitude of the dosage, the number of additions, and the level of saturation. Using the observations by Nömmik and Möller (1981), we can estimate that 12 to 20% may be recovered with additions in the range from 150 to 500 kg, implying that, say, 20 to 60 kg ha^{-1} would remain in the soil, which corresponds to annual N deposition amounts in some areas. Long-term fertilization experiments would thus be of a certain value in illustrating long-term deposition effects.

We have used data from N-fertilization studies by C.O. Tamm (Tamm 1991) who carried out extensive work on Scots pine and Norway spruce forests. For both species, there is a clear variation in chemical composition of needle litter between different fertilizer regimes (Table 4.11, Fig. 4.9). Tamm (1991) initially used annual doses of 50, 100, and 150 kg N ha^{-1}, later reduced to 40, 80, and 120 kg N ha^{-1}. Also with such dosages given once a year, heavy losses occurred, and the amounts retained were comparable to those of N deposition.

The addition of N, either as fertilizer or through N deposition, will result in increased uptake by the trees, and consequently in enhanced concentrations of N in the freshly formed litter. This has been observed by Miller and Miller (1976), and later by Berg and Staaf (1980a). The latter authors, using Scots pine needle litter from a fertilization experiment (Tamm et al. 1974; Tamm 1991), found that N additions at an annual dosage of 80 kg N ha^{-1} resulted in a statistically significant increase in litter N concentrations, whereas the dosage of 40 kg ha^{-1} year^{-1} did not have any significant effect (see Fig. 4.9, Table 4.11). A clear relationship was seen between N dosage and litter N concentration ($R = 0.949$, $p < 0.001$, $n = 8$). The range of N concentrations recorded over several years at one experimental site was about 3.6 and 8.5 mg N g^{-1} needle litter in control and high-dosage stands, respectively.

Table 4.11 Average concentrations of lignin and nutrients in Norway spruce and Scots pine needle litter collected at plots with three fertilization regimes, namely, control, 50, 100, and 150 kg N ha^{-1} year^{-1}. When large amounts of N are added in a single dose, as in this study, much is lost to leaching, volatilization or other mechanisms, but the additions did influence the initial lignin and nutrient concentrations of the needle litters (B. Berg, unpubl. data)

Year of sample	Lig.[a] (mg g^{-1})	N	P	S	K	Ca	Mg
Norway spruce							
Control	355	4.9	0.45	0.73	0.72	17.9	0.65
100 kg N dosage	388	15.3	0.54	0.93	1.04	10.0	0.74
150 kg N dosage	402	16.8	0.55	0.98	1.27	7.7	0.76
Scots pine							
Control	270	3.6	0.14	0.25	0.53	5.3	0.50
50 kg N dosage	260	4.3	0.20	0.33	0.52	5.1	0.55
100 kg N dosage	300	5.8	0.25	0.46	0.59	4.0	0.52
150 kg N dosage	380	8.5	0.30	0.49	0.85	2.9	0.38

[a] *Lig.* Lignin

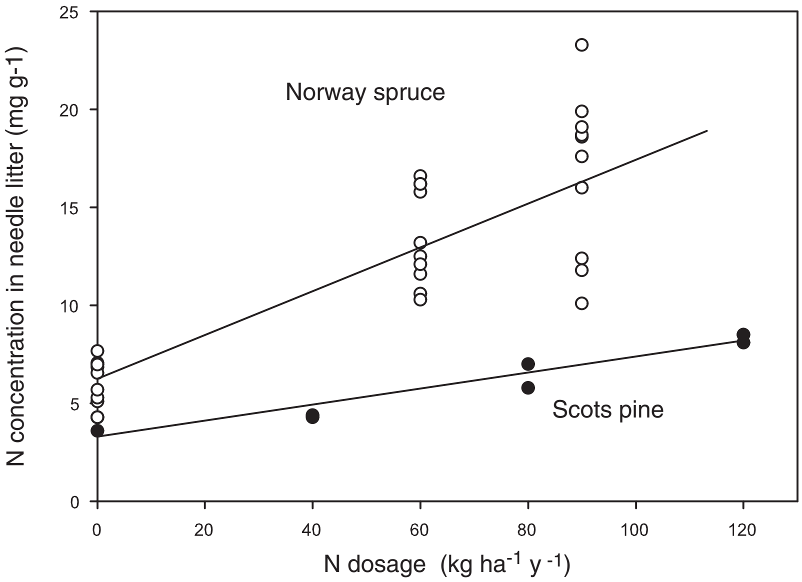

Fig. 4.9 Relationships between dosage of N fertilizer (ammonium nitrate) and concentrations of N in needle litter of Scots pine and Norway spruce. There is a clear difference in letter N concentration following fertilization (B. Berg, unpubl. data)

The variation in N concentration was accompanied by fluctuations in the concentrations of other nutrients as well, producing a relatively balanced nutrient composition (Fig. 4.10, Tables 4.11, 4.12). Thus, P, S, and K concentrations showed positive linear relationships to N concentration, whereas Ca showed a negative relationship, and there was no significant relationship for Mg.

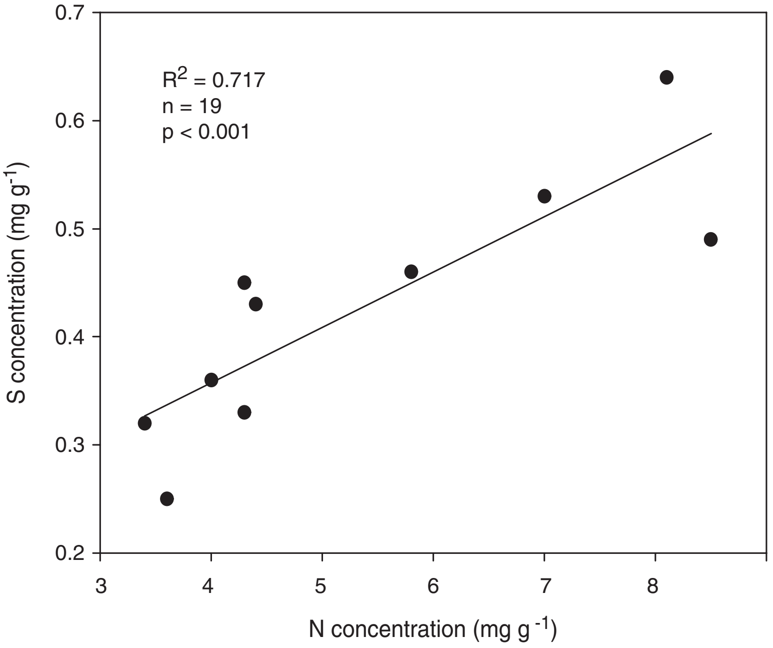

Fig. 4.10 Linear relationship between N and S concentrations in Scots pine needle litter from N-fertilized plots (Berg and Matzner 1997)

Table 4.12 Coefficients of determination (R^2) for linear relationships between concentrations of nutrients, water solubles, and lignin in needle litter of Scots pines subjected to different dosages of N fertilizer. A negative relationship is indicated by (–); $n = 19$ (Reurslag and Berg 1993)

	Component			
	N	P	S	Ca
P	0.550**	-	-	-
S	0.717**	0.932***	-	-
K	0.497**	0.901***	0.773***	-
Ca	(–)0.596***	-	-	-
Lig.[a]	0.517**	-	-	(–)0.728***
Wsol	0.453**	-	-	0.725***

[a] *Lig.* Lignin, *Wsol* water solubles; significance levels: **, $p<0.01$; ***, $p<0.001$

Norway spruce needle litter followed a similar pattern, although litter N had significantly higher concentrations in this case. In general, the concentrations of N, P, and S (Table 4.12, Fig. 4.10) increased with dosage of N fertilizer, although the effect on the concentration of N was most pronounced. The concentrations of N in the litter appeared to be largely in proportion to the dosage of fertilizer, the range being from 4.2 mg g^{-1} in control plots to 18.3 mg g^{-1} in a high-dosage plot (Fig. 4.9). In addition, the concentrations of K and Mg increased, whereas Ca concentrations decreased at higher N concentrations.

We may see (Fig. 4.9) that relative to the dosage used, the concentrations of N in Norway spruce needles increased about three times faster than for Scots pine, thus resulting in needle litter considerably richer in N.

It is noteworthy that concentrations of lignin also varied for both Scots pine and Norway spruce, increasing with dosage of N fertilizer. For Scots pine, the lignin concentrations increased with those of N from 270 to 380 mg g^{-1}. For Norway spruce, the increase was similar, with a range of 242 to 407 mg g^{-1} (cf. Table 4.9). This effect on lignin concentration seems to vary with the kind of system, and appears to be indirect.

The effect of fertilization on lignin concentration could be related to a lack of B in the soil (cf. Sect. 4.3.5). The high dosage of N fertilizer may have "forced" the trees to grow so quickly that the supply of some essential nutrients became inadequate, as the mobile pool in the soil was exhausted. Weathering apparently could not provide a sufficient supply, leading to a lack of this micronutrient in the plant.

4.5.2 Heavy Metal Pollution and Initial Litter Chemical Composition

Heavy metals can be taken up by plants through their roots, or accumulate on their leaf surfaces from atmospheric deposition. In sufficient concentrations, these metals can cause a slowing of decomposition, presumably due to toxicity toward the microbial community.

Berg et al. (1991b) studied this aspect by collecting fresh Scots pine needle litter along a transect of increasing distance from a smelter in northern Sweden. The chemical composition of needle litter collected at each site at abscission varied with distance from the smelter (Table 4.13). A significant positive relationship ($p < 0.05$) was found between the distances from the smelter and Mg concentrations in the

Table 4.13 Concentrations of plant nutrients and heavy metals in local fresh needle litter of Scots pine sampled at six study plots along a smelter pollution gradient in northern Sweden, and needle litter sampled at an unpolluted (control) site. Concentrations of Na, Al, B, Ni, Mo, Sr, and Cd did not vary along this transect (Berg et al. 1991b)

Dist.[a] (km)	Chemical component										
	(mg g^{-1})								(μg g^{-1})		
	N	P	S	K	Ca	Mg	Mn	Fe	Zn	Cu	Pb
2.5	3.78	0.26	0.99	1.43	5.23	0.47	0.79	0.38	0.25	0.100	311
3	3.73	0.24	0.73	1.01	5.70	0.53	0.83	0.36	0.19	0.068	191
7	3.25	0.19	0.49	0.70	6.11	0.46	1.26	0.14	0.11	0.019	44
9	3.71	0.26	0.50	1.08	4.65	0.56	1.10	0.27	0.11	0.012	34
13	3.66	0.25	0.53	1.23	5.65	0.66	1.43	0.12	0.08	0.009	22
30	4.40	0.22	0.51	0.98	5.70	0.67	1.21	0.11	0.07	0.006	12
Control	4.80	0.35	0.41	1.20	5.26	0.49	1.35	0.06	0.05	0.002	1

[a] *Dist.* Distance from smelter

fresh litter. The same tendency was also observed for Mn, meaning that these concentrations increase with distance from the smelter. Of the pollutants, Pb and Zn concentrations showed strong decreases with distance ($p < 0.01$). The same trend was noted for Fe and Cu ($p < 0.05$), and although less marked, for S and Cd ($p < 0.1$). The concentrations of organic compounds, on the other hand, seemed largely unaffected. The completely unpolluted litter had somewhat lower lignin, and higher N and P concentrations than the locally collected needles, as well as very low concentrations of heavy metals.

Chapter 5
Changes in Substrate Composition During Decomposition

5.1 Introductory Comments

There are two principal approaches to studies of the chemical changes in litter during decomposition, namely, to follow the changes in (1) organic chemical composition, and (2) inorganic nutrient composition. We will discuss both.

The decomposition of litter organic components by microbes is selective. Thus, there is a pattern in litter chemical changes over the course of decomposition. This common basic pattern may be modified as a result of the initial chemical composition of a given litter type. The pattern discussed here is based on boreal forest systems, but probably has a wider generality. For example, even in systems as different as a chaparral, decomposition follows a pattern similar to that in boreal forests (Schlesinger and Hasey 1981).

Studies of changes in the chemical components of decomposing litter have to date been unevenly focused, with lignin having received much of the attention. Still, for Scots pine needle litter, more detailed descriptions have been made, including hemicelluloses, cellulose, and different fractions of solubles (Berg et al. 1982a). There are also studies on Scots pine needle litter covering the decomposition process from litter fall to a close-to-humus stage. In this chapter, we describe detailed chemical changes for Scots pine as a case study. We also present data from other boreal species. For K, N, and lignin, specific syntheses have been published, and here these studies are reviewed.

The dynamics of nutrients in litter decomposition has been studied often due to its relationship to nutrient cycling in ecosystems (O'Neill et al. 1975; Anderson and Macfadyen 1976). Several such studies on nutrient dynamics also deal with chemical composition changes during decomposition (Dwyer and Merriam 1983; Dziadowiec 1987; Berg et al. 1987), and the dynamics of the major plant nutrients (Berg and Staaf 1980a, b, 1987; Blair 1988a, b; Rashid and Schaefer 1988). There are few studies, though, that describe nutrient dynamics covering the whole process from newly shed decomposing litter up to the humus stage.

The boundary between the concepts of "nutrients" and "heavy metals" is not clear in the literature. The general view is that nutrients are inorganic elements that are essential for life processes, whereas heavy metals are inorganic elements that,

B. Berg and C. McClaugherty, *Plant Litter*,

in sufficiently high concentrations, can be damaging to life processes. Although heavy metals can be anthropogenic pollutants, they also occur naturally. In this chapter, we treat heavy metals as nutrients in basically unpolluted systems, and discuss their dynamics in a fundamental, natural stage. The role of heavy metals as pollutants is addressed in Chapter 12.

5.2 Organic-Chemical Changes During Litter Decomposition

Litter decomposition is normally studied under different climatic conditions and in different ecosystems, with the result that even identical litter would have different decomposition rates, and thus different concentration changes for a given component. To overcome such problems at least in part, and to make various datasets more comparable in terms of chemical components, we assess litter chemical changes as a function of cumulative litter mass loss, rather than of time.

5.2.1 A Case Study on Scots Pine Needle Litter

Water-Soluble Fraction

The water-soluble fraction is chemically complex, resulting in a far from homogeneous substrate, and the microbial degradability of single components may vary greatly. Generally, for freshly formed foliar litter, this fraction contains high levels of simple sugars, lower fatty acids, and protein remains such as amino acids, and peptides. Most of these components can easily be taken up by microorganisms, and metabolized. As a result, the water-soluble fraction should decompose rather quickly, and its concentration should decrease with time (Fig. 5.1). For Scots pine needle litter in a boreal system, the concentration was found to decrease from ca. 92 to 57 mg g^{-1} in about 1 year, whereas for the sub-fraction of simple sugars and glycosides the corresponding values were 31 mg g^{-1} to undetectable amounts during the same period. Clearly, there are large differences among the rates of disappearance of compounds included in the water-soluble fraction. For some deciduous species investigated to date, the rate of decrease of water solubles may be even more dramatic (Table 5.1); for silver birch leaf litter, the decrease in 1 year was from 321 to 40 mg g^{-1}. For Norway spruce needles, considered to start decomposing when still attached to the tree, the decrease is of a magnitude similar to that of Scots pine and lodgepole pine (Table 5.1). Leaching may also play a role in the decrease in concentrations of water solubles.

Soluble substances are formed during the decomposition of polymer compounds such as holocellulose and lignin, and thus a low level of water solubles is found throughout the decomposition process. In fact, even a rapidly decomposed compound such as glucose has been found in concentrations of up to 1% in Scots pine needle litter that has been decomposing in the field for up to 5 years (Berg et al. 1982a).

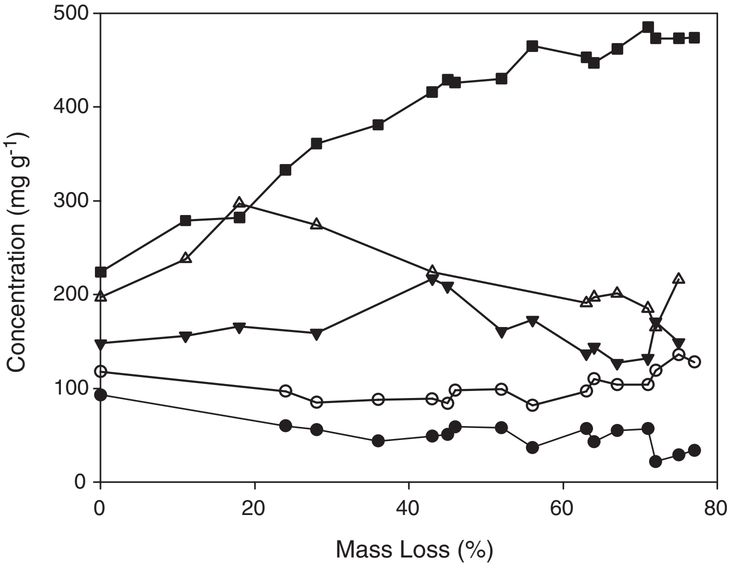

Fig. 5.1 Changes in concentrations of water solubles (●), ethanol solubles (○), cellulose (△), hemicelluloses (▼), and lignin (■) in decomposing Scots pine needle litter (B. Berg, unpubl. data)

Table 5.1 Long-term organic-chemical changes in some different decomposing litter types, expressed as initial concentrations, and as the concentrations when the given mass-loss level was reached[a]

	Wsol (mg g^{-1})		Esol (mg g^{-1})		Holocell. (mg g^{-1})		Lignin (mg g^{-1})		Final
Species	init.	fin.	init.	fin.	init.	fin.	init.	fin.	m.l. (%)
Needle litter									
Scots pine[b]	92	34	120	126	347	92	223	472	77.1
Lodgepole pine[c]	109	44	42	53			366	482	75.3
Norway spruce[d]	114	38	60	31			344	516	51.3
Can. hemlock[e]	181	53	177	36	396	234	206	226	45.1
White pine[e]	162	18	166	46	447	219	225	185	53.2
Leaf litter									
Silver birch[c]	321	40	57	43			263	506	65.4
Grey alder[c, d]	264	33	39	36			264	475	55.5
Red oak[e]	210	55	90	15	452	171	248	213	54.6
Sugar maple[e]	336	41	112	12	431	94	121	99	75.4

[a] *Wsol* Water solubles, *Esol* ethanol solubles, *Holocell.* holocellulose, *fin.* final, *init.* initial, *m.l.* mass loss

[b] Berg et al. (1982a)

[c] Berg and Ekbohm (1991)

[d] Berg et al. (1991a)

[e] Aber et al. (1984)

Ethanol-Soluble Fraction

This fraction includes rather small molecules that are not water-soluble. These are often found to be soluble in either ethanol or acetone, solvents that extract both lower phenolics and higher fatty acids. This fraction sometimes appears to contain compounds that suppress microbial growth (Berg et al. 1980), as seen for single fungal species. Furthermore, mixed microbial cultures have been found to degrade ethanol-soluble compounds more slowly than water solubles. At low pH, negatively charged stable compounds can be leached out of the litter, and the concentration of this fraction will thus decrease, although more slowly than that of water solubles. The individual components of this kind of fraction have as yet not been determined (Chap. 4), and their degradability is thus not known.

Although the concentration of this fraction decreases as litter decomposes, new compounds are added as degradation products from components such as lignin; these have limited solubility in water, and their concentrations often remain high even after some years of decomposition (Table 5.1). For Scots pine, the concentration of ethanol solubles after 3–5 years of decomposition could be of similar magnitude as in the initial litter. For example, in one study of Scots pine, the initial concentration of ethanol solubles was 120 mg g^{-1}. After 4 years of decomposition, the concentration was 126 mg g^{-1}. The same was seen for lodgepole pine, silver birch, and grey alder.

Cellulose

We showed (Chap. 2) that in the early stage of decomposition, the insoluble components cellulose, the hemicelluloses, and lignin were degraded at different rates. Somewhat later in the decay process, the degradation rates of these components were similar (cf. Figs. 2.3, 2.4). The initially different decay rates imply that the concentrations of these components also change at different rates. Thus, the concentration of cellulose decreases slowly (Fig. 5.1). In one case with Scots pine needles, the concentration decreased slowly until, at about 70% mass loss, it became similar to the initial value (Berg et al. 1982a).

In later stages of decay when lignin dominates the degradation process (cf. Fig. 2.2), the degradation rates of insoluble components decrease and maintain similarly low levels. Thus, during this late stage, the concentrations of cellulose remain rather constant (Fig. 5.1; see below).

Hemicelluloses

The most common hemicelluloses decompose in a similar fashion in litter. For the most part, they behave like cellulose, although they may have different positions in the decomposing fibers. This means that the concentrations of, for example, xylans, mannans, arabinans, and galactans decrease in the early stage. In the late, lignin-regulated stages of decomposition, the concentrations reach a similar, constant level. Considering the characteristic structure and complexity of the hemicelluloses, they can be regarded as a group. Using this approach, it was found that the ratio between hemicelluloses and cellulose became constant in the late stages of decomposition (Fig. 5.1).

Lignin

Lignin is not a very clear concept either in fresh or in decomposing litter. Lignin is often defined on the basis of proximate analytical methods, rather than purely chemical criteria. When applied to freshly fallen litter or non-decomposed plant materials, the proximate methods yield results close to what would be chemically defined as lignin. However, in decomposing plant litter, the lignin is modified by humification processes, including condensation reactions, and by partial degradation by microorganisms. This results in the formation of specific decay products that could be included in some common measurements of the lignin fraction, which may raise doubts about the extent to which "true" lignin is being measured in the decomposing litter. In addition, the lignin determined by gravimetric methods will contain, among other things, chitin from fungal mycelium, and an inorganic fraction (ash) that can be of considerable magnitude. Although this fraction for Scots pine lignin is about 1% of the total litter mass, it may amount to some percent in gravimetric lignin analysis. The ash content of newly shed deciduous litter can be much higher, exceeding 10% in some cases. Furthermore, ash concentrations may increase during decay. This ash fraction should be considered when reporting lignin contents of decomposing litter.

We contend that although what is being determined is not always true lignin, it is a chemical fraction with similarities to true lignin. It is important to note that even native (true) lignin is highly variable among species, and even within species. Thus, even native lignin cannot be described with the same chemical precision as is the case for cellulose, or many other plant polymers. Lignin is not a well-defined compound when it is produced, and it remains a poorly defined compound as it is decomposing. A meaningful nomenclature for lignin that has been modified during decomposition is still under debate. A term like "lignins" is sometimes used, and even the misleading term "acid-insoluble substance" is seen in the literature. A more recent suggestion is "non-hydrolyzed remains" (NHR; Faituri 2002). A term like "lignin in decomposing litter" (LDL) would not be correct either, but would at least indicate more clearly the nature of this complex analytical fraction. It should be pointed out that despite this problematical terminology, and although we need methods also to better identify native lignin, the gravimetric "lignin", or "LDL" fraction that contains recalcitrant, "non-hydrolysable remains" is today an important concept in litter decomposition studies. In the course of decomposition when the more easily degradable compounds are decomposed, lignin remains relatively intact for a long time. This means that the litter becomes enriched in lignin, or lignins or LDL (Fig. 5.1), of which the concentration increases. A number of studies have shown that these values may reach even above 50% (Table 5.1). At a certain stage when the open structures of the more degradable holocellulose are decomposed, the remaining fiber will have lignin and its modified products as a protective barrier, and when holocellulose and lignin are degraded at similar rates, the relative proportions of holocellulose and lignin remain nearly constant.

The Analytical Lignin Fraction

Lignin in decomposing litter is a complex concept. Several methods to determine lignin were originally intended for fresh wood (for the paper pulp industry; e.g., Klason or sulfuric-acid lignin). The applicability of such methods for other, more heterogeneous substrates such as foliar litter, both fresh and under decomposition, is not self-evident. Commonly used gravimetric determinations may include components other than lignin, such as ash (containing a.o. Ca, Mg, and silicates), and also recombination products derived from organic components. Still, gravimetric measurements are widely accepted, provided that they have been made correctly. However, unexpected effects have sometimes been observed during decomposition, and even net increases in the lignin fraction have been reported (Berg and McClaugherty 1989). If, for example, humic acids are synthesized and recorded as Klason lignin, then the measured process of lignin mass loss should be regarded as a net process. Norden and Berg (1990) did not find any new peaks in the aromatic resonance region when applying high-resolution ^{13}C NMR to needle litter samples in decomposition stages from 0 to 70% accumulated mass loss. Thus, within a certain range of litter mass loss, there does not appear to be any extensive synthesis of entirely new products. In addition, there was a clearly significant linear relationship between the lignin concentrations estimated using ^{13}C NMR and the level of sulfuric-acid lignin.

The authors compared the lignin analysis method based on Effland (1977) with that of Bethge et al. (1971) (Klason lignin) for fresh and decomposing litter, and found no difference in concentrations (unpubl. data). Data on lignin concentrations from various studies that have used these methods may thus be meaningfully compared, at least from a quantitative point of view. A forage analysis protocol introduced by Van Soest (1963) has also been widely used for lignin analyses. A study by Ryan et al. (1990) compared the Van Soest with the Klason technique as applied to deciduous litters. They found that the two approaches gave somewhat different results, but that these could be interconverted (e.g., Aber et al. 1990). It is important to note that the terminology associated with the definition of “lignin” fractions and their contents is sometimes ambiguous (see Glossary), and that measurements of the lignin fraction using different methods may not give results that are directly comparable.

5.2.2 Other Species

Changes in chemical composition during decay have been studied in several species other than Scots pine, including Norway spruce, lodgepole pine, silver birch, European beech, sugar maple, white pine, Canadian hemlock, red oak, white oak, and bigtooth aspen. The basic patterns as regards water solubles, holocellulose, and lignin are similar. There are initially large decreases in the concentration of water solubles, followed by a decrease in holocellulose concentration and an increase in that of lignin. In the cases investigated to date, the lignin fraction approaches a maximum of 45–55% (Fig. 5.2). One exception to the generally increasing lignin concentrations was found for leaf litter of European beech (Rutigliano et al. 1996), for which there was a distinct decrease in concentration. This litter was rich in lignin and N, and was incubated on an N-rich humus layer (cf. Chaps. 2, 3, 6).

5.2.3 Relationships Between Holocellulose and Lignin

Attempts have been made to describe how the concentrations of cellulose and hemicellulose change during decomposition, compared to that of lignin (cf. Chap. 2). The concentration of holocellulose decreases, and that of lignin increases until a level is reached at which the proportions remain constant. Two such quotients are:

HLQ = holocellulose/(lignin + holocellulose) Berg et al. (1984b)
and
LCI = lignin/(lignin + holocellulose) Melillo et al. (1989)

The former quotient asymptotically approaches a minimum value, which may be different for different litter types (Fig. 5.3). For example, Berg et al. (1984b) found a clear difference between the HLQ values for Scots pine and silver birch.

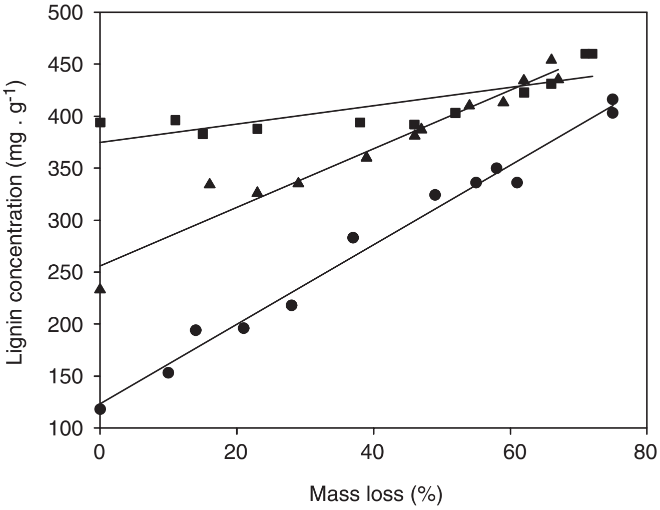

Fig. 5.2 Changes in lignin concentrations during the decomposition of needle litter of Scots pine (▲), lodgepole pine (■), and sugar maple (●) with different initial lignin concentrations. Lignin concentration is plotted vs. litter mass loss (Berg et al. 1997)

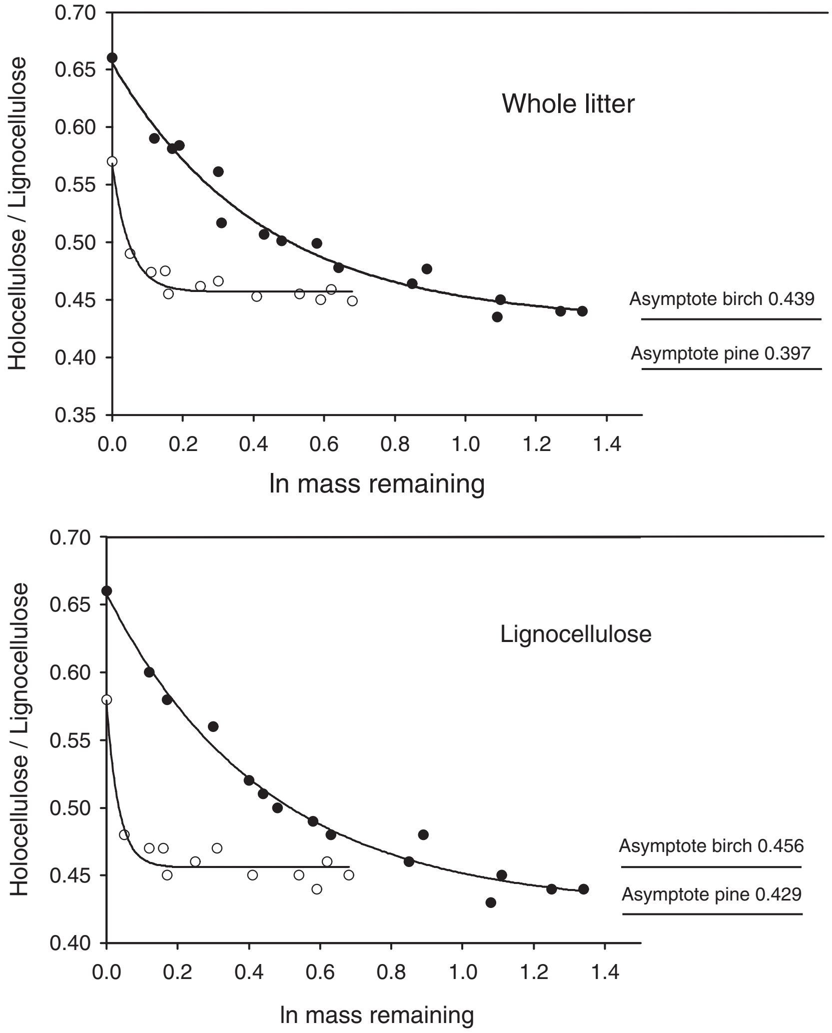

Fig. 5.3 A fitted nonlinear model gives the decrease in the quotient holocellulose/(lignin+holocellulose), HLQ, as a function of the natural log of whole litter mass (*top*), and mass of lignin plus holocellulose (*bottom*) remaining from Scots pine needle litter (●), and leaves of silver birch (○). Also given are the asymptotic values that these approach. The litter was incubated in a nutrient-poor Scots pine forest in central Sweden (redrawn from Berg et al. 1984b)

In an attempt to give a more general view on the concept of LCI, Melillo et al. (1989) introduced the concept "biological filter", and compared the development of the LCI quotient during decomposition, to the quotients found in different humus types (Table 5.2). In their study, the quotients for decomposing red pine needle litter reached 0.67, and the values for the corresponding humus were 0.72 in the forest floor and 0.73 in the mineral soil.

Table 5.2 Lignocellulose index (*LCI*) values from forest soils in the northeastern USA (modified from Melillo et al. 1989)

Species/location	Horizon	LCI
White pine stand/New Hampshire (USA)[a]	Oi	0.50
	Oe	0.66
	Oa	0.73
	A	0.78
	B	0.76
Spruce/Maine (USA)[a]	Oi	0.52
	Oe	0.73
Hardwood–spruce mix/Maine (USA)[b]	Oi	0.45
	Oe	0.63
	Oa	0.78

[a] Waksman et al. (1928)
[b] Waksman and Reuszer (1932)

5.3 Nutrient and Heavy Metal Concentrations During Decay

5.3.1 Changes in Concentrations of Elements in Decomposing Litter

Three principal patterns of nutrient concentrations have been observed in litter during decay, based on the release and accumulation of nutrients. Some nutrients are released from the litter at a rate that is low and proportional to overall mass loss, resulting in a linear concentration increase with cumulative mass loss. Other nutrients may be readily leached from the litter, and disappear faster than the litter mass as a whole, resulting in linear, or curved, negative relationships to mass loss. Finally, some nutrients are strongly retained within, or even imported into the litter–microbe complex, resulting in an exponential increase in concentration vs. litter mass loss. These latter nutrients can increase in both (relative) concentration and absolute amount during decay.

Scots Pine

The leaching of most nutrients from Scots pine litter is generally low, which means that their loss from the litter is more closely related to microbial decomposition processes than to initial leaching. The relationships presented here are considered to be representative for pine litter in a common boreal forest type. To obtain a standard for comparing nutrient dynamics among litter types independently of decay rates, we have plotted nutrient concentrations relative to cumulative litter mass loss, rather than relative to time.

Nitrogen. The concentration of N in litter increases during decomposition. This increase may be described versus time since incubation, or as a function of litter mass loss, in which case we regard the decomposition process of litter as a driving force for the change in N concentration. In this latter case, a positive linear relationship results (Fig. 5.4), allowing comparisons between studies, sites, and experimental treatments. This kind of linear relationship is empirical and has to date not been explained, although it normally has R^2 values well above 0.9.

For boreal Scots pine litter, the N concentration may increase about threefold during decomposition, starting with ca. 4 mg g^{-1} and increasing up to ca. 12 mg g^{-1} (see the special study below).

Phosphorus. The concentration of P in litter increases during decomposition, in a manner very similar to that of N. As is the case for N, this relationship can be described as a positive linear function of litter mass loss (Fig. 5.4). In addition, for P, the linear relationship is empirical. For Scots pine, a fourfold increase from ca. 0.2 to 0.8 mg g^{-1} has been recorded (Staaf and Berg 1982).

Sulfur. As was the case for N and P, the concentration of S in litter increases linearly during decomposition with respect to accumulated litter mass loss. Also in this case, the positive linear relationship is empirical (Fig. 5.4), and for Scots pine an increase from 0.4 to 1.0 mg g^{-1} has been recorded (Staaf and Berg 1982).

Potassium. As K is highly soluble, a proportion of the total is leached very soon after the litter has fallen. Normally by the first sampling in decomposition studies, a large reduction in concentration to a minimum is seen, after which the concentration starts to increase again. Due to the high mobility, rather rapid and large changes in

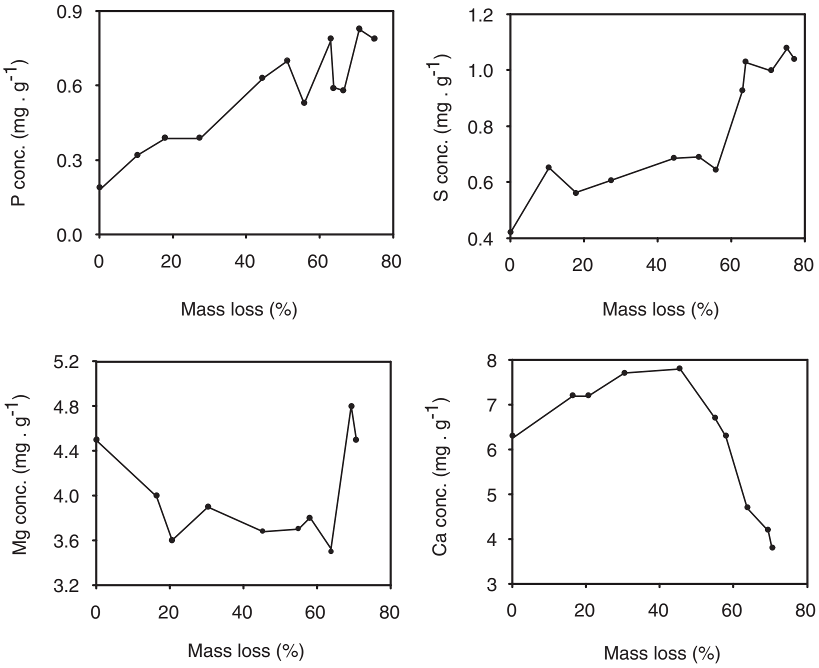

Fig. 5.4 Changes in concentration of phosphorus, sulfur, calcium, and magnesium in decomposing Scots pine needle litter (B. Berg, unpubl. data)

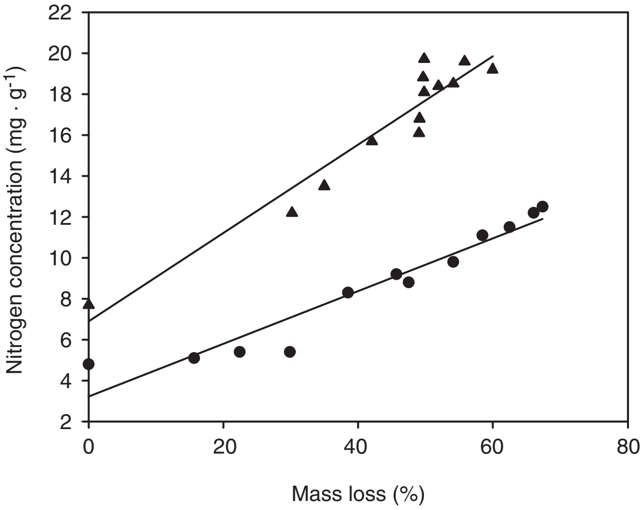

Fig. 5.5 Increase in N concentration of decomposing litter, campared to litter mass loss. The linear relationship, which is empirical, appears to be a good general trend. Still, this is dependent on sampling intensity. Scots pine needle litter (●), having an initially slower decomposition than does silver birch leaf litter (▲), shows a clearer linear relationship. Note the large mass loss for birch litter in the first sampling, indicating heavy leaching (B. Berg, unpubl. data). Changes in concentration of phosphorus, sulfur, calcium, and magnesium in decomposing Scots pine needle litter (B. Berg, unpubl. data)

K concentration may take place, thereby often creating "noisy" concentration graphs that may differ considerably among studies (see also the special study below).

Calcium. A characteristic of the Ca concentration dynamics during decomposition is a peak in concentration followed by a decrease. The turning point corresponds closely to the point in decay at which net lignin degradation begins (B. Berg and C. McClaugherty, unpubl. data; Fig. 5.4).

Magnesium. The concentration of Mg decreases slowly without the fast leaching that was seen for K. However, as for K, the decrease is interrupted, and an increase is observed. As a simplification, the graph may be described as a positive X^2 graph (Fig. 5.4).

Other Nutrients/Heavy Metals. There appear to be too few studies on other metals/elements to allow us to suggest that the graphs presented below are generally applicable. Still, a group of these have similar patterns with clear trends. Studies indicate that the concentrations of most heavy metals increase as the litter decomposes, even up to around 80% mass loss. The nutrients/heavy metals Cu, Pb, Fe, Zn, (Fig. 5.6) as well as Ba, Sr, and Al all have a pattern of increasing concentrations during litter decomposition, essentially following an exponential trend. In all cases, their concentrations increase faster than simply a conservation of the existing amount would suggest. Thus, it is likely that an import takes place. Iron and Pb are known to be relatively immobile over a wide range of soil acidity (Bergkvist 1986), and are characterized by high, exponential concentration increases. In a case study

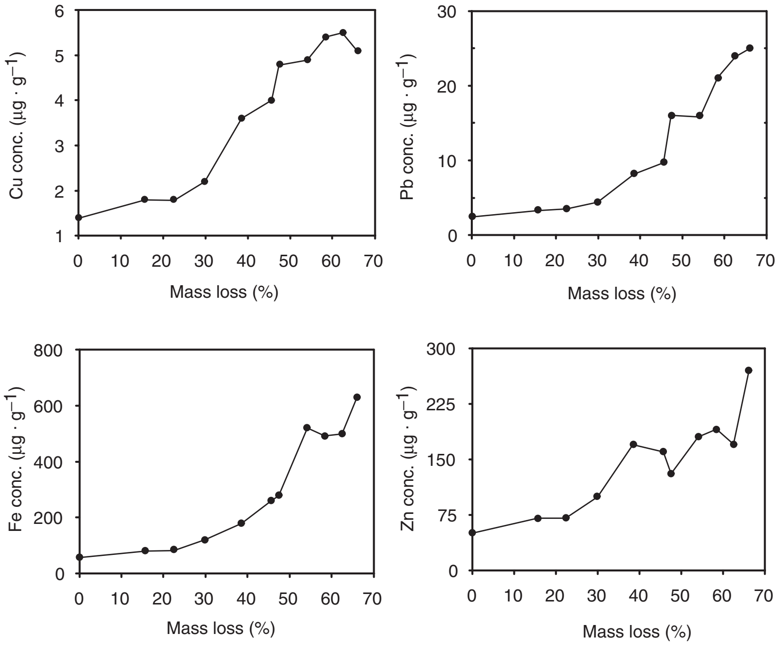

Fig. 5.6 Changes in concentrations of the heavy metals copper, lead, iron, and zinc with mass loss in decomposing Scots pine needle litter (B. Berg, unpubl. data)

for Al, the increase was from initially 280 to ca. 900 $\mu g\ g^{-1}$ at approximately 65% mass loss. For Pb, the corresponding values were 2.5 and 25, for Cu 1.4 and 5, for Fe 55 and 600, for Ba 4 and 28, and for Sr ca. 5 and ca. 10 $\mu g\ g^{-1}$. The concentration of Cd increased from ca. 0.1 to ca. 0.4 $\mu g\ g^{-1}$ at 65% mass loss.

At least two of the nutrients/heavy metals, Mn and Cd, show an increasing solubility and mobility with decreasing pH. They are thus often leached from litter. However, such a property is not independent of the microbial population, and at low concentrations when the metals are not in excess, a low pH does not necessarily mean a high net mobility. The microbial population could retain, or import nutrients in the decomposing litter–microbe complex. Nevertheless, for Scots pine, the typical pattern for Mn was a concentration decrease, at a rate that was proportional to litter mass loss. For other species such as silver birch, the patterns of heavy metal dynamics were similar to those for Scots pine (B. Berg, unpubl. data).

5.3.2 Ash Dynamics

The ash content of litter can vary between litter types and over time. Ash content in, e.g., Scots pine needle litter is initially low, often around 1%, and in the course of decomposition it may increase to 2%. In a study of sugar maple leaf litter, ash contents were initially 11.3% of dry matter, increasing to 19.5% after 1 year of decay, and 26.6% after 10 years of decay (C. McClaugherty, unpubl. data). Ash is normally defined as the fraction of matter that remains after heating a sample to, e.g., 400 °C for 2–3 h, whereby all organic matter (e.g., organic C and N) is volatilized. The concept "ash" is complex, and ash may include, for example, silicates and nutrients such as Ca, Mg, K, and P. It may also include particles such as clay that has entered the litter during incubation. If not considered, high ash contents could seriously affect calculations of percentage mass loss, and of concentrations of N and other substances relative to those of less ash-rich litter types. Litter N contents should thus be consistently related to litter organic matter, rather than to the whole litter, an aspect that is often overlooked or ignored.

5.4 Special Studies on K, N, Mn, and Lignin Dynamics

5.4.1 K Concentration Dynamics

Potassium is an essential plant nutrient, and one of the principal nutrients, along with N and P, that are routinely included in fertilizers. Potassium is one of the most mobile elements in ecosystems, and its presence in dead plant tissues is highly variable. By using available data for foliar litter, Laskowski et al. (1995) found a range of 0.31–15.64 mg g^{-1} in initial concentrations in newly shed litter, corresponding to a range factor of about 50. In their inventory of 139 sets of data for decomposing litter in field studies, they could systemize the dynamics of K concentration changes with decomposition, using data from boreal and temperate forest systems from mainly northern Europe and North America. The litter types investigated (mainly Scots pine, lodgepole pine, Norway spruce, silver birch, sugar maple, and white pine) covered the most common litter types found in forests of northern Europe, and represented some major North American species.

In an analysis using 90 sets of data, Laskowski et al. (1995) found that each set could be subdivided into two phases in terms of K dynamics during decomposition (Fig. 5.7). They distinguished (1) an initial phase with a fast change in concentration, and (2) a later phase with either a slow increase or stabilization in concentration. Usually, the concentration reached its lowest level (C_{min}) on the first sampling occasion, after a few months' incubation in the field. Depending on the litter type and length of incubation, the accumulated litter mass loss at the first sampling varied within a range from 2.5% up to about 40%.

These two phases were not observed for litter types with extreme K concentrations. Thus, for litters with exceptionally low initial K levels (about 0.3 mg g^{-1}), such as Norway spruce needles, an increase in concentration was observed from the very start of the incubation. On the other hand, as discussed in Chapter 6, the Norway spruce litter may already be in a late stage of decomposition at litter fall. For a few litter types with very high initial values, a continuous decrease in concentration

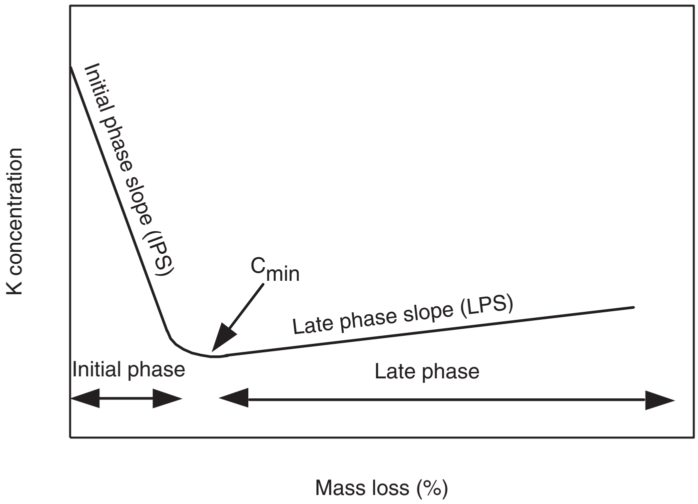

Fig. 5.7 Overview graph for changes in K concentration with accumulated mass loss. Two phases in K concentration changes are identified. The *initial phase* has a rapid release of K. The *late phase* is the consecutive, equally clearly distinguished phase with much slower concentration changes. In the main text, the initial concentration of K is denoted as C_0; the minimum concentration for K reached during its release is denoted as C_{min} (Laskowski et al. 1995)

was observed throughout the whole decomposition period (e.g., for some oak and birch leaf litter).

Initial phase. For the initial phase, Laskowski et al. (1995) obtained a highly significant ($p < 0.0001$) relationship between the initial K concentration and the slope for K release, indicating that the steepness of the slope was highly dependent on the initial K concentration (Fig. 5.7), namely, the higher the initial concentration (C_0), the steeper the slope, suggesting that this could be a general model for changes in K concentrations. The negative relationship had an R^2 value of 0.449 ($n = 90$), indicating that it may explain about 45% of the variability in concentration changes across species and systems.

Coniferous litter as a separate group gave a highly significant, negative relationship with an R^2_{adj} value of 0.557 ($n = 80$), thus improving the relationship in spite of a narrower span of initial K concentrations. Scots pine needle litter revealed a highly significant relationship only between the initial rate and the initial K concentration, C_0 ($R^2_{adj} = 0.427$, $n = 63$, $p < 0.0001$). The studies on Scots pine needles referred to decomposition in Scots pine forests, and the relationship they obtained explained as much as 43% of the change in concentration, the fact that only a very narrow range of initial concentrations was used. In addition, for lodgepole pine needle litter they found a highly significant relationship with $R^2_{adj} = 0.952$ ($n = 7$, $p < 0.0001$). For deciduous litters, they obtained a relatively high R^2 value of 0.58

($n = 10$, $p < 0.02$), especially taking into account that only ten samples were analyzed. For Norway spruce litter, no significant relationship was found.

For deciduous leaves as a group, the relationship between initial K concentration and slope of concentration decrease vs. time in the initial phase was more shallow than that for the coniferous litters, with slopes of −7.89 and −12.73, respectively. In a comparison of the relationships for coniferous and deciduous litters, the linear relationships differed significantly between these, both in the intercept ($p < 0.05$) and in slope ($p < 0.0001$). As the average initial concentration of K was lower for the coniferous than for the deciduous litters, this may be misleading, and at first glance suggests that concentrations of K in the needles drop more quickly than those in the leaves. However, in the very early stage, the deciduous leaves lost mass faster than did the coniferous litter (Berg and Ekbohm 1991), and therefore such a conclusion simply cannot be drawn due to a lack of resolution. In comparison, a laboratory study suggested fast leaching of K from deciduous litter, in combination with a quick leaching of total soluble material (Bogatyrev et al. 1983). From that study, it appears that in most cases a fast decrease in concentration has been observed, and it thus seems reasonable to conclude that mobile K was leached. This agrees with the observations of Bockheim and Leide (1986), Dziadowiec (1987), and Rapp and Leonardi (1988).

For some litter types with exceptionally low initial K concentrations (e.g., Norway spruce litter), they found an increase in concentration from the very start of the incubations, which may mean that leaching was either very low or close to zero. Laskowski et al. (1995) suggest that in these cases the biological retention (buildup of K in microbial biomass) overbalanced any leaching process.

Minimum concentrations. There were significant between-species differences for minimum concentrations (C_{min}) of K in decomposing litter ($p < 0.0001$; Table 5.3). The lowest level was observed for Scots pine needle litter, with an average of 0.48 mg g^{-1}, and significantly higher values were found for the litter of Norway spruce (0.68 mg g^{-1}), silver birch (0.94 mg g^{-1}), oak (0.99 mg g^{-1}), and mixed pine–beech leaf litter (1.52 mg g^{-1}). The latter value was the highest average C_{min} recorded, and differed significantly from that of lodgepole pine litter (0.56 mg g^{-1}; Table 5.3).

Late phase. At the later stages of decomposition, the concentrations of K approached a final level that appeared to be similar for the different litter types, irrespective of litter species, and more similar than the initial concentrations. While the range of initial K concentrations (C_0 values) for the whole dataset was as large as 0.31 to 15.64 mg g^{-1}, with a range factor of ca. 50, the final range was only 0.37 to 1.78 mg g^{-1}, with a range factor of ca. 5. These final values were dependent on the accumulated mass loss at the last sampling occasion for each set, and in order to obtain more comparable values, Laskowski et al. (1995) introduced a value for the concentration of K at 60% mass loss (C_{60}), which was used as a standardized value for comparisons. At 60% mass loss, they considered the litter to be in a humus-near stage.

The standardized C_{60} value gave an even narrower range in late-phase concentrations, with 0.78 and 1.43 mg g^{-1} as extreme C_{60} values, and thus a range factor of ca. 2

Table 5.3 Potassium concentrations in decomposing litters, including both green and brown litter (Laskowski et al. 1995; C_0 is initial concentration, C_{min} minimum concentration, C_{60} the concentration at 60% mass loss, and *n* the number of incubations; standard errors in parentheses)

Litter type	C_0	C_{min}	C_{60}	*n*
All litters	1.48 (0.15)	0.57 (0.02)	1.08 (0.03)	139
Coniferous litters	1.03 (0.06)	0.51 (0.02)	1.06 (0.02)	121
Scots pine needles	0.88 (0.05)	0.48 (0.02)	1.06 (0.03)	97
Lodgepole pine needles	1.03 (0.47)	0.56 (0.06)	1.17 (0.19)	7
Norway spruce needles	1.90 (0.20)	0.68 (0.04)	0.99 (0.04)	17
Mixed pine–beech litter	4.10 (0.54)	1.52 (0.15)	1.18 (0.46)	2
Deciduous leaves	4.54 (0.87)	0.90 (0.08)	1.19 (0.12)	16
Silver birch leaves	5.01 (0.49)	0.94 (0.11)	1.29 (0.23)	8
Grey alder leaves	8.26 (7.39)	0.69 (0.18)	0.97 (0.32)	2
Common oak leaves	2.13 (0.69)	0.99 (0.17)	1.14 (0.09)	3
European maple leaves	4.19	1.34	1.43	1
European beech leaves	1.67	0.69	1.16	1
Mixed oak–hornbeam leaves	3.72	0.52	0.78	1

(Table 5.3). In contrast to the initial concentrations (C_0) and the C_{min} values, there were no significant differences in K concentrations at C_{60} between litter types.

In summary, the initial concentrations were highly significantly different among the litter types. After some decomposition, the differences were smaller, but still significant, and finally at C_{60} no difference was detected. Thus, the initially large and statistically significant differences in average initial K concentrations between coniferous and deciduous litters (average value 1.03 vs. 4.54 mg g^{-1}, respectively) decreased in the late phase, and at C_{60} they had practically disappeared (1.06 vs. 1.19 mg g^{-1}, respectively; Table 5.3).

5.4.2 *Mn Concentration Dynamics*

Manganese is a highly mobile nutrient in acid soils, and that is thus often leached from acidic litter. However, such a property is not independent of the microbial population, and at low concentrations when metals are not in excess, a low pH does not necessarily mean a high net mobility, and the microbial population could retain, or import nutrients in the decomposing litter–microbe complex. For Scots pine litter, the typical pattern for Mn was a concentration decrease, at a rate that was proportional to litter mass loss. The dynamics of Mn in decomposing litter is so far little studied, and we have not been able to make an appropriate synthesis. A comparison of Mn in litter species of different initial Mn concentrations is seen in Fig. 5.8. We may conclude that its concentration may change in a very irregular way, in contrast to, e.g., N.

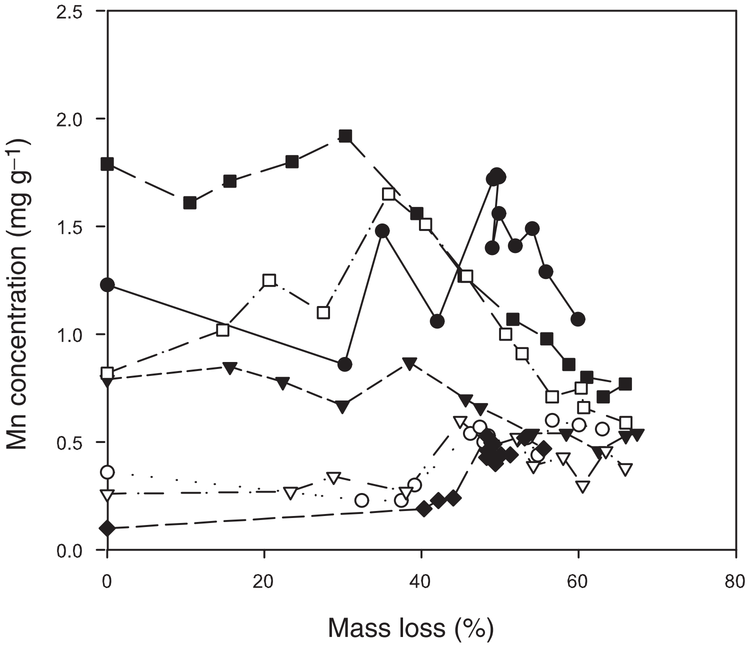

Fig. 5.8 Changes in Mn concentration in relation to accumulated litter mass loss for some deciduous and coniferous foliar litter species (from Berg and Cortina 1995). All samples were incubated in a 130-year-old Scots pine forest: brown Scots pine needles (▼), green Scots pine needles (▽), brown lodgepole pine needles (■), green lodgepole pine needles (□), brown leaves of silver birch (●), green leaves of silver birch (○), leaves of grey alder (◆)

5.4.3 N Concentration Dynamics Along a Climatic Transect

Nitrogen Concentration Increase. That N concentrations increase in decomposing litter is widely known. When the increase in N concentration is related to time since incubation, the result is a curve with an asymptotic appearance. We have related the increasing N concentrations to litter mass loss (cf. above) for several litter types, resulting in a linear increase, possibly until the limit value for decomposition is reached (Aber and Melillo 1982; Berg et al. 1997; Fig. 5.5). Such a linear increase has been found for many species, including foliar litter of Scots pine and Norway spruce. Deciduous litter species, such as silver birch, also give linear relationships, but much mass is lost initially, resulting in a fast increase in N in proportion to mass loss (Fig. 5.5). For Scots pine, the increase in concentration is linear from an initial value of 4 up to 12–13 mg g^{-1} N at about 75% mass loss (Fig. 5.9). Still, the reasons for the straight-line relationships are far from clear, given the simultaneous in- and outflows of N during the decomposition process (Berg 1988).

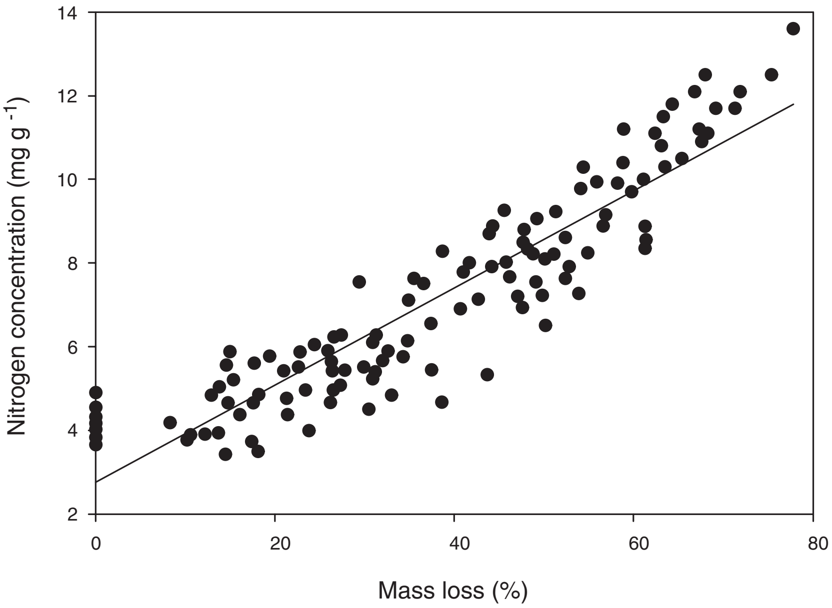

Fig. 5.9 Overall relationship between increasing concentrations of N and accumulated mass loss for decomposing Scots pine needle litter. Incubations were made at one site, a nutrient-poor Scots pine forest. Data are pooled from 14 sets, each representing an incubation of local litter from a different year (Berg et al. 1997)

This linear relationship is an empirical finding, and for systems such as coniferous foliar litter, the relationship appears to be highly significant (Fig. 5.10).

Berg et al. (1997) compared the linear relationship for accumulated mass loss vs. N concentrations among several sets of decomposing Scots pine needle litter in one system (Fig. 5.9). They called the slope of the relationship *the nitrogen concentration increase rate* (NCIR). The litter was naturally produced from the Scots pine monocultural system, and the variation in initial N concentration was the observed annual variation. For one site, the relative increase rates in N concentration showed significant linear relationships to litter mass loss for individual sets of litter, as well as for the average combined from all 14 sets of litter (Table 5.4). The NCIR values in this comparison had an average of 0.1109, and the slopes ranged between 0.055 and 0.129 (SE = 0.0047), indicating that for a given litter type and system the variation in NCIR was somewhat limited.

In a comparison of NCIR values for lodgepole pine needle litter, the slopes of five lodgepole pine datasets gave similar results, with an average slope of 0.1151 and a standard error of 0.0060 (Table 5.4). For needle litter of Norway spruce, the average slope was similar to that of the pine litters, and reasonably consistent among four sets of litter (Table 5.4). The conclusion may be that although the

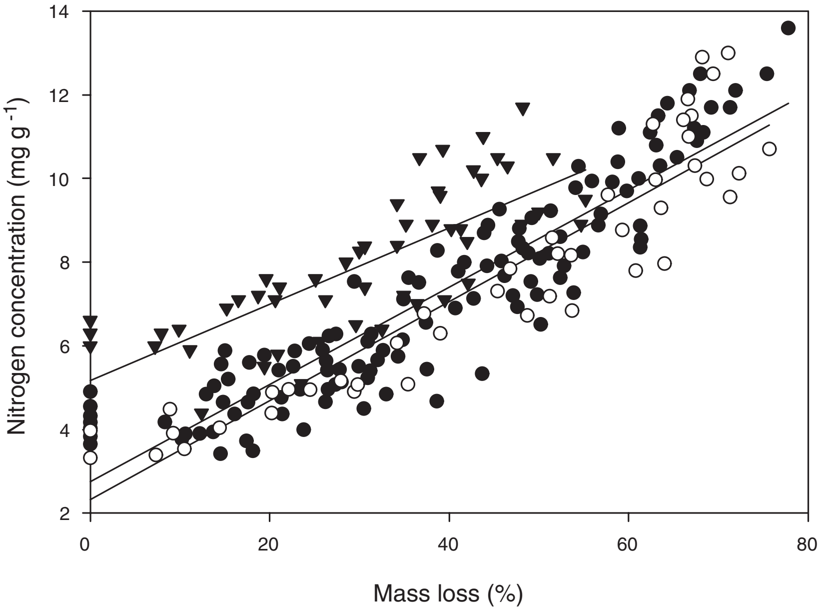

Fig. 5.10 Litter N concentration as a function of accumulated mass loss for decaying coniferous litters: ● Scots pine – 14 sets, ○ lodgepole pine – five sets, ▼ Norway spruce – four sets. Coefficients of determination (R^2) are 0.845 (*n*=131), 0.851 (*n*=54), and 0.638 (*n*=56), respectively (Berg et al. 1997)

increase in N concentration during decomposition is empirical, it is consistently observed. When the three different studies are compared, we see that the two pine species, having similar N levels, increase in parallel (Table 5.4), whereas the Norway spruce litters, as a result of initially higher N concentrations, form a group above the pine litter, while having similar slopes (Fig. 5.10).

The Influence of Litter N Concentrations. Scots pine green needles with a higher initial N concentration had a much larger NCIR than did brown needles, meaning that the increase rate was larger. A similar trend was observed for decomposing Norway spruce needles. Both green needles and N-enriched needles, collected from N-fertilized plots, had higher NCIR values than was the case for the more N-poor regular brown needles. However, the difference between natural and fertilized needles was not significant (Berg et al. 1997). This property of NCIR, to increase with increasing initial N concentration, appeared to be common for different species. Thus, natural needle litter of lodgepole pine and Scots pine had similar initial N concentrations, and the two species also had similar average NCIR values.

Significant relationships between initial litter N concentrations and NCIR values were found within the Scots pine species (Fig. 5.11, Table 5.5), whereas for Norway

Table 5.4 Overall nitrogen concentration increase rates (*NCIR*) for local needle litter of three coniferous tree species incubated at three sites. Comparisons are made both by calculating regressions over the combined dataset, and by taking the average slopes of individual datasets. Nitrogen concentrations were regressed versus litter mass loss (Berg et al. 1997)[a]

Site – species	Intercept (SE)	Slope (NCIR) (SE)	R^2_{adj}	R	*n*	*p*
Scots pine – Jädraås						
All values combined	2.941 (0.985)	0.1107 (0.0042)	0.843	0.919	131	<0.001
Average of 14 slopes		0.1109 (0.0047)			14	
Lodgepole pine – single site						
All values combined	2.762 (1.128)	0.1171 (0.0065)	0.862	0.928	54	<0.001
Average of slopes		0.1151 (0.0060)			5	
Norway spruce – Stråsan						
All values combined	4.769 (1.124)	0.1019 (0.0105)	0.638	0.799	56	<0.001
Average of four slopes		0.1151 (0.0031)			4	

[a] *SE* standard error, *n* number of datasets

Table 5.5 Linear relationships describing the variation in nitrogen concentration increase rates (*NCIR*), compared to the litters' initial concentration of N. The stands are natural systems. The litter species as well as their chemical composition vary between comparisons. Scots pine litter included local, fertilized, and green litters. (Berg et al. 1997)

Combination	Intercept (SE)	NCIR (SE)[a]	R^2_{adj}	R	*n*	*p*<
Scots pine	0.0693 (0.0221)	0.0123 (0.0012)	0.542	0.740	84	0.001
Deciduous – all available	0.1538 (0.0309)	0.0094 (0.0014)	0.860	0.938	8	0.001
Deciduous – no alder	0.0970 (0.0204)	0.0158 (0.0024)	0.880	0.949	7	0.01
All data	0.0767 (0.0367)	0.0105 (0.0009)	0.530	0.724	116	0.001

[a] *SE* Standard error, *n* number of datasets

spruce needles alone, Berg et al. (1997) found no relationship. In an attempt to find a global relationship, they considered all available data both from coniferous and deciduous litters, and indeed found a significant relationship, which seems to hinge on the relatively few extreme points corresponding to green and deciduous litters (Fig. 5.11). Thus, on that scale, NCIR is only weakly influenced by initial N concentrations, except when considering extreme cases. However, to the extent that a

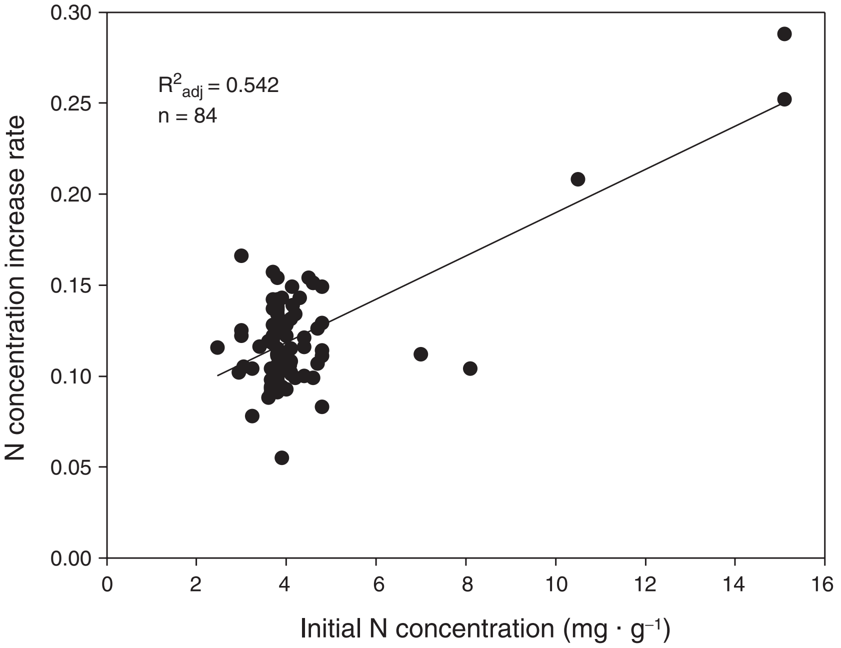

Fig. 5.11 Linear relationship between initial concentration of N in decomposing Scots pine needle litter, and the slope of N concentration vs. accumulated mass loss (nitrogen concentration increase rate, or NCIR). Many individual points are obscured due to overlap (Berg et al. 1997)

relationship does occur, it is a positive one. This means that N concentrations increase to a somewhat greater extent with accumulated mass loss when initial N concentration is higher. Berg and Cortina (1995) also recorded this when comparing NCIR for seven very different litter types incubated in one system (Fig. 5.12).

One mechanism for conserving N in decomposing litter could be via covalent bonding to macromolecules during the humification process. An example of this is the ammonium fixation described by Nömmik and Vahtras (1982). Thus, if the initial amount of N in the litter were higher, then there would be more N available for fixation, giving a higher NCIR. Such a conclusion is reasonable, since Axelsson and Berg (1988) found that N availability limits the rate of the process.

A transect of Scots pine systems. For local natural Scots pine needle litter, and a unified Scots pine needle litter preparation, the relationship between NCIR and AET was investigated across a climatic transect in Sweden, with AET ranging from 380 to 520 mm. There was a highly significant relationship for Scots pine ($R^2_{adj}=0.640$, $n=31$, $p<0.001$), indicating that the N concentration will increase faster (relative to mass loss) under a warmer and wetter climate. This correlation was significant when both local and unified needle litter was used, and also when using only local needle litter ($R^2_{adj}=0.517$, $n=18$, $p<0.001$).

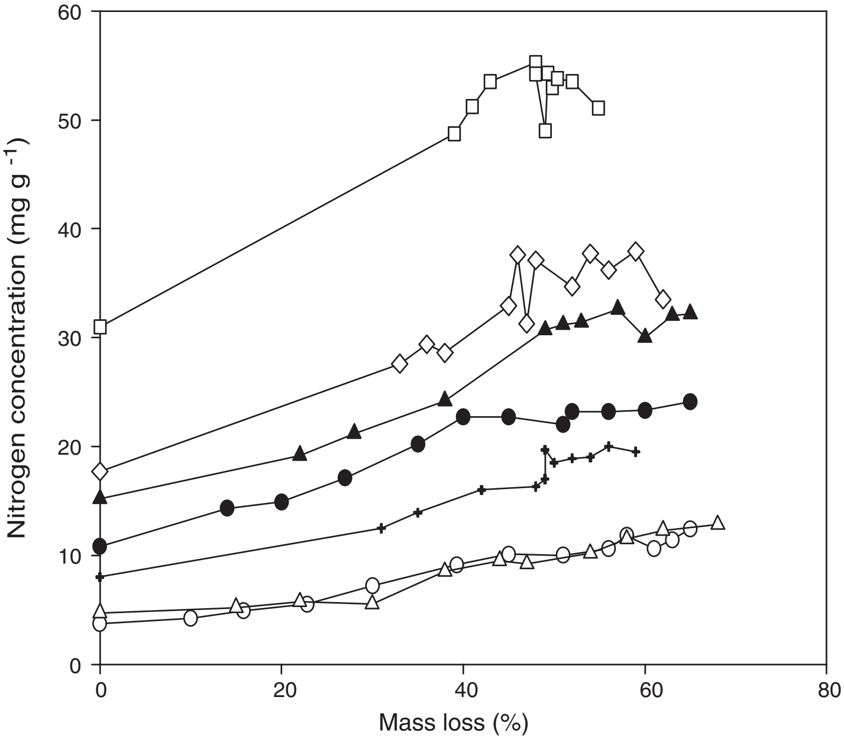

Fig. 5.12 Changes in N concentration as related to accumulated litter mass loss for seven litter types incubated in a 130-year-old Scots pine forest (Berg and Cortina 1995): brown Scots pine needle litter (△), green Scots pine needles (▲), brown needles of lodgepole pine (○), green needles of lodgepole pine (●), brown leaf litter of silver birch (+), green leaves of silver birch (◇), and green leaves of grey alder (□)

Over a large group of litter species, and for litter collected over a broad region, the initial N concentration had minor influence as a regulating factor on NCIR. It was found (Berg et al. 1995a) that initial N concentrations in Scots pine needle litter varied over a large region, and could be related to the climatic index AET. In the above analysis comparing NCIR to initial N levels, the pines formed a cluster (Fig. 5.11) with relatively low initial N concentrations, and low NCIR values.

A transect of Norway Spruce Systems. Norway spruce litter was investigated separately (Berg et al. 1997). Along a climatic transect in Sweden, the NCIR values increased with increasing AET values, and the relationship was highly significant ($R^2_{adj}=0.534$, $n=14$, $p<0.01$).

A General Relationship Among Species. Berg et al. (1997) found that for Norway spruce, NCIR increases slightly more with increasing AET than for Scots pine litter (slopes of 0.00055 and 0.00038, respectively; Fig. 5.13), but the difference was not significant. In the comparison between NCIR and initial N concentration, there were differences between the Norway spruce litter and that of pine. They

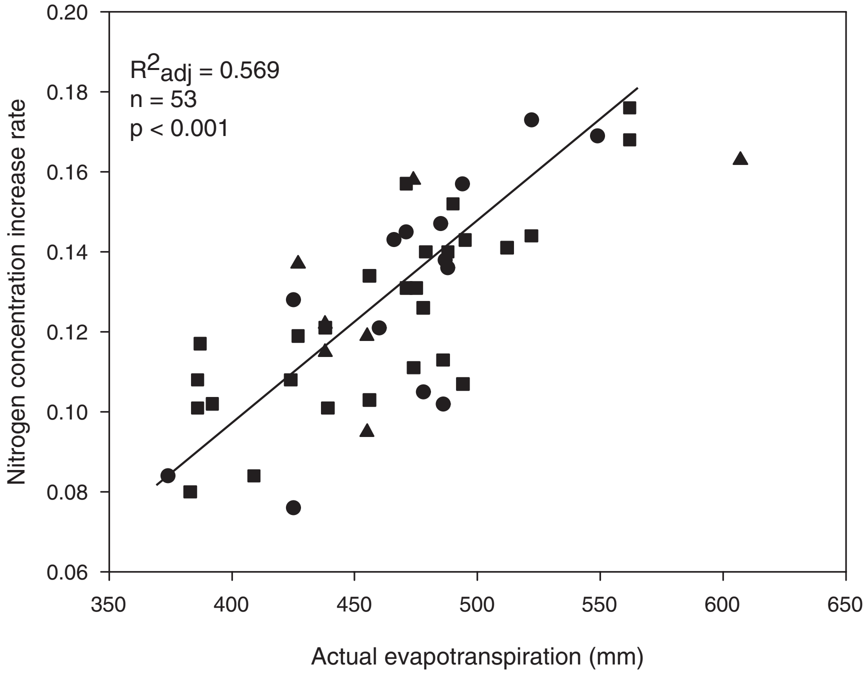

Fig. 5.13 Linear relationship between the climatic index *actual evapotranspiration* (AET) and the nitrogen concentration increase rate (NCIR) in decomposing needle litter of ● Scots pine, ■ Norway spruce, and ▲ other pines (lodgepole pine and white pine; Berg et al. 1997)

concluded that in the analysis vs. climate, the relationships for Norway spruce and Scots pine were sufficiently similar to allow a stepwise combination of data. In a first step, the values for Scots pine and Norway spruce were combined, resulting in a highly significant relationship with a low standard error ($R^2_{adj}=0.604$, $n=45$, $p<0.001$). This means that for both Scots pine and Norway spruce, the climatic factor was more important in explaining the increasing concentration of N in litter than were the species or the initial N concentration.

In a second step, they combined all brown coniferous litter, and obtained a highly significant linear relationship with $R^2_{adj}=0.569$ ($n=53$, $p<0.001$; Fig. 5.13). It may be worth pointing out that the white pine needle litter data came from a more southern site with a relatively high AET, but nevertheless did not deviate from the general relationship.

Finally, in an analysis combining coniferous and deciduous litters, the relationship was still highly significant ($R^2_{adj}=0.628$, $n=59$, $p<0.001$). Deciduous litters departed from the pattern exhibited by coniferous litters, but the overall relationship remained significant. Thus, climate, as indexed by AET, is a significant factor in controlling the rate of N concentration increase in decomposing leaf litter. As these increases were calculated on the basis of accumulated mass loss, rather than time, the results imply that, after a certain mass loss, a particular litter decaying in an area with higher AET will contain more N than does the same litter decaying in an area with lower AET.

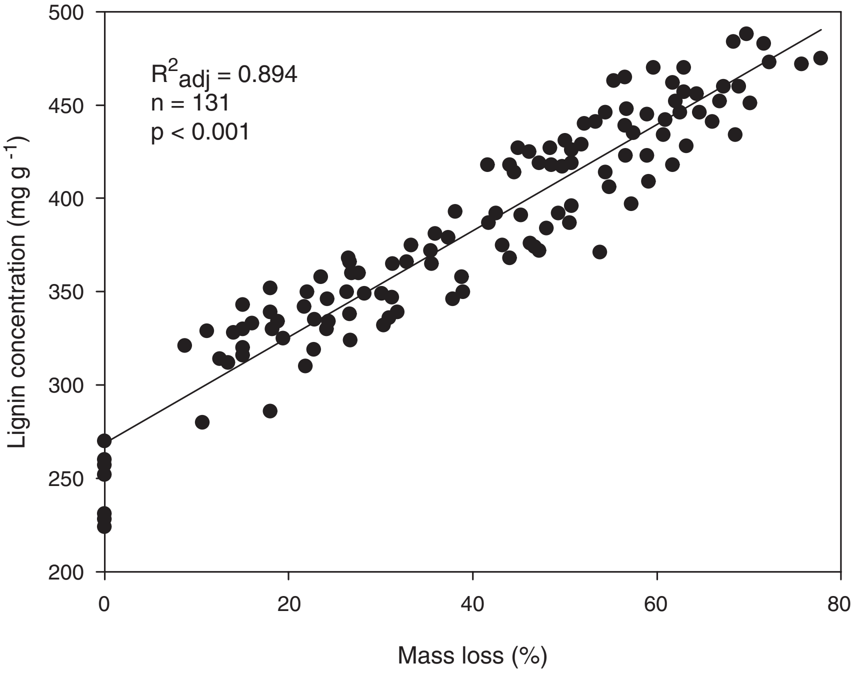

Fig. 5.14 Relationship between the increase in lignin concentration and accumulated mass loss (lignin concentration increase rate, or LCIR) for 14 different incubations of local Scots pine needle litter at a site with Scots pine forest on nutrient-poor soil (SWECON site Jädraås). All measurement points are shown together with the common linear regression line (Berg et al. 1997)

5.4.4 Lignin Dynamics Along a Climatic Transect

Repeatability of Lignin Concentration Changes. Lignin concentration changes may be related to duration of decay, which often can be described by an asymptotic curve. The lignin concentration may, on the other hand, be related to accumulated litter mass loss, resulting in a linear increase (Fig. 5.2). Such a linear increase in lignin concentration has been found for Scots pine, lodgepole pine, and Norway spruce. Deciduous litters such as birch leaves give linear relationships, too, but much mass is lost initially, resulting in a quick increase followed by more constant values (Berg et al. 1984a). For Scots pine, the lignin concentration increases up to ca. 50% and above (Fig. 5.2) for reasons discussed earlier (cf. Chap. 2), and in this interval, the linear relationship is highly significant (Fig. 5.14).

Berg et al. (1997) called this linear increase LCIR (lignin concentration increase rate). The LCIR during decomposition appears to be repeatable within a given stand. Native Scots pine needle litter was incubated annually for 14 consecutive years, and LCIR values for the 14 sets of decomposing needle litter were compared (Table 5.6). The difference between years was the between-year variation in initial chemical composition (Berg et al. 1993e; Johansson et al. 1995; cf. Table 4.4), and the annual variation in climate. Comparing the linear equations for lignin concentration increase among the 14 sets, the differences were found in the intercepts, rather than in the slopes, the intercepts reflecting the initial lignin concentration. The average slope was 3.08 for $n = 14$ (Table 5.7). The slope when using all measurement points in one linear regression was 2.92 with an R^2_{adj} of 0.894 (Fig. 5.14, Table 5.7).

Two other boreal coniferous species were investigated (Berg et al. 1997), namely, lodgepole pine and Norway spruce. These also showed repeatable increases

Table 5.6 Linear relationships between the lignin concentration increase rate (*LCIR*) and litter mass loss for Scots pine needle litter incubated in its own stand (SWECON site at Jädraås). Lignin analysis was made on all samples during decomposition (Berg et al. 1997)

Init. lignin conc. (mg g^{-1})	Intercept	SE	Slope (LCIR)	SE[a]	R^2	*n*
223	249.2	22.9	3.255	0.025	0.932	14
267	251.1	12.8	3.364	0.214	0.972	9
231.4	253.4	13.9	2.783	0.195	0.953	12
270	287.7	16.5	2.298	0.364	0.889	7
227.3	272.8	28.2	2.747	0.765	0.720	7
257	269.8	19.0	2.979	0.373	0.970	4
224	256.2	29.1	2.784	0.550	0.865	6
228.6	248.7	15.3	2.850	0.255	0.947	9
227.3	272.8	28.2	2.747	0.765	0.720	7
257	269.8	19.0	2.979	0.373	0.970	4
224	256.2	29.1	2.784	0.550	0.865	6
228.6	248.5	15.3	2.850	0.255	0.947	9
228.6	250.0	16.3	3.450	0.274	0.952	10
228.6	229.5	9.7	3.123	0.138	0.983	10

[a] *SE* Standard error, *n* number of data points

Table 5.7 Linear regressions of lignin concentration in decomposing litter vs. mass loss for needle litter of three species incubated at their own stands. The slope of the linear relationship corresponds to the lignin concentration increase rate (*LCIR*). Comparisons of LCIR are made both by combining all values from different litter incubations into a single regression, and by taking the average slopes for individual studies (Berg et al. 1997)

Species	Intercept (SE)[a]	LCIR (SE)	R^2_{adj}	*n*	*p*<
Scots pine					
All values	262.0 (20.8)	2.924 (0.089)	0.894	131	0.001
Avg. of 14 slopes		3.08 (0.091)		14	
Lodgepole pine					
All values	370.6 (25.6)	1.24 (0.134)	0.610	55	0.001
Avg. of five slopes		1.21 (0.118)		5	
Norway spruce					
All values	362.7 (18.7)	2.95 (0.174)	0.839	56	0.001
Avg. of four slopes		2.92		4	

[a] *SE* Standard error, *n* number of data points, *Avg.* average

in lignin concentration (LCIR). Thus, for lodgepole pine, five individual incubations at the same main site showed a low variation among slopes (average value of 1.21, $n=5$), while the slope for all five datasets combined became 1.24 ($R^2_{adj}=0.610$, $n=55$; Table 5.7). A similar comparison for native Norway spruce litter, using data for incubated litter at one site, gave straight lines for four combined datasets of decomposing native Norway spruce needle litter, with a slope of 2.95 ($R^2_{adj}=0.841$, $n=56$). When investigating the difference in slope between the five individual incubations, the average slope was found to be 2.92 (Table 5.7).

The Influence of Initial Lignin Concentration. Different litter types have different behaviors with respect to lignin disappearance. For litters rich in lignin – for example, lodgepole pine and Norway spruce needle litter – lignin disappearance begins at, or soon after litter decomposition has started (Berg and Lundmark 1987; Berg and Tamm 1991). Even in these cases, the concentrations of lignin increase as decomposition proceeds. There is, however, variation between LCIR values for different litter species collected at, and incubated in their own ecosystems. At a site with monocultures of lodgepole pine and Scots pine, the litter of lodgepole pine had a lignin concentration of about 350 mg g^{-1}, and that of Scots pine about 290 mg g^{-1}. Both litter types had significant linear relationships between accumulated mass loss and the increase in lignin concentration, the slopes (LCIR) being 1.24 and 2.55, respectively. The litter with initially higher lignin concentrations (lodgepole pine) had significantly lower slopes (see also Table 5.7).

In a comparison of five different datasets each for lodgepole pine and Scots pine, Berg et al. (1997) found a highly significant negative relationship between LCIR and initial lignin concentrations, with an R^2_{adj} value of 0.938, indicating that the higher the initial lignin concentration, the lower the rate of increase. This is probably due to an apparent upper limit for lignin concentration of about 50% (Fig. 5.2). It appears that there is also a more general relationship between initial lignin concentration and LCIR. Over the three pine species, Scots pine, lodgepole pine, and white pine, this resulted in a highly significant negative relationship with $p<0.001$ ($R^2_{adj}=0.471$, $n=69$). Berg et al. (1997) also investigated a larger dataset, and examined the influence of both climate and initial lignin on the LCIR (cf. below).

For Norway spruce, they investigated the relationship between initial lignin concentration and LCIR using data from an intensively studied site (Berg and Tamm 1991). The negative relationship obtained between initial lignin concentrations and LCIR was again significant. The relationship between a higher initial lignin concentration and a lower LCIR slope thus also holds for spruce. The relationship between LCIR and initial lignin concentration still held when they combined all data from coniferous litters ($p<0.001$), associated with an R^2_{adj} value of 0.313 for $n=94$.

Variation in LCIR with Climate. For Scots pine, clear differences have been found in the magnitude of the LCIR between northern and southern sites in Scandinavia. In their studies, Berg et al. (1997) used a unified litter preparation along a transect ranging over most of Sweden and into northern Germany. The

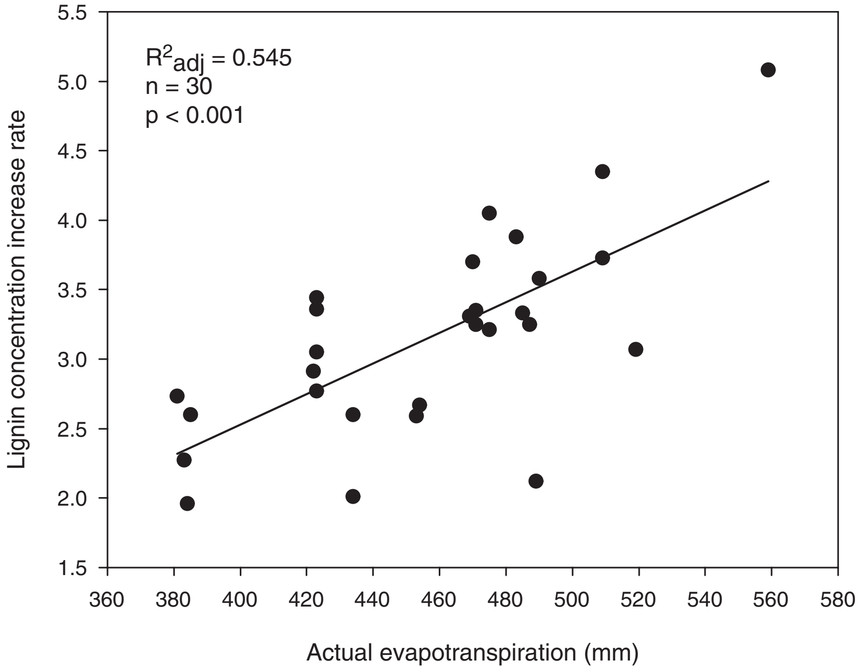

Fig. 5.15 Linear relationship between the lignin concentration increase rate (LCIR) in unified decomposing Scots pine needle litter, and the climate index AET along a climate transect ranging from the Arctic Circle to the northern part of the European continent (Berg et al. 1997)

resulting LCIR values were then related to climate (Berg et al. 1997) using the climate index *actual evapotranspiration* (AET; Meentemeyer 1978). The LCIR for Scots pine gave a highly significant positive relationship with AET, with $R^2_{adj} = 0.545$, and $p < 0.001$ for $n = 30$ (Fig. 5.15).

Combined data for Scots pine, lodgepole pine, and white pine incubated throughout Sweden, and on Black Hawk Island (USA, see Appendix III) showed that the relationship between LCIR and AET was highly significant, and a multiple regression using both lignin and AET gave a strong fit ($R^2_{adj} = 0.697$, $n = 69$). Norway spruce litter shows a similar relationship between LCIR and AET ($R^2_{adj} = 0.546$, $n = 14$, $p < 0.01$; Berg et al. 1997).

In an approach toward a broader relationship, they combined all available data for Scots pine, white pine, lodgepole pine, and Norway spruce, and compared LCIR to AET and added initial lignin concentration (see above). For this combined set of coniferous litter, AET was a moderate predictor of LCIR, but weaker than initial lignin. This regression, including both AET and lignin, gave an R^2_{adj} of 0.697 ($n = 57$) with a highly significant relationship. This means that for four coniferous species along a mainly North European climatic transect, the climatic index AET

Table 5.8 Linear regressions for combined datasets for three stands. The increasing lignin concentration in decomposing litter was regressed vs. litter mass loss, using available data points for each litter type. The resulting slope is the lignin concentration increase rate (*LCIR*). The site Jädraås is a nutrient-poor stand, and the sites Norrliden and Stråsan are more fertile. The stands are located in monocultural systems that are not manipulated (Berg et al. 1997)

Site	Intercept (SE)[a]	LCIR (SE)	R^2_{adj}	R	*N*	*p*<
Jädraås – Scots pine needle litter						
Local natural	262.0 (20.8)	2.946 (0.089)	0.894	0.946	131	0.001
Exper./fertilized	263.0 (21.1)	3.236 (0.14)	0.912	0.956	53	0.001
Green needles	249.5 (16.9)	3.16 (0.26)	0.883	0.967	12	0.001
Norrliden – Scots pine needle litter						
Local natural	276.0 (27.9)	2.989 (0.503)	0.795	0.895	30	0.001
Exper./fertilized	261.1 (24.2)	4.25 (0.22)	0.912	0.96	37	0.001
Green needles	211.8 (8.6)	5.17 (0.12)	0.933	0.974	14	0.001
Stråsan – Norway spruce needles						
Local natural	362.7 (18.7)	2.95 (0.176)	0.839	0.920	56	0.001
Exper./fertilized	393.6 (29.1)	2.90 (0.172)	0.714	0.845	14	0.001
Green needles	288.05 (40.2)	3.39 (0.61)	0.749	0.880	11	0.001

[a] *SE* Standard error, *n* number of data points, *Exper./fertilized* litter from N-fertilized trees

and the initial lignin concentration could explain 70% of the variation in the increase in lignin concentration with decomposition.

Berg et al. (1997) interpreted these findings to mean that at higher AET values, more favorable climatic conditions exist for initial decomposition. With climate less limiting, the faster growing fungi would have an advantage over slower growing lignin degraders (cf. Chaps. 2 and 6). In colder climates, lignin degraders would grow better than those fungi degrading holocellulose. This would result in more lignin being degraded at sites with lower AET. The end result would be that the higher the AET, the more the lignin concentration increased per unit mass lost. In other words, for litters decomposing at sites with higher AET, the amount of lignin and its recombination products (cf. Glossary) occurring in decomposing litter at a particular percent of mass loss is greater than for the same litter at sites with lower AET values.

An alternative and speculative explanation may be connected to the increasing N levels in the same litter types (see above). The increases in litter N levels are also positively related to both the AET (above), and the effect of what in general terms is called the "humification process", which would be faster under warmer and wetter conditions. That would imply that N is more quickly mobilized, thereby increasing the relative N concentration in the soil, and allowing faster transport to the litter. Furthermore, the higher the N concentration, the faster the adsorption of N to lignin remains (Stevenson 1982). Such an explanation is at least possible, since N concentration is the limiting factor in the process of adsorption of N to decomposing litter (Axelsson and Berg 1988).

The influence of N concentration. Some data (Table 5.8) have indicated a higher LCIR value for nutrient-rich litter. Such an observation was judged by Berg et al.

(1997) to be valid, since N has been observed as part of humus formation (Nömmik and Vahtras 1982). Berg et al. (1997) compared three different groups of Scots pine needle litter incubated at a nutrient-poor Scots pine site. The litter sets had different initial nutrient composition, but similar initial organic-chemical composition. The brown, local natural litter had lower levels of N, whereas the needle litter originating from experimental, fertilized plots had higher levels, with the green needles having the highest concentrations. The local natural litter had a composite (LCIR) slope of 2.95 (n=131), and the set of experimental Scots pine needle litter with higher initial nutrient concentrations (Berg et al. 1987) an average slope of 3.24 (n=53; Table 5.8). Finally, the set of green needles had an LCIR value of 3.16 (n=12). Although small, these differences suggested that within the same litter type and at the same site, there may be a difference in rate of increase in lignin concentration when nutrient concentration varies at litter fall. A similar comparison among Scots pine needle litters at a more fertile site (Norrliden; Table 5.8), with Scots pine growing on soil derived from glacial till, revealed more pronounced trends. In this case, the differences between groups were significant. Local, natural brown needles had an LCIR value of 2.99, whereas litter from fertilized trees had a slope of 4.25, and green needles a slope of 5.17 (Table 5.8). Needle litter of Norway spruce exhibited similar (albeit non-significant) trends, with the needles yielding higher LCIR values. Local, natural, brown needles had an LCIR of 2.95, whereas litter from fertilized trees had a slope of 2.90, and green needles a slope of 3.39 (Table 5.8).

There were no significant global relationships between N concentrations and LCIR among any of the data combinations analyzed. It thus appears that even though the nutrient level within a species of litter may affect the rate at which lignin concentration increases, N concentration is not a major factor.

Chapter 6
Chemical Constituents as Rate-Regulating: Initial Variation and Changes During Decomposition

6.1 Introduction

Chapter 5 reviewed the effects of initial litter chemical composition on the pattern of changes that occur during decay. This chapter focuses on the influence of the changing litter quality on the decay processes, and will show that the influences of selected litter chemical components change dramatically during decay, sometimes even reversing the direction of their effect. For this purpose, the three-phase model introduced in Chapter 2 is applied to organize our explanation of the effects of chemical variation on changes in mass-loss rates and decomposition patterns. We also discuss litter types that have been found to have a very short early stage, if any at all (cf. Chap. 2).

Chemically distinct litter species, or litter that has been chemically modified as a result of, e.g., fertilization or pollution will follow different patterns during the decomposition process. Higher concentrations of the main nutrients N, P, and S may increase the initial decomposition rate, and in later stages change the decomposition pattern. The case study litter (cf. Chap. 2) showed a basic pattern, and in this chapter we will describe the effects on this basic pattern of variations in the concentrations of main nutrients. Nutrients other than these main nutrients may be important in some litters. For some foliar litter species, notably Norway spruce and common oak, the patterns differ completely, and initial rates may be related to nutrients such as Mn. These litter species have been the basis for suggesting the flexible early stage in the three-phase model.

The decomposition process normally reaches a stage at which decomposition almost stops, or proceeds so slowly that the stage may be approximately described mathematically by an asymptote, or as a limit value for the decomposition process (cf. Chap. 2). For foliar litter, the limit value normally ranges between 50 and 100% mass loss. The value is negatively related to initial litter N concentrations, which means that the more N-rich (and generally more nutrient-rich) the litter is, the sooner the mass-loss limit is reached, and the less the litter will decompose under comparable environmental conditions. This relationship, which has been generalized for foliar litter types, is developed in this chapter. The limit value is also normally related to litter Mn concentration. There is a general positive relationship between

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the concentration of Mn and the degradation of lignin and modified lignin, as well as litter decomposition. This relationship has not yet been explained experimentally, but Mn is known as a cofactor in lignin-degrading enzymes such as Mn-dependent peroxidase (Perez and Jeffries 1992; Hatakka 2001).

Recent studies have created a new development of the whole model concept. Findings about the role of Mn beginning in the initial stages of decomposition for newly shed litter have modified the concept “early stage”, or “initial stage”. We therefore have developed the three-stage model, and identified three different cases or patterns of decay, especially for the initial stage.

Generally, N concentrations in litter support the process of leaching of C compounds from that litter (Fog 1988). This leaching may begin in the early phase, and continue through the remaining phases to the humus-near stages. There are extreme cases reported, such as an actual disintegration of very N-rich humus that was due to a change in the microflora. This resulted in a very rapid degradation accompanied by a leaching of N-containing compounds (Guggenberger 1994). These findings will receive further attention in Chapter 11.

The intention of this chapter is to demonstrate and systemize the changing effects of several chemical components on rates and patterns of litter decomposition.

6.2 A Three-phase Model Applied to Litters of Different Chemical Composition

The decomposition dynamics in most needle and leaf litters investigated to date follow the model presented in Fig. 6.1. The model appears to be appropriate for needle litter of different pine species, as well as different types of foliar litter, and probably also litter from grasses and herbs. The model thus appears to have a relative generality.

Different plant litter types have different chemical compositions when shed (cf. Chap. 4), and probably the cellulosic fibers are lignified to different extents. Such properties are apparent in the early stage, e.g., in the form of measurable rate-limiting factors. Some of these properties are also reflected in later stages of decomposition, and higher initial concentrations of N and lignin correspond to higher concentrations of these components during the whole decomposition process (cf. Chap. 5). To describe this, we have chosen to apply and develop the three-stage model described earlier by Berg and Matzner (1997). Litters studied so far can be placed into one of three cases under this model, based on the litters’ properties in the early stage, and their behavior in the late stage (Table 6.1). We consider these cases as part of a pattern in development, and expect them to change as new information becomes available. There are thus two cases with a distinct “early phase”, as well as one case in which the “early phase” is so short that it may not always be even possible to measure.

As an initial reference point for early-stage decomposition on which to base further discussion, we consider the decay of Scots pine needle litter. For newly

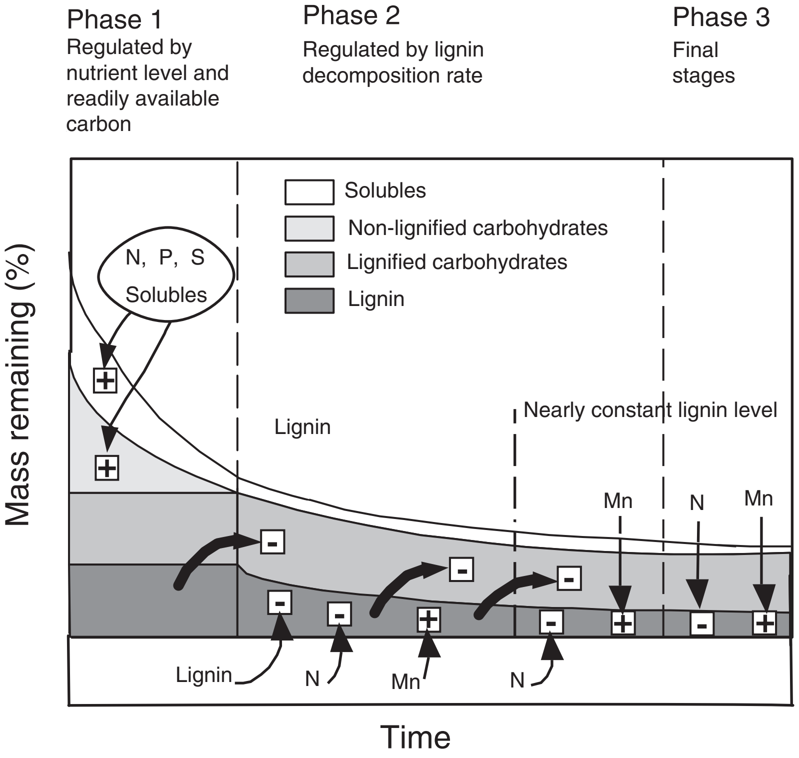

Fig. 6.1 Model for chemical changes and rate-regulating factors during decomposition (modified from Berg and Matzner 1997). The decomposition of water-soluble substances and unshielded cellulose/hemicellulose is stimulated by high levels of the major nutrients (early stage – *phase 1*). When all unshielded holocellulose is decomposed, only lignin-encrusted holocellulose and lignin remain. The early phase has been observed to last up to ca. 40% mass loss (case B in Table 6.1), with a very high mass-loss rate, or leaching. It may also be close to nonexistent, as in case C in Table 6.1. In the late stage (*phase 2*), the degradation of lignin controls the litter decomposition rate. Nitrogen hampers the degradation of lignin, and higher N concentrations suppress decomposition, whereas Mn appears to have a stimulating effect on lignin degradation. Finally, in the humus-near stage (*phase 3*), the lignin level is nearly constant, often at values of 50–55%, the litter decomposition rate is close to zero, and the accumulated mass loss also reaches its limit value

shed Scots pine litter with different nutrient levels, the decomposition rate was linearly related to concentrations of total N, P, and S, until an accumulated mass loss of between 26 and 36% was reached (Fig. 6.2), corresponding to an early phase. We also see cases in which the early stage cannot be distinguished at all (cf. below). The later stages are similar to those described before, and are characterized by a lignin-mediated suppression of the decomposition rate. The late stages of decomposition, and the concept of the limit value are now discussed in terms of varying litter chemical composition. The humus-near stages are explained

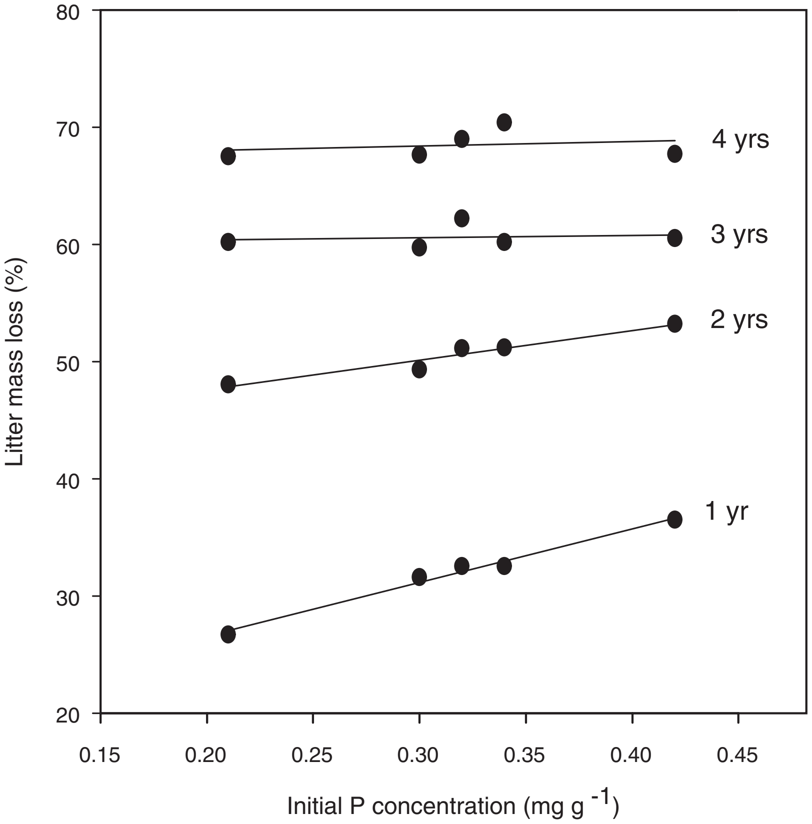

Fig. 6.2 Relationships between initial concentrations of P and increasing mass loss of Scots pine needles. A set of five collections of Scots pine needle litter from N-fertilized plots was used. The slope decreases as the rate-stimulating effect of P decreases, and that of other factors increases. Initial concentrations of N showed a very similar pattern (B. Berg, unpubl. data)

in terms of limit values, and their relationship to the chemical composition of litter. Different litter types, however, have somewhat different patterns in terms of the model, and that is also discussed. We can thus see three different patterns, or cases of foliar litter decomposition, and these patterns appear to be distinct for the groups in mainly the early, but also the late stages. We have given each group a provisionary name: "case A", "case B", and "case C", and they are discussed in that order (Table 6.1).

Even if we can define a reasonably clear border between the early and late stages of decomposition, there is no precise distinction between the late stage and the one that we call the "humus-near", or "limit-value" stage. It is even more difficult to distinguish clearly between litter in the "humus-near" stage and true humus. Several of the functional properties, such as the effect of N on decomposition,

Table 6.1 Overview of a possible division of foliar litter types into groups with different properties, organized into the three-stage model (Fig. 6.1). The names of the groups are provisional. We consider that the properties of the early stage determine to what case the litter belongs

	Stage of decomposition		Examples of litter species
Group	Early stage	Late stage	
"Case A" (cf. Fig. 2.2A)	Low initial leaching ($<2\%$). Decomposition of solubles within the litter structure. A well-pronounced early phase. Initial decomposition rates may be related to initial concentrations of N, P, S. Initial decomposition rates may be related to climate	Slow continuous increase in lignin concentration. Relationship between lignin concentration and mass-loss rate	Scots pine, lodgepole pine
"Case B" (cf. Fig. 2.2A)	High initial leaching ($>5\%$). A well-pronounced early phase with a rapid initial mass loss. Initial decomposition rates may be related to initial concentrations of N, P, S. Initial decomposition rates may be related to climate	Maximum lignin level normally reached quickly. No relationship between lignin concentration and mass-loss rate	Grey alder, silver birch
"Case C" (cf. Fig. 2.2B)	Low initial leaching ($<2\%$). No real initial phase as in case A and B. Slow initial mass loss. Initial mass loss related to lignin or Mn. Influence of climate is probably small	Slow continuous increase in lignin concentration. Relationship between lignin concentration and mass-loss rate not yet clear	Norway spruce, common oak

appear to be common to different stages. Thus, properties of the humus-near stage may persist into the humus stage.

6.2.1 Initial Decomposition Rates for Newly Shed Litter – Early Decomposition Stage in Plant Litter

Background

The initial stage appears to vary with litter species, and so far three main patterns have been reported. The most common case observed is one for Scots pine. This case (case A) has a distinct initial stage in which N, P, or S are rate-determining for the degradation of water solubles, unshielded cellulose, and hemicellulose. Case B appears well represented among some deciduous species with either a high leaching or decomposition of easily degradable compounds, possibly remaining starch. A third case appears to be one in which no real initial phase can be found (case C), and the litter behaves as with lignin being degraded already initially. In this latter case, N, P, and S seem to have no effect on decomposition rate.

To determine rate-regulating factors within a given forest stand, studies are normally designed so that foliar litter types of different nutrient and lignin composition are compared in terms of mass loss over brief periods of no more than 1 year. When evaluating data, the best linear relationship (highest R^2) should show the most limiting factor. However, not all foliar litter should be compared in this manner, since nutrients in litter have different status and availability, and some newly shed litter, such as that from Norway spruce, may be in a late stage of decomposition even before it is shed.

How can Initial Rates be Described?

The majority of studies on litter decomposition found in the literature present results from the early decay stages. These studies often show positive relationships between initial decay rate or CO_2 release from litter, and concentrations of either the group of major nutrients (N, P, S) or the concentration of water-soluble substances. Studies have also found relationships between initial mass-loss rates and concentrations of lignin or Mn.

There are different ways of expressing the decomposition rate in the early stage, and some definitions are therefore useful (see Glossary and Sect. 2.2). For litter types that leach their water-soluble compounds only to a small extent, or not at all, decomposition for a given period (e.g., a month, or a year) is equivalent to microbial decomposition (C mineralization). For litters that leach C compounds initially – for example, several deciduous foliar litter types – mass-loss rates are the result of a combination of microbial decomposition and leaching (see Glossary).

A further way to determine the initial rate of decomposition is to use the mass-loss data from a whole study (Fig. 6.3), ranging from the first sampling of litterbags to the very last one, perhaps after several years. Equation (6.1) is a function that estimates the limit value for decomposition, and also the initial rate as the derivative of the graph at time zero.

$$L = m(1 - e^{-kt/m}) \tag{6.1}$$

In this equation, L is the accumulated mass loss (in %), and t is time (in days). The parameter m represents the asymptote at which the accumulated mass loss will remain constant, and the parameter k is the decomposition rate at the beginning of decay, sometimes indicated as k_{init} (the derivative of the function at $t=0$). This equation illustrates a rate of mass loss that decreases as mass loss proceeds, approaching the asymptote m; note that the asymptote can be 100%. To fit data to this function, a set of litter mass-loss data over time is required. Often 10–12 samplings for a single litter type extending beyond 50% mass loss are required to provide sufficient data for both the limit value and the initial rate to be determined.

The loss of organic matter from newly shed litter achieved by soaking the litter in water may reach rather high values, although this initial leaching can be low in some litter types. For example, Scots pine needle litter may lose only a few percent

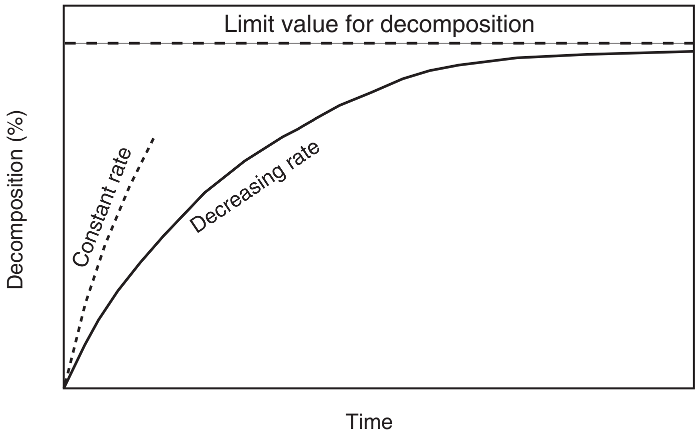

Fig. 6.3 Asymptotic model describing litter mass loss during decomposition. Based on extrapolation, the model serves to estimate a quasi-steady state, or limit value for accumulated mass loss

via leaching (Bogatyrev et al. 1983), while some deciduous litters may leach considerably more, in part because they have a higher concentration of water-soluble substances (cf. Table 4.1). The loss of soluble materials is not wholly due to leaching. In a study of sugar maple leaves on Black Hawk Island (see Appendix III), McClaugherty (1983) determined that most of the soluble carbohydrates and soluble phenols lost during the first year were either consumed by microorganisms, or converted into insoluble compounds. After 1 year, only 21% of the initial soluble carbohydrates remained in the leaves, 15% had been leached, and 64% had been respired or converted. For soluble phenols, the data had a similar pattern: 29% leached, 4% remaining, and 67% consumed or converted. Freeze–thaw cycles increase the leachable amount both of C compounds and of nutrients.

Initial leaching is possibly influenced more by litter type (e.g., coniferous vs. deciduous), or by litter species, freeze–thaw cycles, and concentration of solubles than by litter N levels. Fog (1988) suggested that litter N levels influenced the magnitude of leaching (cf. Sect. 11.3.2). However, this may be more related to leaching in late stages than during initial decay. For a set of coniferous litter, Berg and Matzner (1997) presented data showing a negative relationship between initial levels of N and initial concentrations of water-soluble substances.

Initial Chemical Composition and Different Indices Related to Initial Decomposition Rates

Cases A and B, a Clear Initial Phase. Different approaches have been undertaken to identify a chemical index for the initial decay rate. One index is simply the concentration of a given nutrient, such as N or P. A discussion about which of these main nutrients is rate-regulating in the early stage is not always meaningful,

Table 6.2 Correlation coefficients (R) for linear relationships between first-year mass loss and initial concentrations of some main nutrients, water-soluble substances, and lignin, as well as the lignin-to-N ratio. Scots pine and Norway spruce needles from N-fertilized trees, as well as leaves of common oak were used for a within-species comparison, and a set of different litter types for a comparison over species. Significance levels are given after the R values

	Scots pine[a]	Norway spruce[b]	Norway spruce[c]	Common oak[d]	Multiple species[e]
N	0.446, n.s.	0.305, n.s.	0.045, n.s.	0.467, <0.05	0.643, <0.01
P	0.904, <0.001	0.556, n.s.	0.063, n.s.	0.378, n.s.	0.797, <0.001
S	0.780, <0.01	n.d.	n.d.	n.d.	0.508, <0.05
K	0.899, <0.001	0.511, n.s.	0.126, n.s.	n.d.	0.649, <0.01
Ca	0.148, n.s.	−0.693, <0.05	0.032, n.s.	0.446, <0.05	0.161, n.s.
Mg	0.520, n.s.	0.326, n.s.	0.195, n.s.	n.d.	0.750, <0.001
Mn	n.d.	−0.226, n.s.	0.570, <0.05	0.581, <0.01	n.d.
Wsol[f]	0.217, n.s.	0.888, <0.01	0.265, n.s.	n.d.	0.792, <0.001
Lignin	−0.145, n.s.	−0.663, <0.1	0.122, n.s.	−0.480, <0.05	−0.118, n.s.
Lignin:N	−0.650, <0.05	−0.593, n.s.	0.055, n.s.	n.d.	−0.773, <0.001
n	11	9	14	20	18

[a] Experimental Scots pine needle litter originating mainly from fertilized plots and with increased nutrient levels incubated at the site Jädraås. Data from Berg and Staaf (1980a)

[b] Experimental Norway spruce needle litter originating from fertilized plots and with increased nutrient levels, incubated at the same plot. Data from Berg and Tamm (1991)

[c] Norway spruce needle litter incubated at 14 sites along Sweden with AET ranging from 371 to 545 mm. In that case, no climatic influence could be traced. Data from Berg et al. (2000)

[d] Common oak leaves collected from 20 different stands and incubated on site. Data from Davey et al. (2007). Rate calculated using Eq. (6.1)

[e] Experimental Scots pine litter (cf. above) as well as brown and green leaf litter from Scots pine, lodgepole pine, silver birch, and grey alder. Data from Berg and Ekbohm (1991)

[f] *Wsol* Water soluble, *n* number of samples, *n.d.* not determined, *n.s.* not significant

as other factors can be more dominant. We can see (Table 6.2) that for decomposing Scots pine needle litter, the main nutrients P and S show significant correlations to first-year mass loss, correlations that are improved when more nutrient-rich green needles are included in the measurements. That the relationships to N are weaker does not mean that N is without effect. The different R values for N, P, and S probably reflect differences in availability of the corresponding elements relative to the requirements of decomposer microorganisms. The lower R value for the initial relationship to N could reflect the fact that N is partly stored in litter in forms that are unavailable to the microorganisms that first invade the litter. Contrasting with these three nutrients are the highly mobile ones, such as K, which are highly leachable. Different initial concentrations of these more mobile nutrients appear not to influence litter decomposition rate, or their concentrations in later stages of decomposition.

A positive relationship between a given nutrient and the initial decomposition rate is a crude measure of its rate-regulating function. Part of the N is tied to the lignin fraction (Flaig et al. 1959). About 1/3 of the total N is initially complexed to the lignin fraction in Scots pine needles (Berg and Theander 1984). Such N is then

Table 6.3 Initial N associated with extractable, acid-hydrolysable, and lignin fractions of six foliage litter species collected at Black Hawk Island, Wisconsin, USA (Aber et al. 1984)

Litter	Extractable (mg g^{-1} OM[a])	Acid hydrolysable	Lignin
Bigtooth aspen leaves	4.0	1.5	2.8
Canadian hemlock needles	4.5	1.5	2.3
Red oak leaves	4.1	1.7	2.4
Sugar maple leaves	5.5	0.5	2.3
White oak leaves	4.7	0.7	3.0
White pine needles	2.2	0.0	2.2

[a] *OM* Organic matter

not readily available to the microorganisms that start the decomposition process. Aber et al. (1984) measured the amount of N associated with the solubles, holocellulose, and lignin fractions of six foliar litter species (Table 6.3). They found that between 26 and 38% of total N was associated with the lignin fraction. This means that while a value for total N may be used as an index for available N, it will overestimate the amount of available N. As we may see (Table 6.3), a consequence is that this index may not be very reliable for species with different levels of available N. According to the literature, P and S do not appear to be bound in a manner similar to N, and as a result may be more available to leaching, or microbial uptake (Stevenson 1982).

The C-to-N ratio is another index that conceptually expresses N concentration in organic matter, and gives a good relationship to mass loss for the early stage. This concept of C-to-N as an index was originally developed to be a rule-of-thumb for digestibility of fodder (e.g., fresh hay), but is today in use for soils as a means of predicting N dynamics (see Berg and Ekbohm 1983). For most species of newly shed litter, a low C-to-N ratio usually suggests an initially high decomposition rate.

Another index is the lignin-to-N ratio (Melillo et al. 1982). This ratio was based on the hypothesis that N and lignin had opposite effects on the decomposition rate, whereby N is a rate-stimulating, and lignin a rate-retarding factor. The ratio is generally a good predictor of mass loss during initial stages of decay, particularly for those litter species from which it was derived (cf. Table 6.2). The correlation between the lignin-to-N ratio and first-year mass loss may be significant even if the correlation between either lignin or N taken individually with first-year mass loss is not significant. For late stages (see below; Chap. 2), this index is of little value, since N for the late stages has a rate-retarding effect. The value of this index as a predictor of decay rate thus decreases as the decay process develops.

Indices of initial chemical composition, which represent important rate-regulating factors, vary among litter types (Table 6.2). For Scots pine needle litter, P and S were highly significant, whereas N was not. When combining several litter types, levels of N, P, S, and water-soluble substances all had significant predictive capacity. Potassium and Mg are neglected here as rate-limiting components, since their concentrations decrease strongly immediately after incubation, and there is no indication that they act as limiting nutrients. For Scots pine litter, the lignin-to-N ratio was significant, although neither N nor lignin concentrations alone were. For a combination of different litter species incubated at the same site, N but not lignin was significant, while the ratio was highly significant, and more so than N concentration alone.

For experimental Norway spruce needle litter, the relationships between first-year mass loss and concentrations of lignin and water solubles were significant (Table 6.2; Berg and Tamm 1991), while P was not significant. There was no relationship between N concentration and initial rate of decay, and the lignin-to-N ratio was not significant. For Norway spruce litter incubated along a transect (Table 6.2), no relationship was seen between climate and initial decay, and when comparing substrate-quality factors, only Mn was seen to be related. We discuss this below.

For leaves of common oak, there was a highly significant relationship between initial decomposition rate, calculated by means of Eq. (6.1), and litter Mn concentration. The relationships to Ca, N, and lignin were significant at $p<0.05$. For pine needles, and for different species combined (Table 6.2), concentrations of most of the main nutrients are positively related to litter mass loss. In addition, the concentrations of the main nutrients are normally positively correlated to each other. For example, N, P, and S are all integral parts of basic components such as nucleic acids and proteins, of both plant cells and microorganisms. However, only total concentrations of N, P, and S are normally measured, without regard to availability. This makes any observed relationship between these nutrients more tenuous, because the nutrients do not have the same availability, as discussed above for N.

At a Scots pine site, measurements of first-year mass losses were conducted for several years for the most common litter type (Scots pine needle litter), the annual variation among N, P, and S being given in Table 4.4. The most limiting element for microbial growth and activity can vary among years. Thus, a raised concentration of N may give a response in one year, and not in another. Furthermore, the ratios of N, P, S, and other nutrients vary with time within the same stand and litter (Table 4.4). Cotrufo et al. (1998) found that rates did not increase when the initial concentration of N in litter was proportionately higher than the concentrations of P and S, which were at more normal levels. We cannot exclude the possibility that the proportions of the main three nutrients are a critical factor that may vary among sites and litter types, since both endogenous (in the litter) and exogenous (from the environment) nutrients may influence the microbial community. Furthermore, N, P, and S are not the only nutrients that influence the initial decomposition rate. Ca concentration has also been positively related to initial rates (Van Cleve 1974), although that study was limited in terms of the number of nutrients investigated.

Although N appears to be one of several dominant rate-regulating factors in newly shed litter, the concept “newly shed litter” is neither simple nor clear. Some litter types show differing behaviors, and some litter types – for example, spruce needles, and leaves of common oak – deviate from the three-phase model (Fig. 6.1; cf. below).

Case C, initial phase very short or absent. There are a few studies reporting a deviation from the more traditional pattern with an initial phase in which the initial decay rate is related to the concentrations of major nutrients. Case C (Table 6.1) encompasses litter in which the initial phase, in the sense as described in case A, is absent or very short.

Reports for two litter species show that the initial rate can be best related to litter Mn concentration (Table 6.2), these being a study on Norway spruce needles, and one with common oak (Davey et al. 2007). Davey et al. (2007) related a high initial decomposition rate (k_{init}) to litter Mn concentration, with a high significance ($R^2=0.34$, $p<0.01$), and the relationship to N was also significant, though less so ($R^2=0.22$, $p<0.04$). Likewise, Berg et al. (2000) related the first-year mass loss for Norway spruce needles to Mn ($R^2 = 0.325$, $n=14$, $p<0.05$). The relationships to N, P, and climate factors were not significant along this transect extending from ca. 56 to ca. 66°N.

Two extensive studies on the decomposition of newly shed litter of Norway spruce also indicate a behavior different to that of litter types fitting the case A and B three-phase model. The decomposition rates of newly shed spruce litter are related to the concentrations of water-soluble substances and lignin, rather than to the concentrations of major nutrients (Table 6.2; Berg and Tamm 1991).

When Berg and Tamm (1991) compared the decomposition rates of spruce needles of different chemical composition, there was no statistically significant relationship between initial mass-loss rate and concentrations of nutrients. It appeared, though, that the initial concentrations of water solubles had a significant influence on mass-loss rates (up to about 2 years of decomposition; Fig. 6.4), whereas the initial concentration of lignin had a less pronounced effect (albeit still statistically significant) on first-year mass loss. There was thus no nutrient-regulated early decomposition phase

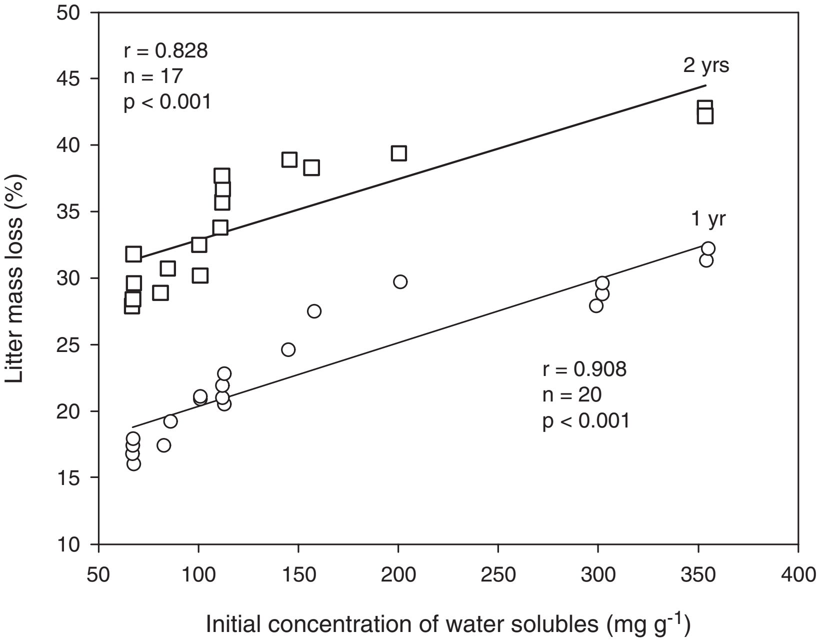

Fig. 6.4 Litter mass loss of Norway spruce needle litter vs. the initial concentration of water-soluble substances: accumulated mass loss after 1 and 2 years (modified from Berg and Tamm 1991)

like that described above. This may be explained by the fact that spruce needles remain on the branches after senescence for several months. We cannot exclude the possibility of a fiber structure with a high level of lignification (cf. Fig. 4.2).

During this early-stage period, leaching of nutrients could take place, and the decomposition of the needles could start, resulting in increased lignin concentrations, and changed concentrations of other nutrients. The implication is that the early phase of decomposition may already have passed before the needles are shed. A possible explanation for the different decomposition pattern of spruce needles is that these are composed of a more heterogeneous material that, in addition, is in a late stage of decomposition when shed. Because they remain attached to the twig for extended periods of time after they senesce, significant decomposition can occur while they are still attached to the tree.

In another study on Norway spruce needles throughout Sweden, carried out at 14 sites along a climate transect (cf. Chap. 7), there was no relationship between first-year mass loss and climate, or climate-related indices, for levels of AET ranging from 371 to 545 mm (Berg et al. 2000). When the data for the sites were combined and compared to substrate-quality factors, the concentrations of the main nutrients (N, P, S) did not give significant relationships, but the concentration of Mn correlated positively with first-year mass loss ($R^2 = 0.325$, $n = 14$, $p < 0.05$; Fig. 6.5). The important role of Mn in lignin degradation has been described in Chapter 3.

Another case is reported by Davey et al. (2007) for leaves of common oak. They collected common oak leaves at 20 stands (Wales, UK), incubated these in one of the

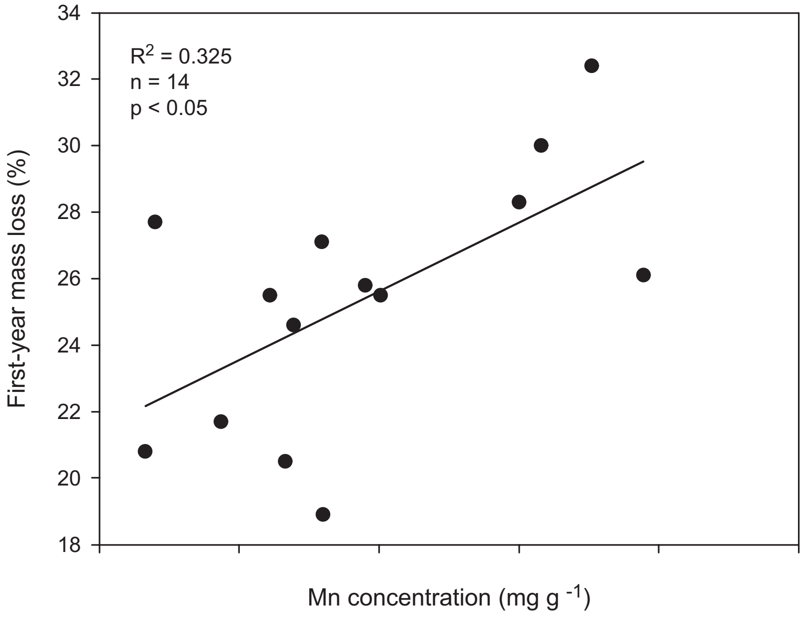

Fig. 6.5 First-year mass loss of local Norway spruce needle litter vs. initial concentration of Mn. The needle litter was incubated at 14 sites along a transect across Sweden (Berg et al. 2000)

oak stands, i.e., under an identical climate, and monitored mass loss for 2.5 years. Using Eq. (6.1), they calculated the initial rates, related to initial concentrations of nutrients, and found that concentrations of Mn (positive) and lignin (negative) gave the best relationships to initial decomposition rate (k_{init}). This supports the earlier studies on Norway spruce litter suggesting that, for some litter species, lignin may be the rate-regulating agent already from the start of the decomposition process. We made a recalculation using the data of Davey et al. (2007), excluding one of their sampled litters from a partly N-polluted area, and found that this strengthened the role of lignin and Mn (Table 6.2), as these relationships became the only significant ones.

6.2.2 Decomposition in the Late Stage – Lignin-Regulated Phase

The Late Decomposition Stage

In an attempt to organize decomposition patterns, Berg and Staaf (1980a) distinguished a late phase in which the decomposition was regulated by lignin decomposition. They noted that when the strong initial effect of the main nutrients diminished, the decomposition rate could be related negatively to the increasing lignin levels. For Scots pine needle litter, they estimated that the shift in phases took place at a mass loss of between 26 and 36% (Fig. 6.1). In a separate study on Scots pine needle litter, Couteaux et al. (1998) determined the change in phases to be at about 25% mass loss. For lodgepole pine needle litter, the early phase was seen to be shorter, and to end at around 20% or less (B. Berg, unpubl. data). Leaves of grey alder, above ascribed to case B, appeared to have an initially high decomposition rate, followed by an abrupt shift from the early to the late stage at ca. 40–45% mass loss. Litter of Norway spruce and common oak can be ascribed to case C, in which the early stage was essentially absent; initial leaching was very low, and initial mass-loss rates were related to lignin and Mn.

The main reason for defining a late stage, or a lignin-regulated phase, is that decomposition in this stage is regulated by the degradation of lignin. Still, the factors regulating the degradation of lignin vary, and we will discuss the present state of our knowledge below.

Some Different Lignin-Related Decomposition Patterns Among Litter Types

We previously introduced three cases (A, B, C) of patterns that appear to be characteristic mainly for the early and late stages of foliar litter decomposition (Table 6.1). Here, we intend to relate lignin dynamics to these groups, or cases. However, for a further understanding, we have organized the description of the late stage around the constituents lignin, N, and Mn.

In the cases reported to date, lignin is resistant to degradation, and an increasing lignin concentration suppresses the decomposition rate of litter in most foliar litter types. The relationship shown above, namely, a decreasing rate for one type of litter incubated at its own forest stand, has been observed by several scientists. One basic method to investigate the possible effect of a chemical component on decomposition rate is to incubate the litter over a series of years, and view the litter that changes with decomposition (cf. Chap. 5) as a new substrate at the beginning of each incubation year. This is an example of a periodic mass loss (see Glossary). In this case, the litter chemical composition at the beginning of each incubation year is associated with the mass loss during the ensuing year. In this approach, the lignin concentration at the start of each 1-year period is regressed against the mass loss over that 1-year period, to obtain a slope for each site describing the effect of lignin. The effect of an increasing lignin level in foliar litter, and its decomposition rate, is thus easily illustrated.

Case A. The mass-loss rate of needle litter is retarded proportionally to lignin concentrations (Fig. 6.6A), an observation that has been made repeatedly in Scots pine ecosystems, as well as in ecosystems of other pine species (Berg and Lundmark 1987; McClaugherty and Berg 1987). In the case of two pine species, Scots pine and lodgepole pine, with similar N levels and growing in systems of same soil richness (Fig. 6.6A), we note that the relative lignin-mediated effects are similar, in both cases being due to a slow and steady increase in lignin concentration during the decomposition process.

Case B. Whereas the pine litter showed negative linear relationships for mass loss vs. lignin for the late stage, with rather slow stepwise changes, such linear relationships are not seen for the case B litter types. There is a clear effect of lignin that can be illustrated by the initial (often first year) decomposition, and that of the following years. After a rather short initial decomposition and leaching phase, the lignin concentration quickly reaches a maximum value that is associated with a lower degradation rate, creating a graph with two clusters (Fig. 6.6B) of points, rather than one showing continuous change, as for case A type litter. This late stage, for case B litter represented by a cluster of points, is thus clearly different from that of, e.g., pine litter, and there is no evident relationship to lignin concentration for this late-stage litter.

Case C. Some litter species appear to lack a distinguishable early phase, thus differing in that respect from the two above types, in which the rate-retarding effect ascribed to lignin has been noted to start after lignin concentrations have increased from an initial value, and probably after all unshielded holocellulose is degraded. In the case C litter types, it appears that the concentrations of Mn have an influence on litter degradation rates, sometimes to such an extent that they show better relationships to mass loss than to concentration of lignin. The effect of Mn is thus hypothesized to take place through the degradation of lignin from about the day of incubation.

Effects of lignin

As decomposition proceeds, the lignin concentrations increase in a very regular way (Berg et al. 1997; Berg and McClaugherty 2003), and the increasing lignin level thus

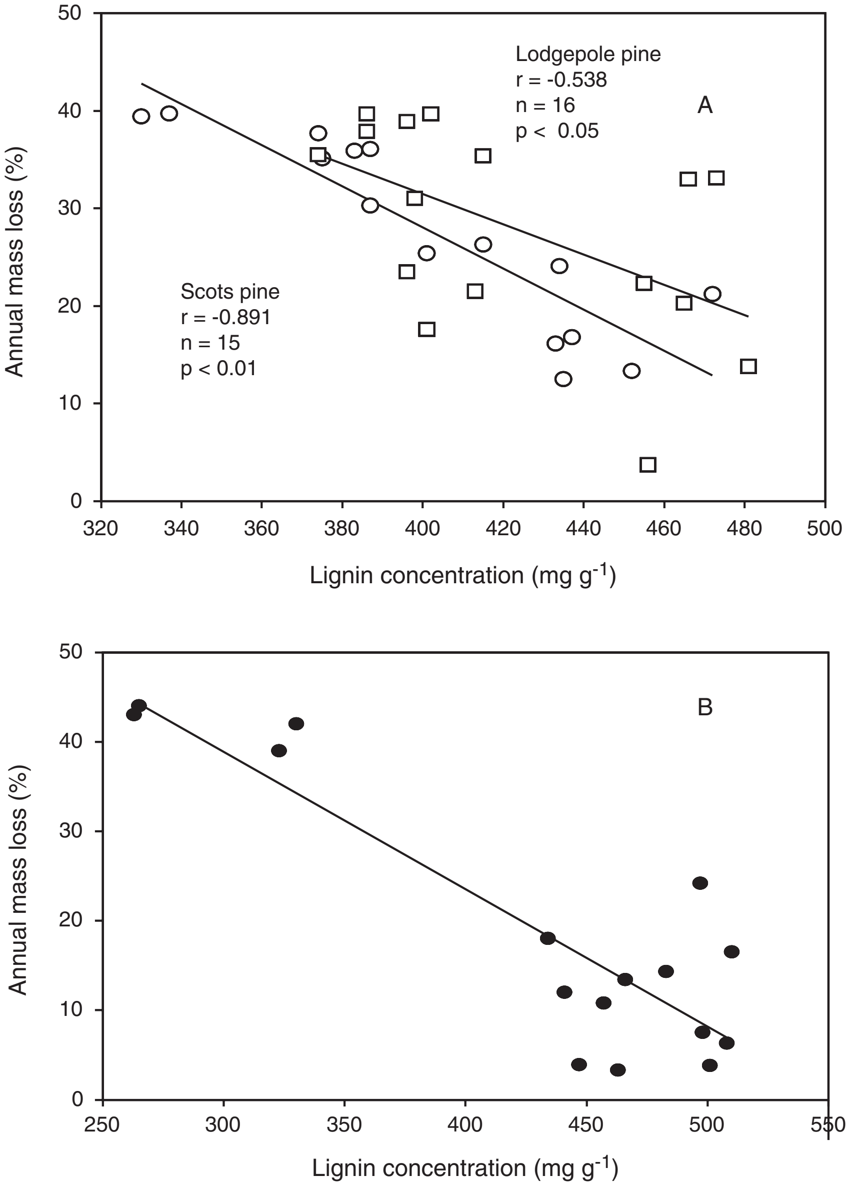

Fig. 6.6 Relationship between lignin concentration at the beginning of a 1-year decay period and the mass loss occurring during the following 1-year period. **A** Scots pine needle litter (○) and lodgepole pine litter (□), both litter species being in the late decomposition stage. **B** Leaf litter of silver birch and grey alder, including both early and late stages. The litter in the late stage forms a cluster with lignin levels above 430 mg g^{-1} litter

Table 6.4 Comparison of R^2 (R^2_{adj}) for the relationships between annual mass loss, and concentration of manganese and lignin in decomposing litter in the late stage. Regressions were made using a stepwise, more narrow interval in lignin concentrations. As the lignin concentrations increase with increasing accumulated mass loss, lignin concentrations, in addition to giving the concentration of a substrate, also index the decomposition level of the litter (from Berg et al. 2007)

Lignin conc. range	Mn			Lignin				Mn conc. range
(mg g^{-1})	R^2	R^2_{adj}	*p*<	R^2	R^2_{adj}	*p*<	*n*	(mg g^{-1})
All available data								
277–509	0.151	0.145	0.001	0.206	0.200	0.001	136	0.04–7.69
>350	0.182	0.175	0.001	0.138	0.130	00.001	115	0.04–7.69
>400	0.215	0.206	0.001	0.059	0.049	00.05	94	0.24–7.69
>450	0.360	0.349	0.001	0.005	-	n.s.	62	0.24–7.69
>475	0.457	0.441	0.001	0.002	-	n.s.	35	0.24–7.69
Norway spruce data only								
>475	0.671	0.653	0.001	0.059	0.001	n.s.	20	0.31–7.69
Data for Scots pine, lodgepole pine, grey alder, and silver birch								
>475	0.115	0.031	n.s.	0.011	-	n.s.	15	0.24–1.90

[a] *n.s.* Not significant

reflects the stage of decomposition. Still, the effect of lignin appears to be related to factors regulating its decomposition, such as N and Mn. Starting with 136 value pairs of lignin concentration and ensuing periodic decay rates representing a variety of foliar litters, Berg et al. (2007) identified different intervals for lignin concentration, stepwise removing the ones with lower lignin concentrations (Table 6.4). This means that the higher concentrations selected also indicated litter material of more advanced decomposition. The reason behind this stepwise selection was simply that an increasing part of the mass loss would be due to lignin degradation. With one exception, the data originated from climatic transects across Sweden from sites with annual average temperatures ranging from –0.7 to 7.8 °C, and precipitation from 410 to 1,070 mm (AET 371 to 520 mm). They observed that the R^2 values for the relationships to Mn increased, although the Mn concentration interval remained the same (Table 6.4). For Scots pine needle litter, it has been shown that the effects of climate on decomposition rate decrease as the litter becomes more decomposed (Johansson et al. 1995). For Norway spruce needle litter along the same climate transect, Berg et al. (2000) did not find any effect of climate on decomposition rate, not even for newly shed litter, viz. the first-year decomposition.

Effects of Nitrogen on Lignin, and Thus on Litter Decomposition

Mass-Loss Rates of Lignin, Compared to Initial Litter N Levels

It has been possible to distinguish differences in lignin degradation rates, and to relate these to litter N concentrations. These estimates of mass-loss rates of lignin were based on measured values for sulfuric-acid lignin (Fig. 6.7A). It was observed earlier that sulfuric-acid lignin in decomposing litter was degraded at very different rates, notably for

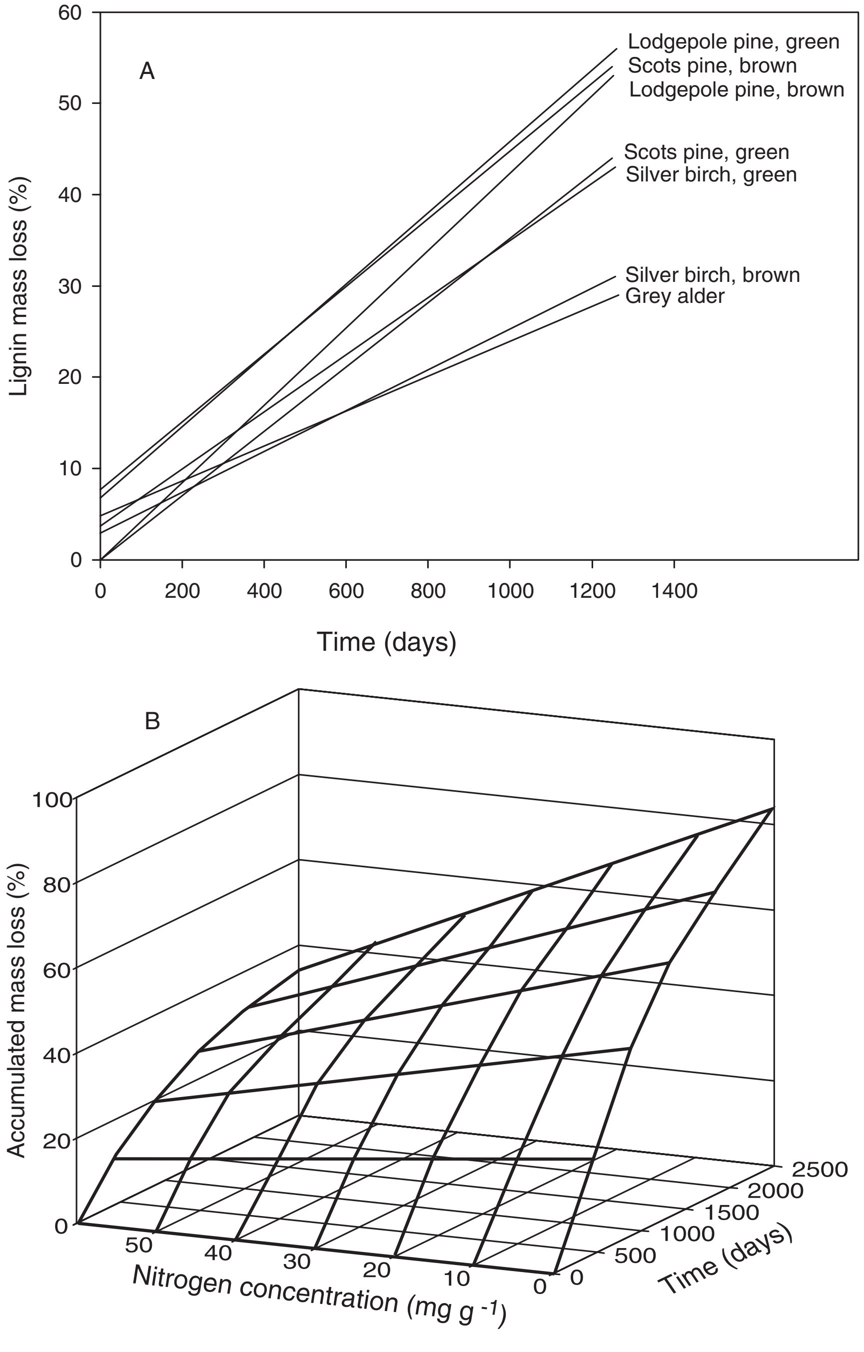

Fig. 6.7 **A** Linear relationships for decomposition of sulfuric-acid lignin versus time in seven litter types of different initial N concentrations incubated in a 130-year-old Scots pine forest (Berg and Ekbohm 1991). **B** Illustration of the negative relationship between accumulated lignin mass loss changing with time, and litter N concentrations (R^2_{adj}=0.677, n=82). Data are for seven litter types incubated experimentally in a Scots pine stand (Berg and Ekbohm 1991)

green N-rich and brown N-poor Scots pine needle litter. The lignin mass-loss rate was lowest for the N-rich litter, and highest for the N-poor litter (Berg et al. 1982b). Berg and Ekbohm (1991) also fitted a linear model incorporating the N concentration of the litters, and found a clear negative relationship between litter N concentration and lignin mass-loss rate (Fig. 6.7A, B).

We have focused on the suppression of lignin-degradation rates by N. There are other nutrients, however, which may influence the lignin-degrading ability of the mixed soil microflora. Such nutrients are likely to include Mn and Ca, although information exists only for pure cultures of lignin-degrading fungi.

Nitrogen – The Biological Regulation and the Chemical Mechanisms

We reviewed the biological and chemical aspects of lignin degradation in Chapters 2 and 3. As discussed above, elevated N levels may suppress the degradation of lignin, and at raised concentrations, the effect may be proportional to N concentration. These two effects, biological and chemical, have so far not been distinguished at the level of litter decomposition, or the level of lignin degradation in litter. However, Berg and Matzner (1997) discussed effects of N additions to humus that suggested that both a biological and a chemical effect could be hampering the decomposition. In Table 2.3, we compared N levels in needle litter with those in pure laboratory cultures that were suppressing lignin degradation. In the relatively N-poor brown Scots pine needle litter, there were between 40- and 100-fold higher N concentrations than those needed to suppress lignin degradation in a laboratory culture. Of course, much of the N in the litter would have been relatively unavailable to the fungi, in contrast to the N in the culture media. Nevertheless, with initial concentrations of N in the litter reaching nearly 3%, litter N levels are up to 800 times as high as those concentrations suppressing lignin degradation in pure cultures of fungi.

The negative effect of added N on respiration rate in humus was seen within hours (Berg and Matzner 1997), indicating a microbial mechanism. We may expect that a repression of fungal ligninase synthesis occurs also in litter, as a result of the relatively high levels of N present. The chemical reaction between N and the decomposing lignin is slow at the low pH values (around 4) of boreal needle litter. Still, in a laboratory experiment the reaction proceeded at a rate of 14–19 μg N day^{-1} g^{-1} litter (Axelsson and Berg 1988). The reaction rate was limited by N availability; using Scots pine needle litter as a substrate, Axelsson and Berg (1988) found that the reaction rate increased with increasing N concentrations. Thus, for long-term decomposition in the field, we can speculate that over a period of years the reaction between N and lignin will become prominent.

How Should we Regard the Retardation of Litter Decomposition Caused by Lignin?

Often the "effect of lignin" on decomposition rate has been illustrated by showing the correspondence between increasing lignin concentrations and decreasing mass-loss rates. A higher concentration of lignin would thus reflect a higher percentage of a compound resistant to decomposition, with a rate that is dependent on litter N concentration, and the kind of organisms that have invaded the litter. We can distinguish some cases that represent extreme possibilities, but our discussion is based on incubation of litter on the forest floor, not in laboratory systems.

If N-sensitive white-rot fungi invade the litter and dominate, we should find that N concentrations, increasing with accumulated mass loss, are hindering the degradation of lignin to an increasing extent. Thus, the overall decomposition of the litter will be increasingly impeded. In this case, raised N levels could result in a lowered litter decomposition rate. The white-rot fungi as a group have the ability to degrade lignin fast when N levels are low, so that any effect of N should be clearly distinguishable (cf. Chap. 3). Such an effect may be expected in a nutrient-poor system in which N-sensitive fungi dominate.

Another possibility is that white-rot fungi that are not sensitive to raised N levels invade the litter. The lignin degradation of such a population would not be hindered by raised N concentrations, and lignin would thus not be a barrier to litter degradation at higher N concentrations. In such cases, either there would be no correlation between raised lignin levels and decomposition rate, or perhaps more likely, there would be no increase in lignin levels.

Brown-rots would not degrade lignin completely, and after the disappearance of the unshielded holocellulose, the raised lignin concentrations would hinder litter decomposition. This would apply to both N-sensitive and N-non-sensitive species.

Considering the decomposition of foliar litter, the most likely scenario when litter is incubated on the ground is invasion by a mixture of fungal species. For example, Osono and Takeda (2001) found over 100 different fungal taxa on the decaying leaves of Japanese beech. Thus, we would expect that both sensitive and non-sensitive white-rots and brown-rots would participate in the degradation. Such a mixture of species would result in a moderate suppression of lignin degradation at low N levels, while higher N levels would have a stronger effect. Differences between systems would be reflected in the slope of the decomposition rates for lignin, and for litter (Figs. 6.6 and 6.7). Thus, a high initial litter N level would have a stronger rate-retarding effect on litter decomposition than would be the case for a litter with lower N incubated under the same conditions. We also speculate that a system richer in N would have relatively more fungi not sensitive to N, while truly nutrient-poor systems would have a relatively high frequency of N-sensitive fungi, thus allowing a stronger retardation of litter decomposition in the latter type of system (Eriksson et al. 1990; Hatakka 2001).

Based on cases reported in the literature, suppression is normal for foliar litter. In fact, there may be only one case reported for which lignin degradation is not hampered. In a paper on lignin decomposition in beech leaf litter, Rutigliano et al. (1996) reported that lignin concentrations decreased immediately from the start of the study. Later, the concentrations started to increase slowly from a level much lower than the initial one. The system was very rich in nutrients (cf. the humus contained ca. 3.7% N in organic matter; Berg et al. 1996b), and it is possible that the system was dominated by white-rot fungi that were largely unaffected by raised N levels.

It is a well-known phenomenon that as litter decomposes, the N level increases (cf. Fig. 5.5). The rate of increase observed in N concentration is normally proportional to the initial concentration (cf. Chap. 5), implying that the higher the initial N level, the greater the increase in N concentration with increasing mass loss.

During decomposition, there is an increase in the concentration of the normally resistant compound lignin, and its recombination products (cf. Fig. 5.2). Traditionally, this has been explained by the fact that the lignin-degrading microorganisms usually grow very slowly, and that lignin as a chemical compound is largely resistant to decomposition, while the unshielded cellulose and hemicelluloses in litter are decomposed considerably faster. This traditional picture of lignin resistance to degradation appears to be valid only under certain circumstances, however, and the degradation rate of lignin in litter has been related to the concentrations of N and Mn in litter (cf. Chap. 2), and the physiology of the lignin-degrading organisms present (cf. Chap. 3). Most studies on litter decomposition are made on foliar litter where the levels of N have been high enough to influence the microbial degradation of lignin, and possibly the formation of more-resistant, N-containing humus compounds, thus creating an image of lignin as being more recalcitrant (Table 2.3).

When the decomposition has reached a certain magnitude, the (foliar) litter contains material that is rich in lignin and its condensation products. At this stage, the remaining cellulose and hemicelluloses are enclosed and protected by lignin and humins (cf. Chaps. 2 and 5). As a consequence the late-stage degradation rates of cellulose and the various hemicelluloses are similar to that of lignin, whereas they are higher during earlier stages (cf. Chap. 2). Thus, through the effect of N in the late decomposition stages, the degradation of lignin and humification products regulates the decomposition of the whole litter (Berg et al. 1987; Berg and Ekbohm 1991).

We may speculate that part of the rate-retarding effect of lignin could be dependent on the increasing N level of the decomposing litter, N exerting a suppressing effect on lignin degradation (cf. Fig. 2.2). Still, we do not know whether this rate-retarding effect of increasing lignin levels should be ascribed to the simultaneously increasing N concentration in the litter. For decomposing Scots pine needle litter, the same lignin level showed a stronger retardation at warmer and wetter sites than at colder and drier ones (cf. Fig. 2.8). The concentration of N increases faster at warmer and wetter sites (cf. Fig. 5.12), which means that higher N concentrations do occur in litter at sites where the proposed effect of lignin is stronger. The suppressing effect of N on the degradation of lignin, as well as on the decomposition of whole litter, has been observed in a variety of studies, and is based on both organic-chemical observations (Nömmik and Vahtras 1982) and on microbiological-physiological data (Eriksson et al. 1990). The retarding effect of N should not be assumed to apply more generally across different ecosystems, but at least it has been observed and confirmed in the cases described here (cf. Chap. 11).

Effects of Manganese on Litter Decomposition – Some Case Studies

The effects of Mn on lignin degradation are well established on the level of organisms (Chap. 3). Still, on the level of litter decomposition it appears that as yet unknown factors may influence what we can measure, and rather than synthesizing and generalizing these data, we prefer to present a set of case studies.

Manganese has an initial concentration range different from that of N, and behaves in a very different manner during decomposition. Thus, the initial Mn levels over a number of European litter species ranged by a factor of almost 100, from 3.9 mg g^{-1} in silver birch in Sweden to 0.04 in stone pine in Italy (Berg et al., DELILA database, Appendix IV). Whereas it has been possible to identify regular patterns in lignin and nitrogen dynamics, it has not been possible to distinguish any consistent pattern for the variation in Mn concentrations during decomposition (cf. Sect. 5.4.2, and Fig. 5.8). Even for a single litter species decomposing in its own system, the pattern varies among years.

The effect of Mn on degrading fungi should be expected to be more complex to interpret than that of N, at least in terms of the values of total Mn that normally are available for litter-decomposing fungi. We thus cannot say that an observed decrease or increase in total Mn concentration generally has an effect on decomposition rate.

Norway spruce. For Norway spruce, Berg and Tamm (1991) compared the effect of lignin concentration on litter mass-loss rate for individual incubation years, and found significant relationships only in the first year, and none in years 2, 3, and 4 (Table 6.5). When investigating the late phase, and comparing annual mass loss and lignin concentrations, they found that the concentration of lignin had a rate-regulating effect on litter decomposition when present in a concentration range from 350 to 450 mg g^{-1}, causing a decrease in annual mass loss of 24 to 10% (Fig. 6.8, Table 6.5). Above a lignin concentration of 500 mg g^{-1}, the scatter in annual mass-loss values increased considerably, with no pattern evident. Berg et al. (1987) noted a similar phenomenon, though less pronounced, for Scots pine needle litter in a very late stage of decomposition.

Considering that there was no lignin effect in litter with lignin concentrations above 450 mg g^{-1}, and that the lignin concentration did not increase much above that, we can conclude that at high concentrations of lignin, near its maximum value, other rate-regulating factors begin to emerge (Berg et al. 1984b; cf. Chap. 5). This would imply that the influence of N on the lignin-degrading microflora can be

Table 6.5 Correlation coefficients (R) for the linear relationship between annual mass loss of Norway spruce needle litter and initial concentrations of lignin at the start of each 1-year period. Analyses are based either on incubation year, or grouping of litter vs. lignin concentration (cf. Fig. 6.8; Berg and Tamm 1991)

Variable	R	*n*	*p*<
Incubation year	`		
1st year	–0.894	10	0.001
2nd year	–0.482	11	n.s.[a]
3rd year	–0.234	11	n.s.
4th year	–0.376	8	n.s.
Lignin conc. range			
<450 mg g^{-1}	–0.873	16	0.001
<475 mg g^{-1}	–0.774	22	0.001

[a] *n.s.* Not significant

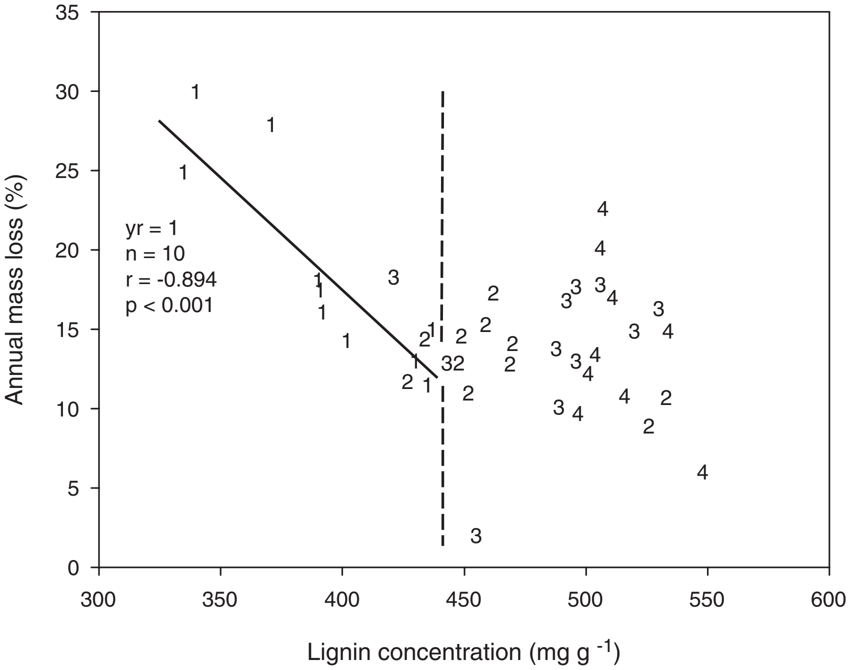

Fig. 6.8 Annual mass loss of Norway spruce needle litter, compared to lignin concentration in litter at the start of each 1-year period. Data are for an experiment in N-fertilized plots (Berg and Tamm 1991), and for two control plots at which N-fertilized litter was incubated. The *number* indicates the approximate incubation year, the *vertical line* an approximate limit for the effect of lignin

outweighed by that of other rate-retarding factors. Alternatively, the reactions between N and lignin degradation products that build a chemical barrier may have ceased, possibly due to saturation by N. We may speculate that in these late stages, the influence of some other component may dominate lignin degradation.

In a transect study with locally collected Norway spruce needles, only some sites showed an increasing lignin concentration followed by a decreasing annual mass loss, thus reflecting the pattern described for pine (Berg et al. 2000). Lignin concentrations correlated negatively with litter decay rates for seven of 14 sites. For the seven other sites, no such lignin effect was seen. Thus, two groups of sites could be distinguished (see also transect no. 4 in Sect. 7.5). Berg et al. (2000) combined the data within the two groups of sites (Table 6.6). Group I sites had significant relationships between lignin concentration and annual litter mass loss. Group II sites showed no significant relationships between lignin concentration and mass loss. The litter of group I ($n = 55$) had a highly significant, negative relationship between annual mass loss and concentrations of lignin (Fig. 6.9A, Table 6.6). For group II ($n = 33$), only the relationship between mass loss and litter Mn concentration was significant

Table 6.6 Linear regressions for combined data of decomposing Norway spruce needle litter. Data are from a transect study with 14 sites (cf. Chap. 7). At seven sites, negative, significant relationships were seen between lignin concentration and annual mass loss. The data from these sites are combined into group I (n=55). Group II (n=33) represents sites at which no significant relationships were seen between lignin concentration and annual mass loss (Berg et al. 2000)

	Group I (sign. relationships)			Group II (non-sign. relationships)		
	R	R^2	$p<$	R	R^2	$p<$
Lignin	−0.775	0.600	0.001			n.s.[a]
Wsol	0.673	0.453	0.001			n.s.
N	−0.608	0.37	0.001			n.s.
P	−0.498	0.24	0.01			n.s.
K	0.330	0.109	0.05			n.s.
Mg	0.554	0.307	0.001			n.s.
Mn	0.316	0.100	0.1	0.526	0.277	0.01
Ca	0.281	0.079	0.1			n.s.

[a] *n.s.* Not significant, *Wsol* water-soluble substances

(R^2=0.277, $p<0.01$; Fig. 6.9B). For this group, there was no significant relationship between annual mass loss and concentrations of lignin, water solubles, N, P, K, Mg, or Ca (Table 6.6).

The effect of Mn becomes even more pronounced when combining all available data for annual mass loss of Norway spruce needle litter (first year excluded). The best linear relationship was obtained for annual mass loss vs. Mn concentration (R^2=0.356, n=95; Table 6.7). For the entire dataset, neither N nor lignin had a significant effect.

We have already discussed (Chap. 2) the effect of N (Eriksson et al. 1990) and Mn (Perez and Jeffries 1992; Hattakka 2001) on lignin degradation. Lignin decay, and therefore litter decomposition rates may be limited if one or more of the essential elements required for microbial degradation of lignin are lacking. Likewise, high concentrations of an element such as N could suppress the microbial degradation of lignin. Such nutrient interactions may be complex, but the composition and activity of the microbial community, including the lignin-degrading fungi, depend greatly on the concentrations of nutrient elements. It appears possible that the differing concentrations of Mn in litter could be dependent on site (soil) properties (Berg et al. 1995a).

Synthesis, spruce and pine species. Berg et al. (2007) used a set of decomposition data from Norway spruce, Scots pine, lodgepole pine, Aleppo pine, silver birch, and grey alder. All data were taken from litter that clearly was in a late stage of decomposition, viz. data for litter for the 2nd, 3rd, 4th, and 5th years of decomposition. In all, they used 136 values of which 32 were for Scots pine, 75 for Norway spruce, 16 for lodgepole pine, four for Aleppo pine, six for silver birch, and three for grey alder. They used the concentrations of nutrients and lignin at the

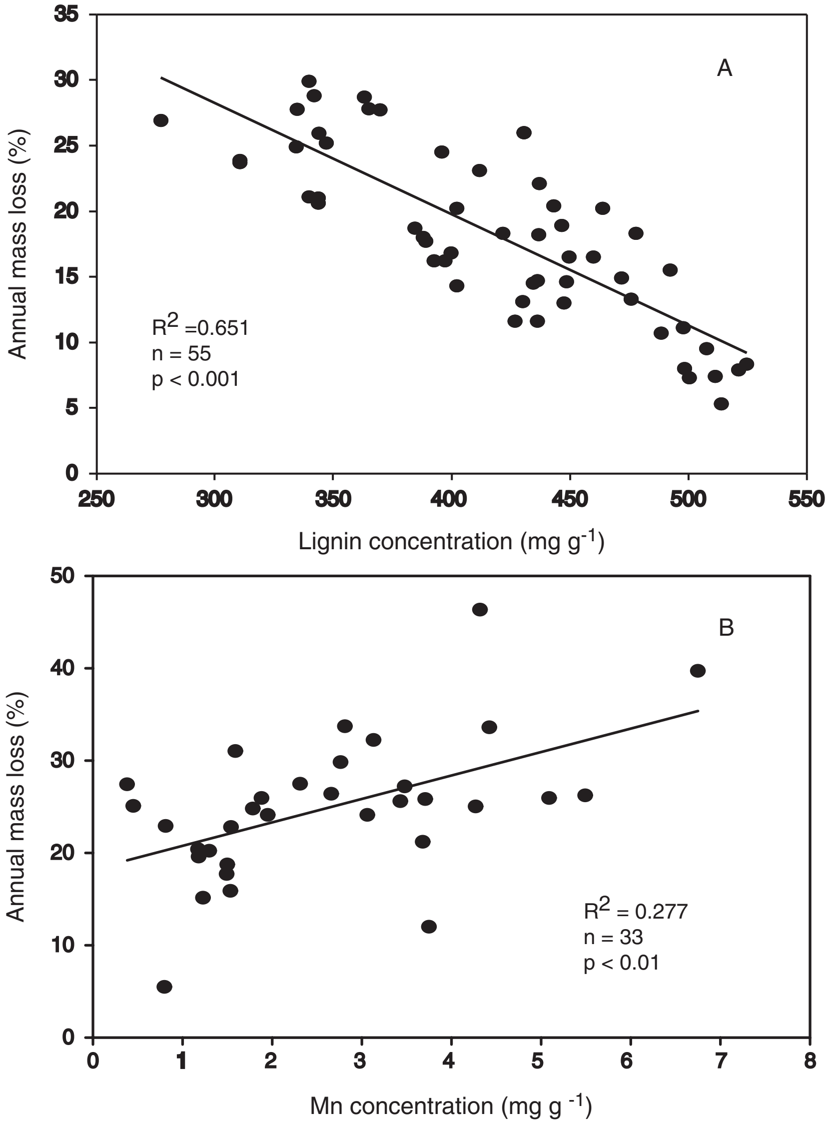

Fig. 6.9 Annual mass loss vs. substrate-quality factors at the start of each year for local Norway spruce needle litter in late decomposition stages incubated in 14 Norway spruce forests across Sweden. Lignin and Mn concentrations at the start of each 1-year period were related to the litter mass loss in the following 1-year period. **A** Annual mass loss vs. lignin concentration at those seven sites where negative linear relationships between lignin concentration and annual mass loss were recorded. **B** Annual mass loss vs. Mn concentration at those seven sites where no relationship between annual mass loss and lignin concentration was recorded (cf. Tables 6.6 and 7.9; from Berg et al. 2000)

Table 6.7 Linear relationships between all available data for annual mass loss of Norway spruce needle litter and concentrations of chemical components in the litter. The data covered all litter of a Norway spruce transect (Berg et al. 2000), and that from an experimental site, and included mass losses during the second through the fifth years. Concentrations of N and lignin did not have significant relationships (B. Berg, unpubl. data). *n*=95

Variable	R	R^2	$p<$
Mn	0.597	0.356	0.001
Mg	0.487	0.237	0.001
Wsol[a]	0.454	0.206	0.001
K	0.367	0.135	0.001
Ca	0.254	0.065	0.05
P	0.230	0.053	0.05
All components	0.712	0.507	0.001

[a] *Wsol* Water solubles

start of each 1-year period. The concentrations of Mn in litter at the start of such 1-year periods ranged from 0.04 to 7.69 mg g^{-1}, and for lignin from 277 to 509 mg g^{-1}, corresponding to range factors of 192 and 1.8, respectively.

Most of the litter had Mn concentrations below 2 mg g^{-1} (Fig. 6.10), and included mainly litter of pine species, birch, and alder. The main part of the litter with Mn concentrations above 2 mg g^{-1} came from Norway spruce.

In a first step they regressed all the annual mass-loss values to the litter lignin concentration, which resulted in a negative linear relationship ($R^2=0.210, p<0.001$). We may thus see that for all litter combined, a negative relationship was found between lignin concentrations and litter mass loss. In a second step, they regressed all annual mass-loss values to litter Mn concentration at the start of each year. All available data ($n=136$) gave a positive linear relationship ($R^2=0.151$, $p<0.001$; Fig. 6.10, Table 6.4). We may note that the data did not show a natural distribution, as most data points had an Mn concentration of less than 2.0 mg g^{-1}. A logarithmic transformation gave linear relationships with R^2 values of 0.201 and 0.150 for lignin and Mn concentrations, respectively, both highly significant. When combining Mn and lignin concentrations in a multiple regression, the relationship improved ($R^2=0.349, p<0.001$).

Berg et al. (2007) also made a subdivision of the whole dataset ($n=136$), and investigated the litter with Mn concentrations below and above 2 mg g^{-1} seperately. Using an Mn concentration interval of 0.04 to 2.0 mg g^{-1}, they could not find any relationship between litter Mn concentration and litter mass loss, despite a range factor of 50. When investigating data with Mn concentrations below 2 mg g^{-1} for relationships between lignin concentration and litter mass loss, they obtained a highly significant relationship ($R^2=0.410$, $n=81$, $p<0.001$).

By stepwise selecting a narrower interval in lignin concentrations, Berg et al. (2007) progressively obtained a litter substrate that was more decomposed. For all data, with lignin concentrations ranging from 277 to 509 mg g^{-1}, a significant relationship was found to litter lignin concentration ($p<0.001$), as well as to Mn concentration (Table 6.4). We may see (Table 6.4) that the narrower the lignin

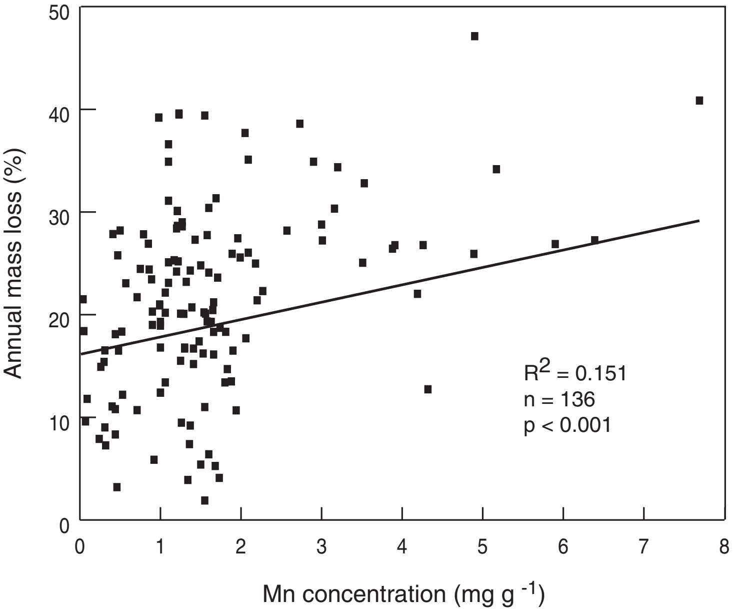

Fig. 6.10 All available data for annual mass loss of foliar litter in late stages were related to litter Mn concentration at the start of each year. Mass-loss data are for sites distributed over the whole of Sweden, plus another two sites in northern Libya (from Berg et al. 2007)

concentration interval was, the more the relationship to Mn improved (cf. R^2_{adj} increased). At a lignin concentration interval of 475 to 509 mg g^{-1}, the R^2 value for the relationship between litter mass loss and Mn concentrations was 0.457, whereas the relationship for the influence of lignin had become insignificant, likely due to the narrow concentration interval. This reduced dataset ($n=35$) encompassed nine values for Scots pine, one for lodgepole pine, 20 for Norway spruce, three for grey alder, and two for silver birch. They divided this dataset ($n=35$) into two main groups, one for Norway spruce litter (Mn concentration range from 0.31 to 7.69 mg g^{-1}), and one for the other litter types combined (Mn concentration range from 0.24 to 1.9 mg g^{-1}). For Norway spruce needle litter, the relationship between Mn concentration and annual mass loss gained an R^2 of 0.671 ($R^2_{adj}=0.653$) with $n=20$, and for the other, combined litter types, the R^2 was 0.109 ($R^2_{adj}=0.028$, $n=15$, n.s.). For this whole dataset ($n=35$) with lignin concentrations >475 mg g^{-1}, we may see that all data basically fit the linear relationship (Fig. 6.11). The main difference between the groups appears to be that the Norway spruce litter had a wider concentration interval with a range factor of 24.8, whereas that for the other litter types was considerably narrower with a range factor of 7.9.

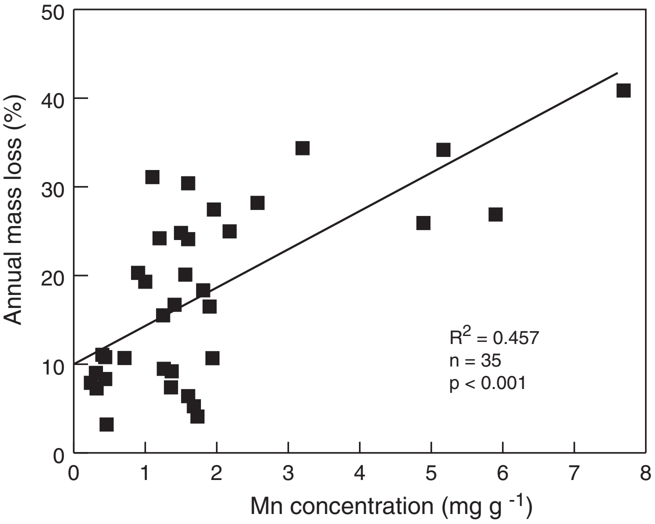

Fig. 6.11 Annual mass loss of foliar litter in late stages of decomposition, compared to litter Mn concentrations. The dataset was restricted to decomposition stages with lignin concentrations above 475 mg g^{-1}, including values for Norway spruce, lodgepole pine, Scots pine, grey alder, and silver birch (cf. Table 6.4; from Berg et al. 2007)

Lodgepole pine litter. A smaller dataset for lodgepole pine needle litter was investigated by Berg et al. (2007). When regressing litter mass loss vs. lignin concentrations, they obtained a negative linear relationship with $R^2=0.491$ and $p<0.05$. In a linear regression between Mn concentration (range 0.71–2.7 mg g^{-1}, range factor 3.8) and annual litter mass loss, they obtained a positive relationship with $R^2=0.290$, $n=10$, which was not significant. When lignin and Mn were combined in a linear regression, the R^2 increased to 0.726 ($p<0.01$). The two stands where this litter was incubated were very similar, and had monocultures of lodgepole pine.

Scots pine needle litter. When using a set of data for decomposing Scots pine, a highly significant and negative relationship to lignin concentrations was found ($R^2=0.436$, $n=32$, $p<0.001$). A regression between mass loss and Mn concentrations with a range of 0.5 to 1.9 mg g^{-1} showed no evident relationship ($R^2=0.087$, $n=32$, n.s.).

It is possible that the suggested complex "mechanism" for Mn as a coenzyme (cf. Chap. 3) is not reflected only by its concentration, as a concentration range factor for lodgepole pine litter of 3.8 was wide enough to give a significant effect (Berg et al. 2007), whereas factors of 7.9 for Scots pine and 32 for a mixture of different litter types were not wide enough in terms of range in concentrations. The full range of Mn concentrations for newly shed litter varied by a factor of 96 (cf. above).

6.2.3 *Litter at a Humus-Near or Limit-Value Stage*

General Comments

Limit values for decomposition may be calculated for many litter species, provided that decomposition has been followed far enough through the decay process (cf. Chap. 2). After an inventory of existing decomposition studies, Berg et al. (1997) and Berg (2000b) published a total of 128 limit values, of which 106 originated from forest sites that were natural, and not from manipulated sites. When calculating values for different litter types, the limit values were found to differ (Howard and Howard 1974; Berg and Ekbohm 1991). Berg et al. (1996b) found that limit values were related negatively to initial litter N concentrations, and positively to initial Mn concentrations. They presented the hypothesis that the amount of litter remaining at the limit value was regulated by lignin remains that had become recalcitrant, due to complexation of low-molecular-weight N compounds that was in turn enhanced by the raised litter N levels. The relationships were empirical, and suggestions for causal relationships included factors that influence lignin degradation, and modify lignin structure. These were attempts to build a theory about the nature of the recalcitrant remains. Currently, we can state that the empirical relationships have been found to be more general, and the recalcitrance of the remaining litter has been validated, but still there is no clear theory. In a search for possible factors regulating the limit value, relationships have been found with litter concentrations of N, Mn, Ca, and lignin, all of which have a potential causality. Reviews containing increasing numbers of limit values have been published (Berg et al. 1996b, 1997; Berg 2000b), and the main patterns observed have been repeatedly confirmed.

General Relationships

Higher N levels in the litter give lower limit values and lower rates of decomposition. When the existing 106 limit values for foliar litter decomposing in natural systems were regressed against concentrations of nutrients and lignin, it was seen that N concentration showed a highly significant, negative relationship (Fig. 6.12, Table 6.8). The possible reasons for the relationships between limit values and N have been discussed in Chapter 2. The relationship using all available data from natural systems was negative ($R^2=0.323$, $n=106$, $p<0.001$), implying that the higher the initial concentration of N, the lower the limit value, with a smaller proportion of the litter being decomposed. Behind this observation may be a causal relationship that is valid both for litter in late decomposition stages and for humus. The discussion that was applied to "litter in late stages" (cf. Chap. 2) may also be used in this case. After further inventories, 128 limit values have been estimated (Berg 1998a, b), and combined still show a highly significant relationship to initial N levels.

The fact that, in this large dataset, the relationship to N concentration was significant indicates a general effect of N over an appreciable number of species in

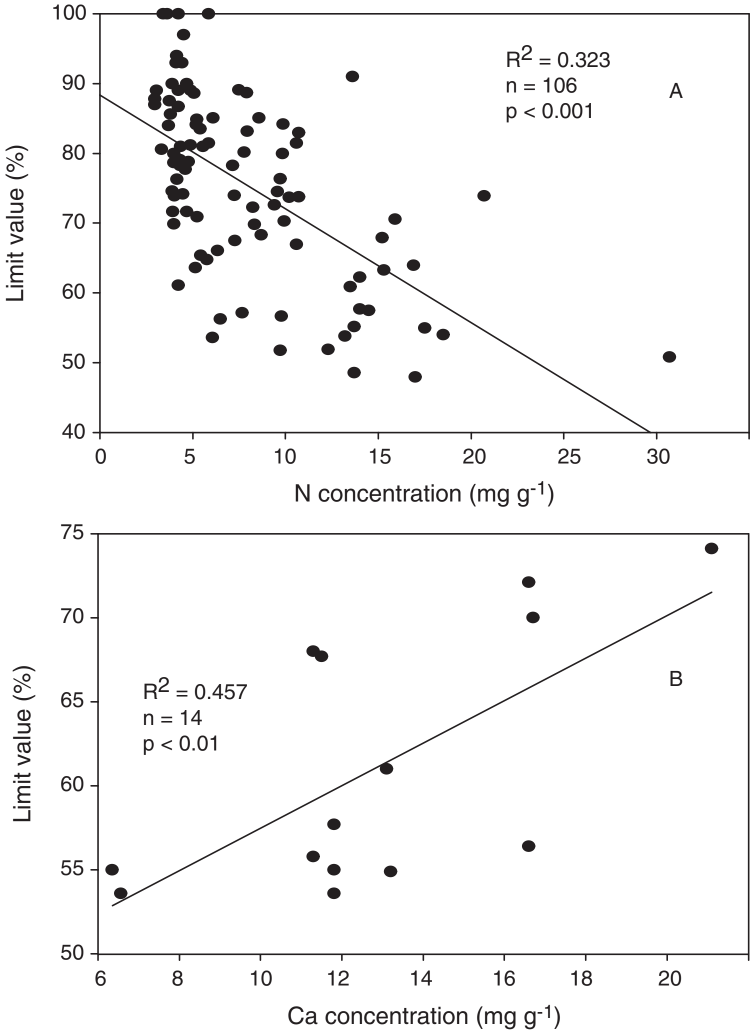

Fig. 6.12 Linear relationships between limit values for decomposition, and initial concentrations of N and Ca in foliar litter. **A** Available data from natural forest systems vs. litter N concentration (Berg 2000b). **B** Available data from Norway spruce forests vs. litter Ca concentration (Berg 2000a)

deciduous and coniferous ecosystems in boreal and temperate forests. In addition, initial litter N concentrations ranged from 0.3 to 3.0%. Although significant, the R^2 value was still low (0.324) when including all 128 limit values. This probably depends on the fact that, in this broadly based dataset, there are several factors potentially influencing the limit values, which presumably increased the variability of the data. Since data were collected for different forest ecosystems, with litter being incubated on soils with different properties and in different climate zones, this is not surprising. In the large dataset, several species were represented, and Berg (2000b) calculated the average limit value for the eight dominant species, and compared this to their average N concentration (cf. Fig. 11.3, Table 11.5). Analysis of this subset of data showed a clearer relationship between initial N levels and limit values. The litters in the complete dataset were often significantly different in terms of both N level and limit value (see also Chap. 11). As different forest humus systems have different levels of nutrients, this may be expected. The large difference between two such systems is illustrated in Table 11.4, namely, a Scots pine system with a humus N level of 11.8 mg g^{-1}, and a silver fir system with an N level of 38.2 mg g^{-1}, and a generally higher level of other nutrients. With such differences, the soil microorganism populations would have adapted to the different nutrient levels.

Higher Mn values are related to higher limit values. When the relationship between limit values and initial Mn concentrations of the litters was investigated, Berg et al. (1996b) showed a clearly significant, positive relationship ($R^2=0.529$, $n=17$, $p<0.001$; cf. Chap. 2) for natural, undisturbed systems. With 83 limit values, litter Mn concentrations gave a highly significant, positive relationship ($R^2=0.269$, Table 6.8). For selected groups of litter such as deciduous ($n=13$) and coniferous ($n=74$), positive relationships were seen between Mn and limit values, with $R^2=0.382$ and 0.263, respectively. In addition, for Scots pine needle litter

Table 6.8 Correlations between limit values, and initial concentrations in litter of N, P, S, K, Mg, Mn, Ca, and lignin. With data from all sites pooled, the extent of available chemical analyses determined the amount of data in the statistical analysis of each nutrient (different *n* values; Berg and Johansson 1998)

Nutrient/litter group	R	R^2	*n*	*p*<
Natural systems – all data				
N	−0.568	0.323	106	0.001
Mn	0.519	0.269	83	0.001
All deciduous litter				
N	−0.438	0.192	30	0.05
Mn	0.618	0.382	13	0.05
Ca	0.675	0.456	18	0.01
All coniferous litter				
N	−0.660	0.436	86	0.001
Mn	0.513	0.263	74	0.001
Scots pine needle litter alone				
N	−0.683	0.466	42	0.001
Mn	0.485	0.235	35	0.01
Norway spruce needle litter				
Lignin	−0.742	0.551	11	0.01
Ca	0.636	0.404	11	0.05

alone, a significant relationship was seen (R^2=0.235), whereas limit values for spruce needles did not have any significant relationship to Mn (Table 6.8).

Higher lignin values are related to lower limit values. Using all available limit values, Berg et al. (1997) noted a negative relationship to initial lignin concentrations in litter. Such a relationship may be expected, as lignin appears to be an important component in the nucleus of the recalcitrant part. When all litter types were investigated, the relationship was weak, with an R^2 value of 0.044 for 112 measurements, whereas for individual litter types, e.g., spruce litter, the relationships were stronger (R^2=0.551 in this case; Table 6.8). The relationship between lignin concentration and limit values is not necessarily a simple one; although lignins may strongly influence limit values, this role is influenced by variables such as N, and Mn.

Heavy metals. A very N-rich system could be expected to have a higher percentage of lignin-degrading organisms that are not sensitive to N (cf. Chap. 3). This could mean that the limit values are less strictly controlled (or not at all) by the concentration of N, while other factors such as the levels of heavy metals may be more important. Heavy metals have been measured, and relationships noted in data originating from two very contrasting sites (Berg et al. 2003). No clear global relationships were apparent from these studies, but negative relationships between limit values and litter Cd and Zn concentrations were evident at a moderate level of significance (p<0.1).

Nutrient and heavy metal concentrations as indicators. The fact that significant relationships exist between limit values and initial concentrations of N and Mn suggests a rate-regulating mechanism. However, until a causal mechanism is demonstrated, the effects of initial concentrations of these elements should be viewed as empirical indices only.

These indices should be regarded in different ways. For a nutrient such as N, concentrations increase linearly with accumulated mass loss, and mainly proportionally to the initial concentration (see Chap. 5; Berg et al. 1999b). Thus, the use of initial N concentration as an index should not cause any problem. Similar reasoning may be applied for some heavy metals. For heavy metals such as Cu, Pb, and Fe, the concentrations in later stages reflect the initial ones, as their concentrations increase (cf. Chap. 5). However, for some nutrients and heavy metals, Mn being an example, mobility is pH-dependent. With these elements, an increase does not normally take place during decomposition, and it remains to be determined how we should interpret the relationship between limit values and their concentrations. Although new findings have been reported in the domain of regulation of enzymatic activity by Mn, these studies have not yet led to a clear understanding of the effects of Mn in more complicated litter and soil systems.

Groups of Litter Species have Different Empirical Relationships

The observed relationships between N and Mn concentrations, and limit values were also seen for selected groups of litters (Berg et al. 1996b, 1997). Berg and Johansson

(1998) made a first subdivision into coniferous and deciduous litter types. However, such an approach disregards the effects of site quality (cf. below).

The coniferous litters as a group gave a highly significant relationship between limit values and litter N concentrations ($R^2 = 0.436$, $n = 86$, $p < 0.001$; Table 6.8), as did Mn ($R^2 = 0.263$, $n = 74$). Berg (1998a) also found enough studies using Scots pine to allow a special investigation of the factors regulating the limit value for that specific litter species; there was a highly significant, negative relationship between N concentrations and limit values ($R^2 = 0.466$, $n = 42$, $p < 0.001$). Needle litter from fertilized trees with raised levels of N and other nutrients showed the same general pattern, the best relationship being to N. Manganese, Ca, and lignin gave significant relationships as well.

For Norway spruce needles from undisturbed systems, a highly significant, negative relationship was found between limit values and the concentrations of lignin ($R^2 = 0.551$, $n = 11$, $p < 0.01$; Table 6.8), and Ca in litter. However, there was no relationship to either N or Mn concentrations. When investigating spruce needle litter from N-fertilized plots, Berg (2000a) found relationships between both litter Ca and Mn concentrations, and limit values. Davey et al. (2007) reported that limit values for leaf litter of common oak were best related to initial Ca concentrations. We may speculate that the groups suggested above (e.g., Table 6.1) would be applicable to the limit-value stage. These two litter species thus would belong to case C.

For deciduous litter as a separate group, the limit values were positively related to litter concentrations of Mn ($R^2 = 0.382$, $n = 13$, $p < 0.05$), and Ca ($R^2 = 0.456$, $n = 18$, $p < 0.01$; Table 6.8).

Do limit values indicate a stable fraction? Can we describe the properties of the recalcitrant remains? Do limit values indicate a more or less complete halt in the litter decomposition process? Although limit values for litter mass loss have been estimated for a variety of litters by using asymptotic functions, we cannot conclude that such limit values indicate that the remaining organic matter is completely recalcitrant to degradation by biological agents (see below). Rather, the residual organic matter could very well consist of a moderately stabilized fraction that decomposes very slowly, or a fraction that simply does not decompose in a given environment, whereas a changed environment, or a disturbance could facilitate further degradation. However, this would not mean that the discovery of an apparent final mass-loss value should be considered trivial, especially if the limit value can be related to climate and litter properties, such as lignin concentration, nutrient status, or other environmental factors.

Couteaux et al. (1998) applied both a three-factorial model (Chap. 10) and a limit-value function to direct CO_2 measurements of decomposing Scots pine needle litter close to the limit value, and to the humus formed in the same stands. They measured k values for decomposition of a stable fraction in the magnitude of 0.0001 to 0.00001% per day. These k values correspond to a decomposition rate of about 1% per 30 and 300 years, respectively. That study included an analysis of stable, meta-stable, and labile components (cf. Table 11.7), where the stable fraction comprised ca. 80% of the material, and may be considered as rate-limiting.

The estimated limit values may thus illustrate a fraction that is highly stabilized, and thus decomposes at a very low rate. Even if this should be the case, the limit-value concept is no less useful, especially if we can link this recalcitrance in litter to its chemical properties – for example, to the initial concentrations of lignin or some nutrient – or possibly to climate (cf. Chap. 11).

6.3 Does Chemical Composition Influence Leaching of Compounds from Humus?

In the literature, observations indicate the existence of a disintegration or decomposition mechanism for humus that appears to be initiated by high acid or high N loads in the soil system. Very high N loads – for example, from atmospheric N deposition – appear to promote a disintegration of humus, probably as a consequence of strongly increased microbial activity. This theory was forwarded by Fog in 1988. He suggested that a higher concentration of N in litter/humus would result in an increased production of soluble organic matter (DOM, or DOC). His ideas were based on the functioning of that group of lignin-degrading organisms that are called “soft-rots” (cf. Chap. 3). Worrall and Wang (1991) briefly reviewed the literature, and added their own observations to show that at least some soft-rot fungi need high levels of N in their surroundings in order to carry out decomposition. Therefore, in an N-rich environment they can, to a certain extent, replace white-rot organisms. Soft-rot degradation of lignin yields remains of incompletely degraded lignin that react with organic N compounds, a reaction that leads to water-soluble products. Fog’s (1988) conclusion was that high N concentrations increase the formation of water-soluble compounds, resistant to degradation, but decrease the amount of humus that is formed, as might occur in a mor layer. Ulrich (1981) has described a similar process, calling it a “disintegration of humus”. David et al. (1989) reported higher concentrations of soluble organic matter with increasing acidity.

Guggenberger (1994) concluded that the mobilization of DOC is not ruled exclusively by a low pH. On the contrary, he makes the reasonable conclusion that high inflows of total N suppress the complete lignin degradation carried out by white-rot organisms, but increases the general microbial activity. He supports the conclusion by Fog (1988) that the more N-tolerant soft-rot fungi produce partial degradation products that are more water-soluble, especially the N-containing compounds. He also proposes that a generally higher microbial activity will give a greater production of microbial metabolites.

We may compare this to the isolation of N-tolerant white-rot fungi (cf. Chap. 3) from N-rich surroundings, and conclude that the phenomenon described by Guggenberger (1994) and Fog (1988) could be due simply to a wider spectrum of fungal species. The common property among these fungi could be a tolerance of high N levels. Connected to the above observations is a comparison of amounts of humus in mineral soil under Douglas-fir and red alder. Cole et al. (1995) found that in the more N-rich alder stand, greater amounts of C compounds were leached into the mineral soil from the humus layer. While it is difficult to base wider conclusions on this study alone, the observation that an N supply in a naturally richer environment is part of a mechanism for the formation of DOC that subsequently precipitates in the mineral soil does fit Fog's (1988) hypothesis.

Chapter 7
Climatic Environment

7.1 Introduction

Climate has a dominant effect on litter decomposition rates on a regional scale, whereas litter quality dominates on a local level (Meentemeyer 1984). Thus, at a given site and climate, one should expect differences in mass-loss rates of litters to be related primarily to their chemical and physical properties. Many studies have demonstrated such relationships (Fogel and Cromack 1977; Aber and Melillo 1982; Upadhyay and Singh 1985; McClaugherty et al. 1985; Dyer 1986). As the decay of litter progresses through time, the constituents that regulate the rate of mass loss can change. Berg and Staaf (1980a) presented a schematic model of these litter decay stages, later modified by Berg and Matzner (1997; cf. Chap. 6). Thus, early-stage decomposition is controlled primarily by concentrations of limiting main nutrients, especially N and P, whereas lignin decomposition exerts the dominant control in the later stages. The delivery of heat and moisture to the litter will exert a control over the rate at which the decay phases postulated by Berg and Staaf (1980a) can proceed. Thus, in one climatic regime, the early, nutrient-controlled phase could persist, while in other regimes this phase could be quickly passed (Dyer et al. 1990).

Analyses of decay dynamics have been conducted using widely different litter types, at sites in different climatic regimes and in different forest types. Thus, when considering the regulation of decomposition, it is difficult to separate the influence of climate from the influence of litter quality. With increasing emphasis on understanding the impact of climate changes on the broad-scale patterns of biological processes, we need to expand our consideration of the decomposition processes from substrate- and site-specific studies to a broader, regional context. At this larger geographic scale, our attention must turn to climate.

In this chapter, we have focused on litter decomposition in stands with monocultures, and use results from five main climatic transects with either Norway spruce, or solely Scots pine, or a mixture of Scots pine and other pine species. We suggest that the results are sufficiently contrasting to illustrate that different patterns should be expected among species along climatic transects.

B. Berg and C. McClaugherty, *Plant Litter*,

7.2 Microbial Response to Temperature and Moisture

The soil microbial community encompasses several hundred species in the soil of a particular stand (Torsvik et al. 1990; Bakken 1997). The microbial community has a rich adaptability to both different moisture and temperature regimes (cf. Chap. 3), but both moisture and temperature can be limiting. Unless there is enough moisture, often above about 10% water-holding capacity, water may be so limiting that raising temperatures would not result in higher microbial activity. Likewise, in an energy-limited system, such as at low temperatures, higher moisture would not necessarily result in higher activity.

The microbial response to temperature should be regarded as the sum of responses from the entire microbial community. Those bacteria and fungi having their temperature optima at, say, 15 °C are less active at 10 °C, and nearly inactive closer to freezing point. However, at zero °C and even below, psychrophilic organisms carry out a clear heterotrophic activity. These organisms belong to species completely different than those active at higher temperatures. In systems in cold climates, the microorganisms would thus be adapted to the prevailing climatic conditions.

A microbial response to variability in climate would thus be dependent on the availability of both nutrients and carbon sources (see review by Panikov 1999). A lack of an essential nutrient, or available carbon source relative to the needs of the microbial population would result in a lack of response to a variation in climate. In situations where substrate quality poses a severe limitation on decomposition, changes in climate can have relatively little effect on decomposition rates.

7.3 Early-Stage Decomposition of Scots Pine Needle Litter

7.3.1 Decomposition at one Site

Within a single site, there is a clear variation in litter decomposition rates among years that may be due to fluctuations in weather**.** When Scots pine needle litter was incubated at its own site, the first-year mass loss (as determined over 19 measurements) ranged from 21.1 to 33.8% (Fig. 7.1), giving a range factor of 1.6. There was no difference in annual mass loss between litter samples incubated in the spring and in late autumn immediately after litter fall. Average values for both sets were close to the general average value of 27.8% year^{-1} mass loss.

However, there are differences in decomposition rates between periods of the year that are determined by temperature and rainfall patterns, and intensity. A model was constructed that related soil water and temperature quite well to litter mass loss (Jansson and Berg 1985; Table 7.1), with R^2 values ranging between 0.85 and 0.99, indicating that the annual variation in climate may dominate the annual

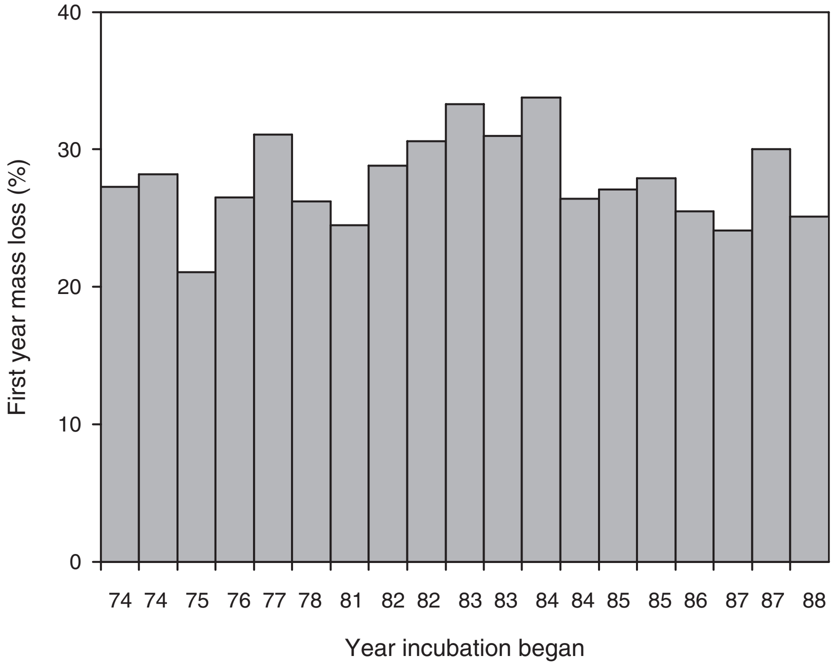

Fig. 7.1 First-year mass loss from Scots pine needle litter incubated in an 120- to 150-year-old Scots pine forest at the former site of the Swedish Coniferous Forest Project (SWECON) at Jädraås, Sweden. The first incubation was made in 1974, and the latest in 1988. In some years, incubations were made in both spring and autumn (B. Berg, unpubl. data; B. Andersson, unpubl. data)

variation in mass loss. The model calculated soil climate on a daily basis. When soil water and soil temperature were combined into a single factor, this had clearly superior predictive power as compared to either of the single factors alone (Table 7.1). The model predicted a soil climate over a period of 6 years that included a large variety of weather patterns. Thus, soil moisture and temperature also exhibited large variability. Two summers were characterized as warm with extended drought periods, whereas the other summers were moist. The variations in soil temperature were much more pronounced between different winters than between summers. Of the winters, three had soil temperatures well below zero °C, which also caused high water tension in the soil. The other winters were both moister and warmer, mainly because of thicker snow packs, which prevented the soil from becoming completely frozen. Under these conditions, the soil water never froze, which implies that decomposition was possible under the snow cover. In fact, for one particular 1-year period, the main part of the decomposition took place during the winter. As indicated earlier, the initial chemical composition was variable (cf. Table 4.4), but the model, based on climate, explained decomposition quite well.

Table 7.1 Coefficients of determination (R^2) obtained from correlations between observed decomposition rates and different soil climate estimates as independent variables. Scots pine needle litter was used and incubated annually at its own site (Jansson and Berg 1985)

	Year of incubation		
Independent variable	First	Second	Both
Actual evapotranspiration (AET)	0.41	0.74	0.55
Soil temperature	0.37	0.77	0.52
Soil water tension	0.78	0.97	0.81
Soil water content	0.68	0.96	0.77
Soil temp. and water tension	0.90	0.98	0.89
Soil temp. and water content	0.85	0.99	0.87

7.3.2 Decomposition Along Transects

We will review several major studies on decomposition along different climatic transects in northern Europe. Five of the studies investigated needle litters, and one investigated root litter.

- Transect 1 with Scots pine, located mainly on glacial till in which local Scots pine needle litter was incubated once or twice. Twenty-two stands/sites were located between 66°08′N, near the Arctic Circle, and 55°39′N, at about the latitude of Copenhagen in southern Scandinavia (Table 7.2).
- Transect 2 with Scots pine on sediment soil, in which unified Scots pine needle litter was incubated annually for periods lasting from 6 to 19 years. The transect had 13 sites between northernmost Finland (69°45′) and central Holland (52°02′N). This transect had highly standardized sites with nutrient-poor Scots pine stands on sandy sediments, and thus on flat ground. At each of these sites, however, a special set of experimental litter was incubated.
- Transect 3 was composed of pine forests located mainly on sediment soils in which unified Scots pine needle litter was incubated. Transect 1 was included, and sites with stands of Austrian pine, Corsican pine, stone pine, maritime pine, and Monterey pine. This transect included 39 sites ranging across Europe from northernmost Finland (69°45′N) to southernmost Spain at (38°07′N), and southernmost Italy (39°24′N).
- Transect 4 with Norway spruce stands located on glacial till in which local litter was incubated once. Fourteen sites were used, located between 66°22′N, close to the Arctic Circle in Scandinavia, and 56°26′N in southernmost Sweden.
- Transect 5 with Scots pine. This transect had sites along a west-to-east gradient of continentality. Sites were located between 52° and 53°N, and from Berlin in the west (12°25′E) to the Russian/White Russian border in the east (32°37′E).
- A transect with root litter in a northeast-to-southwest orientation, which included 25 stands with Scots pine and lodgepole pine, and 12 stands with Norway spruce. The sites ranged from near the Arctic Circle in Scandinavia to Berlin (52°28′N; see Sect. 7.6).

Table 7.2 Calculated slope coefficients for the relationship between annual mass loss and increasing lignin concentration in litter at the start of each 1-year period (cf. Figs. 2.8, 7.6; *n.s.* not significant). Data are taken from a transect with local Scots pine needle litter incubated at sites extending from the Arctic Circle in Scandinavia, to Lüneburger Heide ca. 100 km south of Hamburg, Germany (Johansson et al. 1995)

Site	Slope	SE	R^2	R	*n*	*p*<
2 Harads	–0.0231	0.0144	0.076	–0.276	33	n.s.
3:1 Manjärv	–0.0216	0.0421	0.036	–0.189	7	n.s.
3:2 Manjärv	–0.060	0.0597	0.173	–0.416	9	n.s.
3:3 Manjärv	–0.132	0.0209	0.278	–0.527	8	0.05
4:23 Norrliden	–0.0815	0.0217	0.453	–0.673	19	0.01
6:51 Jädraås	–0.0734	0.0240	0.227	–0.476	34	0.01
17:2 Kappsjön	–0.1751	0.0473	0.774	–0.880	6	0.05
18:2 Anundberget	–0.1874	0.0551	0.794	–0.891	5	0.05
103:1 Tomta	–0.045	0.0593	0.055	–0.235	12	n.s.
102:1 Kungs-Husby[a]	–0.107	0.0353	0.568	–0.754	9	0.05
105:1 Remningstorp[a]	–0.166	0.043	0.65	–0.806	10	0.01
101:1 Grensholm[a]	–0.148	0.0518	0.577	–0.760	8	0.05
107 Sänksjön[a]	–0.166	0.043	0.65	–0.806	8	0.01
8 Nennesmo	–0.230	0.0516	0.665	–0.815	12	0.01
10:1 Mästocka	–0.228	0.0533	0.901	–0.949	4	n.s.
13 Ehrhorn	–0.250	0.0334	0.846	–0.920	12	0.001

[a] Set contains some data from N-enriched litter

The decomposition data from transects 1–5, and that for root litter were related to both climate and substrate-quality data, the former calculated according to Meentemeyer (1978). The climate indices are listed in Table 7.3 with their acronyms along with acronyms for substrate quality.

Scots Pine Monocultures

Local litter. When investigating the data of transect 1 ranging over Scandinavia, Johansson et al. (1995) determined the effect of climate and litter-quality variables on mass-loss rates. They used long-term average climatic values when relating first-year mass loss to climate variation (Table 7.4), and found that average annual temperature (AVGT) gave the best fit, with an R^2_{adj} value of 0.518. Annual actual evapotranspiration (AET) gave almost as good a fit, with an R^2_{adj} of 0.505. Potential evapotranspiration and average temperature in July were also significantly related to mass loss, but annual precipitation, water surplus, and water deficit did not give any significant relationships. AET had previously been distinguished as a superior climate index at broad, continental scales (Meentemeyer 1978, 1984; Berg et al. 1993a, b). As the R^2_{adj} value for AET was close to that obtained using annual average temperature, Johansson et al. (1995) used this as a basis for further analysis.

On this scale, they found no relationships between first-year mass loss and initial concentrations of water solubles, N, P, and lignin. None of these factors was

Table 7.3 Climate and substrate-quality variables against which litter mass loss was regressed in studies of litter decomposition along transects (transects nos. 1–4, and transect with root litter). The climate variables were calculated according to Thornthwaite and Mather (1957), and Meentemeyer (1978). For convenience, these acronyms are used in this chapter

Acronym	Description of variable
LOSS	Annual mass loss of litter (%) either as first-year or as annual mass loss in later decomposition stages
Climate variables	
JULT	Average temperature for July (°C)
AVGT	Average annual temperature (°C)
PRECIP	Total annual precipitation (mm)
PET	Potential annual evapotranspiration (mm)
AET	Actual annual evapotranspiration (mm)
SUR	Soil moisture surplus (mm)
DEF	Soil moisture deficit (mm)
Substrate-quality variables	
WSOL	Concentration of water solubles at the start of each year (mg g^{-1})
LIGN	Lignin concentration, initial or at the start of each year (mg g^{-1})
NITR	Nitrogen concentration, initial or at the start of each year (mg g^{-1})
PHOS	Phosphorus concentration, initial or at the start of each year (mg g^{-1})
POTA	Potassium concentration, initial or at the start of each year (mg g^{-1})
CALC	Calcium concentration, initial or at the start of each year (mg g^{-1})
MAGN	Magnesium concentration, initial or at the start of each year (mg g^{-1})
MESE	Manganese concentration, initial or at the start of each year (mg g^{-1})

Table 7.4 Linear relationships between first-year litter mass loss, and climate factors along a climatic transect from the Arctic Circle in Scandinavia (northeast) to the latitude of Copenhagen in the southwest (transect 1). Local Scots pine needle litter was incubated at 22 stands/sites. All climate and substrate-quality variables listed in Table 7.3 were tested ($n=28$; Johansson et al. 1995)

Climate factor	Slope (SE)[a]	Intercept (SE)	R^2_{adj}	$p<$
AVGT	2.729 (0.498)	20.869 (5.812)	0.518	0.001
AET	0.134 (0.025)	−30.162 (5.890)	0.505	0.001
PET	0.143 (0.027)	−37.522 (5.955)	0.493	0.001
JULT	3.871 (1.787)	−28.6645 (7.856)	0.120	0.05

[a] *SE* Standard error, R^2_{adj} adjusted for different degrees of freedom between comparisons

significant, probably because the variation in climate across the 28 sites outweighed the control by substrate quality. Thus, for this litter type, the first-year mass loss supports the traditional image.

Unified litter. In a more specific approach, a set of sites with numerous observations was investigated. This set of 13 sites in Scandinavia and the northwestern part of continental Europe had mass-loss measurements over a period of between 6 and 19 years (transect 2). Of the individual climate factors, AET gave a highly significant relationship ($R^2_{adj}=0.867$, $p<0.001$; Table 7.5). It is likely that the multiple years of observations gave an average calculated mass-loss rate more representative of the climatic norms used in this study, compared to the one-time incubation in

Table 7.5 Coefficients of determination for linear correlations between first-year mass loss of unified Scots pine needle litter and selected climatic factors, as well as some substrate-quality factors. Sites, from transects 2 and 3, were grouped and investigated separately as well as in combinations of groups. All correlations presented here are significant at $p<0.001$. For acronyms, see Table 7.3 (Berg et al. 1993a)

Independent variables	R^2	R^2_{adj}	Types of pine stands in transect
Scandinavian–northwestern European sites ($n=13$)			
AET	0.878	0.867	Scots only
AET, NITR	0.895	0.885	
Scandinavian–continental Europe north of the Alps and the Carpathians ($n=23$)			
AET	0.647	0.630	Scots only
AET, WSOL	0.748	0.736	
Scandinavian–northwestern European sites plus Atlantic sites ($n=22$)			
AET	0.916	0.912	Scots, Austrian, Monterey, and maritime
Mediterranean plus central European and North American sites ($n=17$)			
AET	0.753	0.736	Scots, stone, Monterey, and red
AET, WSOL	0.766	0.750	
AET, JULT	0.761	0.745	

transect 1. Part of this transect (ten sites) was placed in standardized Scots pine forests on level ground in nutrient-poor sediment soils. This part of the transect gave a fit to AET at the same level as that of all the 13 sites ($R^2_{adj}=0.866$, $n=10$, $p<0.001$).

Substrate-quality factors alone did not give any significant relationships, but the inclusion of NITR or WSOL as a substrate-quality index improved the relationship somewhat; for AET plus NITR, an R^2_{adj} value of 0.885 was obtained (Table 7.5). The addition of other climatic factors added very little to explain the observed variation. This part of the world's boreal forests is energy-limited (Berg and Meentemeyer 2002), and the relationships may be improved by selected temperature functions.

Monocultural Pine Stands of Different Species

All sites. Using 39 pine sites (transect 3), Berg et al. (1993a, b) incubated needle litter samples in regions with AET ranging from ca. 330 to 950 mm, and with a highly standardized site selection and design. The sites ranged over differing climates across western Europe, from boreal northernmost Finland to southern Spain, and the contrasting subtropical southern Georgia (USA). Unified litter was incubated two or three times a year at the different sites. First-year mass loss ranged from about 10% at the northernmost boreal site to 56% at the subtropical one.

The best positive correlations were obtained for the relationship between first-year mass loss and AET ($R^2=0.509$), and the total annual precipitation (PRECIP, $R^2=0.323$), both with $p<0.001$, and average temperature (AVGT, $R^2=0.203$, $p<0.05$).

Table 7.6 First-year mass loss of unified Scots pine needle litter in 39 pine forests (transect 3) as a function of some single climatic factors as well as multiple ones. A broad regional scale was used across Europe, from an Arctic site close to the Barents Sea to southern Spain and southern Italy, and the data included subtropical sites in southern Georgia, USA (for acronyms, see Table 7.3; Berg et al. 1993a)

Independent variables	R^2	R^2_{adj}	*p*	Comments
AET	0.509	0.496	<0.001	
PRECIP	0.323	0.304	<0.001	
AVGT	0.203	0.181	<0.01	
PET	0.187	0.165	<0.05	
DEF	0.097	0.073	<0.05	DEF gave a negative relationship
AET, JULT	0.689	0.681	<0.001	JULT gave a negative relationship
AET, JULT, AVGT	0.716	0.708	<0.001	JULT gave a negative relationship

Of the other climatic variables, water deficit (DEF) also gave a weak, but significant correlation (Table 7.6).

First-year mass loss was plotted against the best single variable (AET) using all sites (Fig. 7.2). The progression in rates from the Arctic to the subtropical sites is readily apparent. Some of the scatter can be attributed to the use of long-term climatic means, rather than information about the weather during incubation. For example, the Georgia sites should have had higher rates of mass loss in normal years than those that were observed, because incubation occurred in an extremely dry year. Some of the variation must also have been caused by variations among local site conditions and litter quality. Although the litter originated from the same site (unified litter), there were some differences in chemical composition among years. The N concentration in the incubated litter ranged from 3.4 to 4.1, P from 0.19 to 0.21, S from 0.32 to 0.38, and Ca from 2.3 to 7.1 mg g^{-1} (cf. Table 4.4).

Atlantic climate sites. This climate, with rainy summers and moderate winters, encompasses all Scandinavian–northwestern European sites. The 13 highly standardized sites in the long-term Scandinavian transect (transect 2), the sites of transect 3 with an Atlantic climate ($n=7$), and data from two eastern Finnish sites had similar relationships between mass loss and AET (Fig. 7.3). All of these sites had low water deficit, with the exception of one that was located very close to the coast. With these similar responses, the 22 decomposition values were combined for an analysis vs. climate. Comparing AET and first-year mass loss gave a very good fit ($R^2_{adj}=0.912$; Fig. 7.3A). This relationship was not improved by the addition of other climatic factors or substrate quality.

Sites with warm, dry summer climate. The relationships obtained for the Atlantic climate sites were significantly different from those for Mediterranean and inland sites. Although AET had similar ranges for the two climate types, the pattern and temporal distribution of temperature and precipitation were of importance. Combining the mass-loss values for the sites characterized by dry and warm summers resulted in a set of sites encompassing those with a Mediterranean climate, and those in central Europe and in the American Midwest. A linear regression of mass

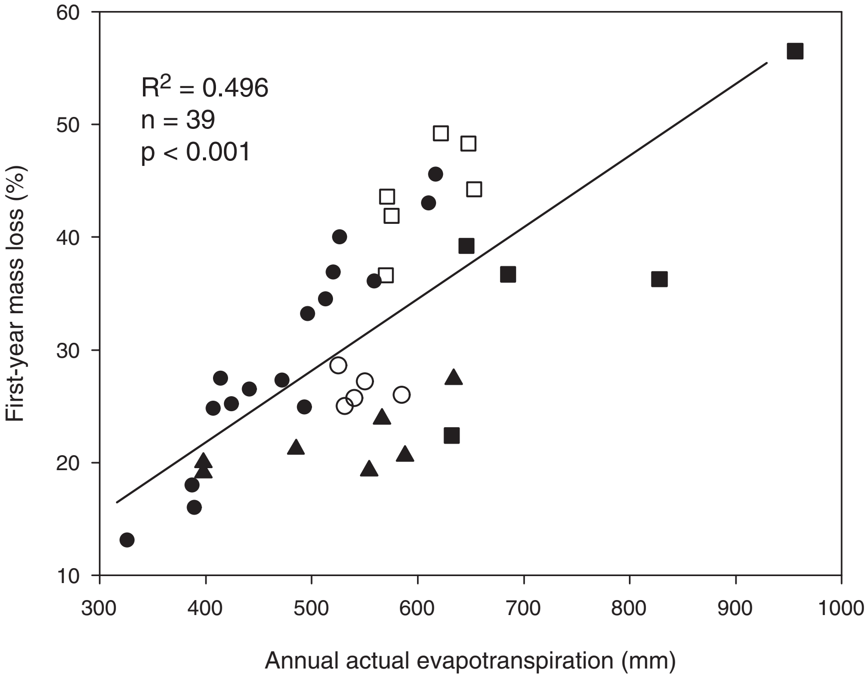

Fig. 7.2 Bivariate plot of average first-year litter mass loss vs. actual annual evapotranspiration. ● Scots pine sites along an intensively studied Fennoscandian-NW-continental transect extending from northern Finland to central Holland, □ pine sites close to the European west coast, or sites relatively exposed to Atlantic climate, ▲ pine sites around the Mediterranean, ○ central European Scots pine sites (Poland) with characteristics of inland climate, ■ pine sites in the eastern inland of the USA ($n = 39$, Table 7.5; Berg et al. 1993a)

loss vs. AET gave a significant relationship ($R^2_{adj} = 0.736$, $n = 17$, $p < 0.001$; Fig. 7.3B). The relationship was not improved by climatic factors, indicating little contribution to the relationship by seasonality or by substrate-quality factors.

Latitudinal transect. In a different approach, Breymeyer and Laskowski (1999) investigated a latitudinal transect (transect 5) oriented along a gradient of increasing continentality, ranging from Berlin in the west (12°25′E) to the Russian/White Russian border in the east (32°37′E). With increasing continentality, the annual average temperature decreased, temperature amplitudes and precipitation increased, while in the same direction, the first-year mass loss decreased. Their experiment thus indicated that the distribution of climate over the year is of importance for mass-loss rate, which was also seen in the comparison of Atlantic and inland climates (cf. above).

Comments on regional comparisons. Berg et al. (1993a, b) showed that general broad-scale climatic control of mass-loss rates in pine needle litter could be

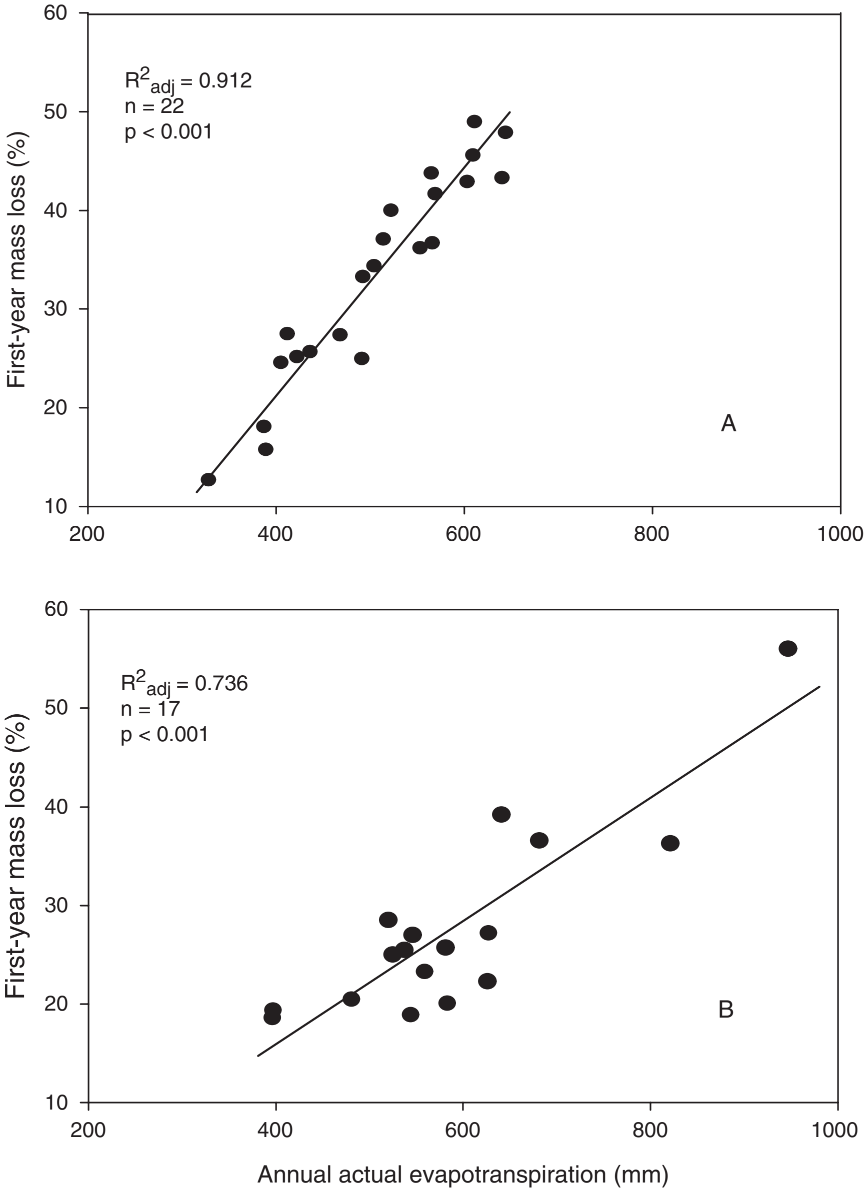

Fig. 7.3 Bivariate plot of average first-year litter mass loss vs. actual evapotranspiration. **A** Scots pine sites along a Fennoscandian-NW-continental transect, and pine sites close to the European west coast, relatively exposed to Atlantic climate (n=22). **B** Mediterranean, central European, and North American sites (n=17). A unified Scots pine needle litter was used (Berg et al. 1993a; cf. Table 7.5)

modeled. Their results also show that regions have differing responses that may be related to climate patterns. This means that the slopes and intercepts of the relationship can vary between different climates (Fig. 7.3). Effects of climate patterns may be direct or indirect. Forest floor environments are indeed different under pine forests of different regions, even though macroclimatic AET values are similar. Increasing continentality may result in changes in the composition of ground vegetation (Roo-Zielinska and Solon 1997, 1998), which may change the ground climate and other environmental conditions important for decomposition.

In this comparison, climatic variables that respond to seasonality and continentality were included, but none of these variables could help explain lower rates at the Mediterranean and inland sites. The mixture of years and sites used suggests that this is not simply the result of experimental error (Berg et al. 1993a). Furthermore, the results using the Fennoscandian and Atlantic sites are very similar to those found by Meentemeyer and Berg (1986) using earlier datasets for Fennoscandia, and weather records for the actual incubation period. Their regressions using AET vs. needle litter mass loss had intercepts and slope coefficients as well as R^2 values similar to those found here. The functional basis for these differences among climatic zones remains unclear.

7.3.3 Soil-Warming Experiments

As part of the international Climate Change Experiment (CLIMEX), Verburg et al. (1999) incubated downy birch leaf litter in southern Norway in soils with temperature elevated by 3 to 5 °C. They found no effect of soil warming on litter mass remaining after a 1-year period, and concluded that any effect of increased temperature had been offset by that of decreased moisture.

In the Adirondack Mountains of northeastern New York, USA, McHale et al. (1998) incubated litterbags containing leaf litter of American beech and sugar maple. The bags were incubated for 2 years in plots maintained at 2.5, 5, and 7.5 °C above ambient soil temperatures during the snow-free season. Decomposition of beech leaf litter did respond to temperature, the mass loss after 2 years being significantly greater in the 7.5 °C plots than in the control plot (58 vs. 41% mass loss, respectively). Sugar maple leaves showed smaller differences between the same plots, with 58 vs. 51% mass loss, respectively.

Rustad and Fernandez (1998) conducted a similar experiment in Maine, USA, with red spruce and red maple foliage litter, using a 5 °C warming. Red maple leaves showed a slightly increased mass loss during the first 6 months of decay, but after 30 months, the elevated temperature had no effect. Red spruce needles behaved in the opposite way, with significant differences in mass loss appearing only after 30 months of incubation. Unfortunately, these studies took place during a particularly dry period, and moisture may have been limiting in the control as well as in the heated plots.

Both these latter studies led their authors to suggest that temperatures will have the greatest effect on the early stages of decay, when labile materials are being degraded. In later stages, as litter quality becomes limiting, temperature seems to have less impact.

7.3.4 Local Topography

Topography, notably slope and aspect, can influence microclimate. Slope position can influence water dynamics, and possibly litter accumulation. Topography is clearly important in soil formation, but its role in decomposition dynamics is not as well documented. In a forest, the canopy often moderates microclimate in the forest floor (see above), and microrelief assumes importance as a rate-regulating factor.

Topographic heterogeneity can have a large effect on the distribution of litter on the forest floor (Dwyer and Merriam 1981). In an American beech–sugar maple forest in southern Quebec, Canada, Dwyer and Merriam (1981) observed that the mass of litter accumulated on the forest floor varied from 416 g m^{-2} at high sites, to 1,210 g m^{-2} at ground level and 2,438 g m^{-2} at low sites, i.e., by a factor of nearly six. The three sites also had very different levels of soil moisture and soil temperature. After 16 months, mass loss ranged from 10% at high sites to nearly 40% at low sites. Examination of bacterial populations revealed the same trend, the lowest abundances having been recorded at the high sites. Thus, topography influenced the accumulation of litter and the microclimate, which in turn influenced the microbial community and resulted in altered initial decay rates. Even though decomposition was faster at the low sites, the downslope movement of litter more than counterbalanced the enhanced decay, and increased litter accumulation. The accumulation rate of soil organic matter was not reported.

In many northern forests, pit and mound topography creates a microtopography with sufficient relief to influence decomposition. The results of studies on the effects of pit and mound topography seem to contradict the results of Dwyer and Merriam (1981, cf. above). For example, Beatty and Stone (1986) found that decomposition was slower in pits, and McClellan et al. (1990) found no difference between decomposition of cellulose (filter paper) in pits and mounds. Dwyer and Merriam (1981) worked in a site that had warm, dry summers, in contrast to McClellan et al. (1990) whose sites were in cool, wet southeast Alaska where water was unlikely to be limiting. Less clear is why Beatty and Stone, working in New York State, USA, found lower decay rates in pits. Perhaps the pits in their study held water so well that the soil became hydric, and decomposition decelerated during periods of anaerobicity.

When these studies are taken together, it becomes clear that the underlying factor influencing decomposition rate is really the microclimate. Whether or not microtopography influences decay rates and nutrient cycling depends on whether or not the topography causes variation in microclimate, especially moisture.

7.4 Effect of Substrate Quality on Mass-Loss Rates along Scots Pine Transects

7.4.1 Early Stage

At a given site, different litter materials decay at rates that are largely dictated by their chemical and physical properties (Berg and Staaf 1980a; Berg and Ekbohm 1991). These relationships may be unique to a site and its decomposer organisms. Therefore, predictions of decay rates for other sites cannot confidently be made on the basis of effects of substrate quality at a single site. The analysis of decay dynamics at a site must include the combined effects of both climate and litter-quality variables.

In part of transect 2, litters of different qualities were incubated at 11 sites (Table 7.7). This transect included sites in Finland, Germany, The Netherlands, and Sweden. For each site, the litter-quality variables (concentrations of N, P, and water-soluble constituents) were regressed against annual mass loss (Berg et al. 1993a). Despite the low number of litter types at each site, most of the regressions were significant ($n=4$, $p<0.1$). Examination of the intercepts and slope coefficients for each regression equation at each site suggested a consistent change in coefficients that was influenced by climate, similar to that found by Dyer (1986).

Berg et al. (1993a) analyzed the set of intercepts and slope coefficients for the 11 sites in terms of each climatic variable. Their analysis revealed the degree to which the coefficients varied with climate. For concentrations of both N and P, the intercepts were strongly and positively related to annual potential evapotranspiration (PET), and the slope coefficients were related to precipitation at the site. Thus, the intercepts appear to be controlled mostly by annual temperature (cf. temperature is a main component of PET), and the slopes of the relationships (mass loss vs. quality) by gross water supply (precipitation).

These relationships were described empirically using derived linear equations based on data from a boreal-to-temperate climatic transect (Berg et al. 1993a):

$$\text{Mass loss}_{\text{Phos}} = \left(-29.3 + 0.111(\text{PET})\right) + \left(0.749 + 0.013(\text{PRECIP})\right)\left(\text{PHOS}\right) \quad (7.1)$$

Table 7.7 Chemical composition of four experimental Scots pine and lodgepole pine needle litters incubated at sites along transect 2 (Berg et al. 1993a)

	Wsol	Esol	Lig.	N	P	S	Mg	Ca	Mn	K
Litter type	Concentration (mg g^{-1})									
Scots pine										
Brown, natural	164	113	231	4.8	0.33	0.55	0.49	4.42	0.79	1.07
Brown fertil.	135	91	265	7.0	0.33	n.d.	0.37	2.50	0.70	1.02
Green natural	199	63	284	13.4	1.47	0.98	0.85	2.82	0.41	4.90
Lodgepole pine										
Brown natural	103	42	381	3.9	0.34	0.62	0.95	6.35	0.95	0.56

Equation (7.1) shows the relationship between mass loss rates and PET, and initial phosphorus concentration. The first term in parenthesis is actually an intercept determined by the site's PET (mm). The second term is the slope coefficient, determined by the annual precipitation at the site (mm). The initial P concentration (PHOS) is the independent variable.

$$\text{Mass loss}_{\text{Nitr}} = \left(127.3 + 0.100(\text{PET})\right) + \left(-0.067 + 0.0022(\text{PRECIP})\right)\left(\text{NITR}\right) \quad (7.2)$$

Equation (7.2) is completely analogous to Eq. (7.1), and demonstrates the relationship between climatic variables, N concentrations (NITR), and annual mass-loss rates.

The expanded model for the influence of initial concentrations of N and P at any particular site may be expressed as nomograms (Fig. 7.4, Eqs. 7.1 and 7.2). This nomogram was constructed from Eq. (7.1). Selected PET values are shown on the left vertical axis, annual precipitation on the horizontal axis, and predicted mass-loss rates on the right vertical axis. The figure provides predicted loss rates for PET values between 400 and 600 mm, variable precipitation (200–650 mm), and initial P concentrations of (a) 0.15, (b) 0.30, (c) 0.60, and (d) 1.20 mg g^{-1}. Thus, PET determines the intercepts, and precipitation (PRECIP) determines the slopes. Using this nomogram, the mass-loss rate at a given site can be predicted on the basis of initial P concentrations.

These relationships (Fig. 7.4, Eqs. 7.1 and 7.2) also suggest that most of the regional variation in early-stage mass-loss rates in Scots pine forests across northern Europe is driven by temperature/heat constraints (Berg and Meentemeyer 2002). As precipitation increases, the differences in mass-loss rates for litter of differing P concentrations became larger. The sites used in this investigation all had an Atlantic climate (cf. above), and we could expect that the corresponding relationships for Mediterranean and continental sites would be different.

Figure 7.4 illustrates an alternative approach to comparing the roles of climate and litter quality in determining mass-loss rates across a large geographical area. Even small changes in climate can produce greater changes in early-stage decay rates than do large differences in litter quality. Thus, it is not surprising that in this type of system, quality variables are important at local scales, but their influences are less significant when viewed over a larger scale. Nevertheless, the equations described here should permit predictions of the influence of litter quality across a broad area of northern European pine forests, especially those with Scots pine.

7.4.2 Late Stage

Lignin concentrations increase during decomposition of litter (cf. Chap. 5), and raised lignin concentrations have been related to decreased litter decomposition rates (Fogel and Cromack 1977). The rate-dampening effect of lignin concentrations on litter mass-loss rates can be described with a negative linear relationship (Berg and Lundmark 1987), which for pine litter may begin as early as 20% mass loss. In

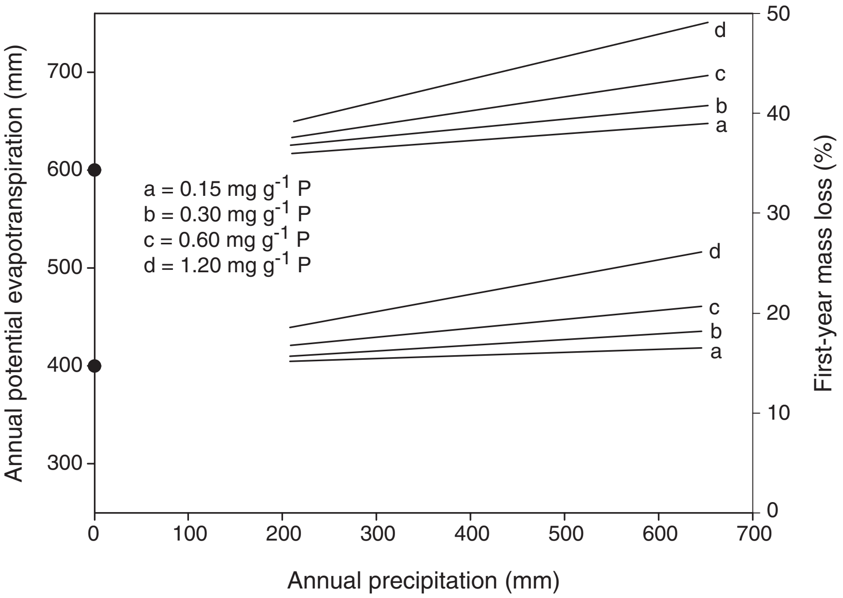

Fig. 7.4 Relationships among annual mass loss (%), potential evapotranspiration (PET), annual precipitation, and initial P concentration in litters. To investigate the effect of differing litter qualities under different climates, four chemically different litter types were incubated at 11 sites (part of transect 2, Table 7.7). The nomogram was constructed from Eq. (7.1). Selected potential evapotranspiration (PET) values are shown on the *left vertical axis*, annual precipitation on the *horizontal axis*, and predicted mass-loss rates on the *right vertical axis*. The figure provides predicted loss rates for PET values of 400 mm (*lower set of graphs*) and 600 mm (*upper set of graphs*), and four initial P concentrations of *a* 0.15, *b* 0.30, *c* 0.60, and *d* 1.20 mg g^{-1} (Berg et al. 1993a)

earlier work, Meentemeyer (1978) and Berg et al. (1993b) related mass-loss rates to lignin concentrations, and demonstrated a variation with geographic location.

Johansson et al. (1995) calculated slopes for the relationship between lignin concentration and annual mass loss along a 2,000-km-long climatic transect (part of transect 1), and found negative relationships. The steepest slopes were obtained for the southern sites that were warmer and wetter, and thus had initially higher mass-loss rates than did the more northern ones (Fig. 7.5). In fact, for three dry, nutrient-poor northern sites, the slopes became so shallow that the R^2 values became very low (Table 7.2). Thus, the slope for the southernmost site, no. 13 at Lüneburger Heide, Germany (Fig. 7.5), was –0.250% mg^{-1} g^{-1}, but a value of –0.023% mg^{-1} g^{-1} was determined close to the Arctic Circle in Sweden. The slopes for the sites in south and central Sweden were in-between (Fig. 7.5). The lengths of the lines in Fig. 7.5 define the intervals between the highest and lowest lignin concentrations used for the relationship.

The range in lignin-concentration values could influence the slope. However, Johansson et al. (1995), using two sets of data (for sites 13 and 6:51; Fig. 7.5) to isolate a range with the same lignin-concentration interval, made a comparison of the slopes and found that they remained the same. In a further step, they used the slopes at each site and compared these to climate. They performed a second set of linear regressions, and found that the best fit was that between slope and AET (Fig. 7.6), with an R^2 of 0.559. Other climatic variables gave significant correlation with slope as well, e.g., PET and annual average precipitation with values for R^2_{adj} of 0.413 and 0.405, respectively. They also combined all data in a multiple regression analysis with AET, lignin, and their product as independent variables. This analysis showed a strong significance for all three terms in the model, and an adjusted coefficient of determination (R^2_{adj}) of 0.346 ($n = 196$, $p < 0.0001$), thus explaining 34.6% of the variation. This offers support for the conclusion that the relationship between litter mass-loss rate and lignin at a site is dependent on, or related to, the values of the climatic factors, especially AET. However, this relationship is empirical, and the underlying causal factors are not known.

The causal mechanisms behind the relationship between lignin concentration and mass-loss rate could depend on the litter N concentration (Chap. 6). That the mass-loss rates were affected more strongly by increasing lignin concentrations in warmer and wetter climates means that the degradation of lignin was more hampered at such stands. The litter N concentration increased more quickly in litter incubated in stands

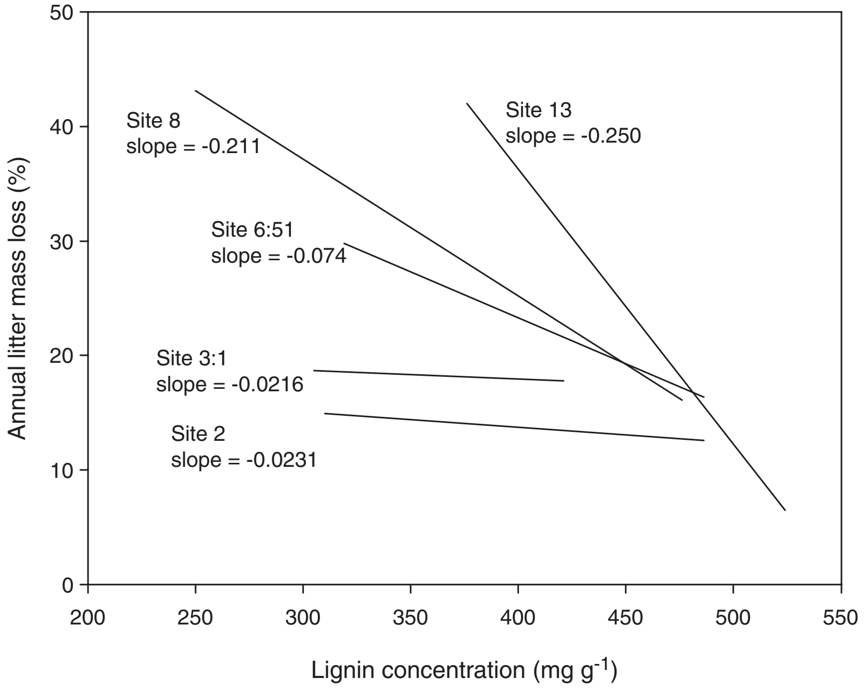

Fig. 7.5 Plot of annual litter mass loss versus litter lignin concentrations at the start of each year. The forest stands ranged between the Arctic Circle in Scandinavia, and Lüneburger Heide ca. 100 km south of Hamburg, Germany (Table 7.2)

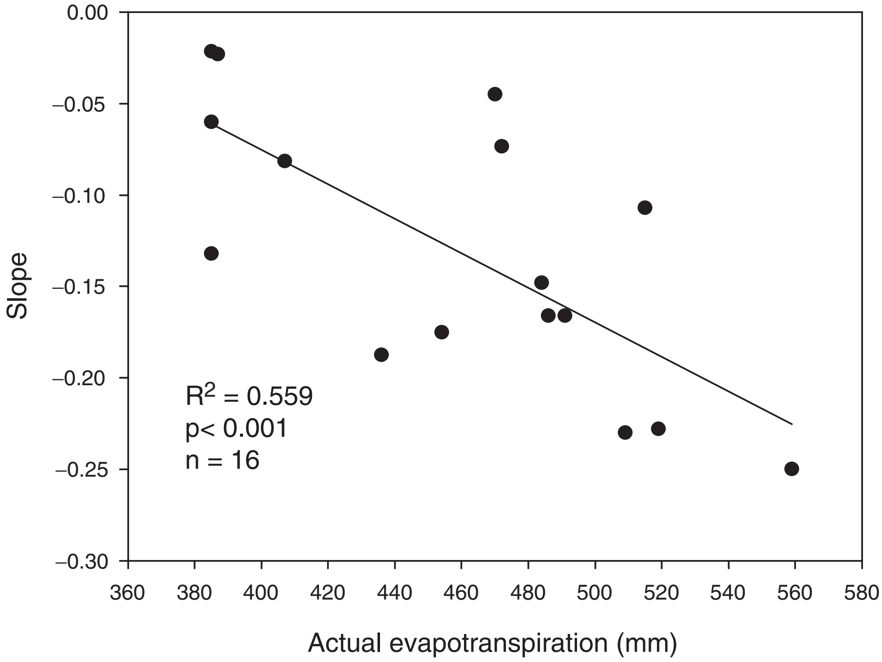

Fig. 7.6 Bivariate plot of slope coefficients (Table 7.2) versus actual annual evapotranspiration (AET) for 16 sites along a climatic transect. The slope coefficients originate from the relationship between litter lignin concentration and annual litter mass loss (modified from Johansson et al. 1995)

located at higher AET (cf. Chap. 5), which may be a partial explanation. Furthermore, in the initial stages, the same litter types incubated at the same sites responded very differently toward climate (Fig. 7.3). We can reiterate that conditions that are initially rate-stimulating may, in later stages, become rate-inhibiting.

It appears that when litter has entered late decomposition stages, its decomposition rate is affected more by increasing lignin concentrations at sites with higher AET values, namely, under warmer and wetter conditions. It also seems that the slopes of the lignin vs. mass-loss relationship tend to converge at a lignin concentration a bit higher than 500 mg g^{-1} litter, suggesting that the mass-loss rates approach a similar value at this level of lignin concentration, irrespective of climate. Thus, at very late, humus-near stages, decomposition rates would not be driven principally by climate factors.

An experiment by Dalias et al. (2001) may confirm this observation. They investigated the effect of different temperatures on the decomposability of the residual litter substrate. Using humus from five coniferous sites along a transect from 64°00′N in Sweden to 43°07′N at the Mediterranean, they incubated a ^{14}C-labeled straw material at 4, 16, and 30 °C. They let the straw decompose to the same level of mass loss in all cases (as measured in terms of released $^{14}CO_2$). Then, the material was re-incubated, and the release of $^{14}CO_2$ showed that the highest mineralization rate took place in samples that had been originally incubated at 4 °C, and the lowest in those originally incubated at 30 °C (Fig. 7.7). Their interpretation was that when litter decomposed under higher temperatures, its residual compounds were more recalcitrant.

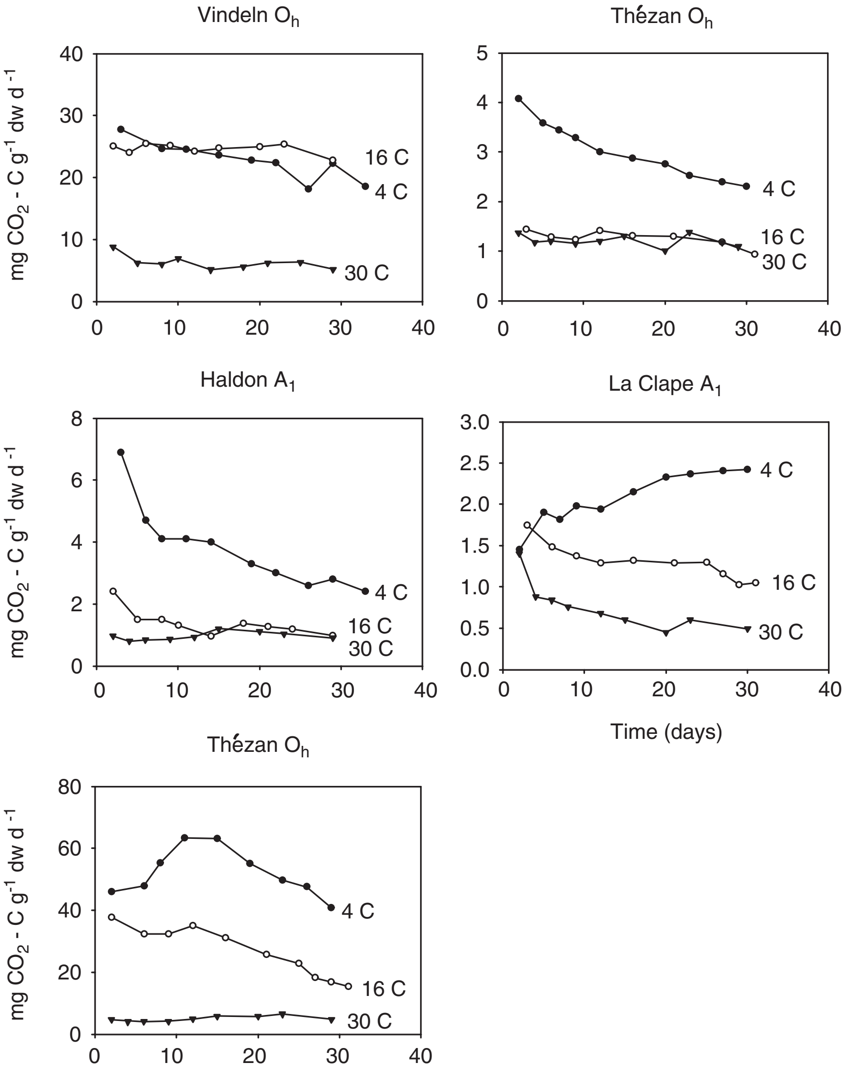

Fig. 7.7 Mean daily respiration of $^{14}CO_2$ per gram dry, partly decomposed wheat straw. Wheat straw had been incubated, and was partly decomposed in the humus at five sites along a climatic transect. The straw was re-incubated at 4, 16, and 30 °C in the laboratory. Decomposition was allowed to proceed until about the same mass loss in all cases (as measured from $^{14}CO_2$), the litter was re-incubated at the standard temperature of 23 °C, and the activity was compared among the litters incubated at different temperatures. The highest activity was found for litter that had been incubated at the lowest temperature (Dalias et al. 2001)

7.5 Climate and Decomposition of Norway Spruce Needle Litter

7.5.1 *Climate Versus First-Year Mass Loss*

Along a climatic transect (transect 4), the decomposition rate of Norway spruce needle litter was more closely related to substrate quality than to climate. Norway spruce needle litter is a substrate with properties very different from those of various types of pine needle litter (cf. Chaps. 4 and 6) and along the transect this was reflected in a switch from climate control to one of substrate quality. For example, in a north–south transect along Scandinavia from the Arctic Circle (66°22′N) to the latitude of Copenhagen (56°26′N), climate indices did not show any significant relationship to first-year mass loss.

The lack of a climatic influence on the decomposition of Norway spruce litter, both for the first year of incubation and in later years, makes it differ greatly from previous studies using other litter types, notably Scots pine needles (Berg et al. 1993a, b). In other words, the decomposition of Norway spruce litter does not depend on site-specific energy and water inputs to the ecosystem, but on other, more powerful influences. For Norway spruce litter, site climate based on long-term averages was very poorly related to decomposition rate, even though the variation in AET along the 1,600-km-long transect ranged from 371 to 545 mm. This suggests that soil microclimate is not an important control on litter decay rates in Norway spruce stands.

For some of the Norway spruce plots along this transect, Berg et al. (1984a) reported that first-year mass loss of a standardized preparation of Scots pine needles was not correlated to climatic indices. They had incubated unified Scots pine needle litter in paired stands of Norway spruce and Scots pine, and although decomposition of the litter incubated in the Scots pine stands was regulated primarily by climate, the decomposition of that incubated in the nearby stands of Norway spruce, on the same soil and under the same climate, was not related to any climatic factor.

Soil microclimate in spruce forests is poorly described by local temperature, precipitation, and water-balance variables. Spruce trees produce dense canopies, but in a transect study, Berg et al. (2000) found no effect of canopy cover and basal area indices on litter decay. In contrast, the decomposition of Scots pine litter incubated in a pine stand reflects ground microclimate fluctuations very well (Jansson and Berg 1985). Compared to Scots pine stands, the results suggest that other factors may be involved in spruce, such as substrate quality, and possibly different microflora. Ground climate in the spruce forests may not be related as closely to macroclimatic factors and averages as in the adjacent pine forest (Johansson et al. 1995). Under the dense spruce canopies, water could be limited due to interception, in which case temperature differences would have little effect. This appears to be a reasonable conclusion, since decomposition of Scots pine needles in spruce stands was also unrelated to climate.

Dead Norway spruce needles may stay on the branches for long periods, and become partly decomposed before being shed. This means that the early phase of decomposition (Berg and Staaf 1980a) occurs before litter fall, and that at least part of the litter was already in a late phase of decomposition when collected. Hence, the concentrations of compounds such as lignin, N, and P will be higher than in directly shed litter, and concentrations of water solubles will be lower. Furthermore, mobile nutrients, such as K, will be leached, resulting in lower concentrations (Laskowski et al. 1995). Thus, a dominant influence of the substrate cannot be excluded. However, only one of eight substrate-quality factors, namely, initial Mn concentration, correlated positively with first-year mass loss ($R^2 = 0.325$, $p < 0.05$; Table 7.8, and also see Fig. 6.5). The relationship between Mn concentration and first-year mass loss is based on a causal relationship for the role of Mn as a rate-stimulating agent for lignin degradation (cf. Chaps. 2 and 6).

7.5.2 Late Stage

Individual sites. Along transect 4, Berg et al. (2000) compared annual mass loss for Norway spruce needle litter to current litter lignin concentrations in the same way as was done for Scots pine needle litter (cf. Fig. 7.5). We can compare these two approaches using slope coefficients for the negative relationship between changes in lignin concentration with time, and annual mass loss. For Norway spruce needle litter, the lignin concentration at the start of each 1-year period was regressed against the mass loss over that 1-year period, to obtain a slope for each of the 14 sites, describing the effect of lignin concentration on litter mass loss. The values included were clearly those of the late stage (years 2, 3, 4, and 5). Lignin concentration correlated negatively with litter decay rate for seven of the 14 sites. Berg et al. (2000) combined these into one group (group 1, Table 7.9). For the seven other sites (group 2), there were no such effect related to lignin (Table 7.9).

The significant, negative slopes (group 1, Table 7.9) for annual mass loss vs. lignin concentration were tested for relationships to climate and other substrate-quality variables. None of the tested climatic factors (Table 7.3) was significantly related. However, initial lignin concentration gave a significant, negative relationship with slope coefficient ($R^2 = 0.677$; Table 7.10), and the best fit (positive) was found for the empirical relationship between litter Ca concentration and slope

Table 7.8 Linear relationships of first-year mass loss of Norway spruce needle litter vs. climatic and substrate-quality factors. The litter, collected locally, was incubated along a climate transect (transect 4) extending from the Arctic Circle in Sweden to the latitude of Copenhagen ($n = 14$). All climate and substrate-quality variables listed in Table 7.3 were tested

Variables	R	R^2	$p<$
MESE	0.570	0.325	0.05
AET, MESE, MAGN	0.644	0.415	0.05

Table 7.9 Equations for the linear relationship between annual mass loss in years 2–5 and lignin concentrations at the start of each year in decomposing Norway spruce needle litter incubated at 14 sites in Scandinavia (transect 4; Berg et al. 2000)

Site	Slope	Intercept	R	*n*	*p*<
Significant relationships (group 1)					
5 Stråsan	−0.09631	55.5266	−0.709	18	0.001
111 Hässlen	−0.07393	48.2824	−0.851	13	0.001
113 Tönnersjöheden	−0.09399	57.0367	−0.973	5	0.01
10 Mästocka	−0.11077	65.05364	−0.960	5	0.01
114 Farabol	−0.10636	65.16445	−0.969	5	0.01
104 Tveten	−0.10874	66.37035	−0.955	5	0.05
102 Kungs-Husby	−0.03942	38.60125	−0.933	4	0.1
Non-significant relationships (group 2)					
109 Ätnakobbo	0.04882	2.90427	0.801	4	n.s.
108 Västbyn	0.03572	15.61122	0.197	5	n.s.
112 Månkarbo	−0.03309	38.60966	−0.911	3	n.s.
103 Tomta	0.013382	19.7723	0.207	5	n.s.
100 Dimbo	0.037064	12.28549	0.386	5	n.s.
101 Grensholm	0.021138	12.904	0.351	4	n.s.
105 Remningtorp	0.002265	28.00804	0.063	5	n.s.

Table 7.10 Linear relationships between the slope coefficients from the group 1 litter in Table 7.9 and substrate-quality variables. Only statistically significant (p<0.05) slopes were used in this investigation. n = 7 (Berg et al. 2000)

Equation	R	R^2	*p*<
Slope = f (Ca)	0.946	0.895	0.01
Slope = f (lignin)	−0.823	0.677	0.05

coefficient ($R^2 = 0.895$). This indicates that the higher the initial concentration of Ca, and the higher the slope coefficient, the lower the effect of lignin on litter decay rates.

Groupwise combination of data. Berg et al. (2000) performed another set of regressions, comparing the data of group 1 and group 2 in terms of substrate-quality variables, namely, concentrations of lignin, N, Ca, Mg, Mn, and water solubles (cf. Table 6.6). For the group 1 litter ($n = 55$), they found highly significant, negative relationships between the annual mass loss, and concentrations of lignin and N (cf. Fig. 6.9), and positive relationships for other variables including concentrations of water solubles. That water solubles correlated positively with litter mass-loss rate suggests that energy was a limiting factor.

For group 2 ($n = 33$), they compared annual mass loss and substrate-quality variables (cf. above) as potential rate-regulating factors. The relationship to Mn concentration was highly significant ($R^2 = 0.277$, $p < 0.01$; cf. Fig. 6.9), but there were no significant relationships between annual mass loss and the other substrate-quality factors. In both groups, the intervals for lignin concentrations were similar, with 227 to 524 mg g^{-1} for group 1, and 286 to 513 mg g^{-1} for group 2.

The litter in group 2 had a wide range in Mn concentrations (0.41 to 7.7 mg g^{-1}; cf. Fig. 6.9). For group 1, the range was clearly narrower (0.3–3.0 mg g^{-1}). When Berg et al. (2000) selected the corresponding range in Mn concentrations for the group 2 litter, by excluding all data outside the interval 0.3 to 3.0 mg g^{-1}, no significant relationship to Mn concentration was found.

Combined data. When combining all data for late stages (group 1 and group 2) with the Mn concentration interval from 0.3 to 7.7 mg g^{-1}, Berg et al. (2000) found a highly significant relationship between Mn concentrations and mass loss ($R^2 = 0.372$, $n = 59$, $p < 0.001$). The effects of Mn on lignin degradation have been discussed above (cf. Chap. 3). Using all the data for late stages (group 1 plus group 2), including all transect data plus all data from an experimental site (B. Berg, unpubl. data, $n = 95$), they found that Mn concentration correlated positively with annual mass loss ($R^2 = 0.356$, $p < 0.001$; cf. Table 6.7).

7.6 Climate and Decomposition of Root Litter

A study of coniferous root litter was undertaken along a climatic transect across a large region ranging from the Arctic Circle (66°N) in Scandinavia to Berlin (52°N) in NE Germany. The study was carried out in coniferous monoculture forests. Berg et al. (1998) used data from 37 sites at which root litter of three coniferous species, namely, Scots pine, lodgepole pine, and Norway spruce, had been incubated.

When they combined all data, the linear relationships to climatic factors and chemical composition were poor. In spite of the considerable climatic difference between sites, there were no strong relationships between any climatic variable and the first-year mass loss (range 17.0–40.9%). For the first-year mass loss, the average annual temperature (AVGT) was the most important rate-regulating factor for all litter combined, with an R^2_{adj} value of 0.186. Substrate-quality indices had a weak influence. Thus, for the whole region, lignin concentration was significant with an R^2_{adj} value of 0.142. When combining average temperature and lignin concentration, the R^2_{adj} value was 0.262.

They distinguished between pine and spruce litters, and found that for the separate groups the values for R^2 increased, but still the effect of average annual temperature dominated. For the pine group, the R^2_{adj} reached a value of 0.346 (Table 7.11). Also over the region, the N concentration in the fresh pine root litter gave a significant relationship ($R^2_{adj} = 0.232$).

For the root litter of Norway spruce, the average temperature in July was the strongest rate-regulating climatic factor (Table 7.12), with an R^2_{adj} value of 0.381. A combination of temperature in July (JULT) and the initial P concentration in the litter gave an R^2_{adj} value of 0.713 for spruce root litter, thus explaining about 71% of the variation. Temperature in July and initial Ca concentration explained about 45%. Berg et al. (1998) concluded that the decomposition of spruce root litter was

Table 7.11 First-year mass loss of local root litter from both Scots pine and lodgepole pine, incubated along a climatic transect, as a function of climatic and substrate-quality factors. The root litter had an approximate diameter of 2–3 mm (Berg et al. 1998)

Variable	R	R^2_{adj}	*n*	*p*<
Climatic factors				
AVGT	0.612	0.346	25	0.01
PET	0.563	0.287	25	0.01
AET	0.553	0.276	25	0.01
JULT	0.454	0.171	25	0.05
Substrate quality				
NITR	0.536	0.232	17	0.05
Climate and substrate quality				
AVGT, NITR	0.603	0.322	17	0.05
AVGT[a]	0.592	0.308	17	0.05

[a] Uses data for which both AVGT and NITR are available

Table 7.12 First-year mass loss of local Norway spruce root litter incubated along a climate transect as a function of some single climatic and substrate-quality factors (Berg et al. 1998)

Variable	R	R^2_{adj}	*n*	*p*<
Climate factors				
JULT	0.661	0.381	12	0.05
AVGT	0.588	0.281	12	0.05
AET	0.497	0.172	12	0.1
Substrate quality				
PHOS	0.569	0.239	10	0.1
CALC	0.568	0.238	10	0.1
Climate and substrate-quality factors				
JULT, PHOS	0.861	0.713	12	0.01
JULT, CALC	0.713	0.454	10	0.05

more dependent on energy input than that of pine, and that for both groups, energy was the main rate-regulating factor. However, fine root decay is perhaps less sensitive to temperature changes than is foliage litter decay (Silver and Miya 2001; cf. Chap. 9).

7.7 A Series of Limiting Factors

In later stages of decay, increasing lignin concentrations have been found to correlate negatively with lower decay rates. However, there are nutrient factors that may influence the prevailing microflora, thereby influencing both the degradation rates of lignin and the substrate. The succession of the latter may be regulated by the composition of nutrients. The effects of N (Eriksson et al. 1990) and Mn (Perez and Jeffries 1992; Hatakka 2001) have been discussed earlier (cf. Chap. 6). Lignin degradation rates, as reflected in lignin concentration, may limit litter decomposition rates if one or more of these essential elements required for microbial degradation of lignin (e.g., Mn) are limiting. At the other extreme, high concentrations of an element such as N could suppress microbial degradation of lignin. Such nutrient interactions may be complex, but the composition of the microbial community, including the lignin-degrading fungi, depends greatly on both litter degradability and concentrations of nutrient elements. If the degradation of lignin is the primary rate-regulating factor in later decomposition phases, factors such as the concentration of nutrients that influence lignin degradation will also influence the decomposition of the whole litter.

For the litter of Norway spruce, the effect of lignin was related to Mn concentrations. Within a narrow concentration interval (0.3–3.0 mg g^{-1}), Mn was not related to litter degradation rate. However, within the wider range of litter Mn concentrations (0.4–7.7 mg g^{-1}), mass-loss rates appear to be influenced by the litter concentrations of Mn, and the relationship was better. At high Mn concentrations, microbial lignin degradation may thus be facilitated. Lignin concentration itself was less important, but would increase in importance when Mn was limiting. The differing concentrations of Mn in litter could be dependent on site (soil) properties (Berg et al. 1995a), and the availability/mobility of Mn in the mineral soil could thus be an important site property for determining the rate of litter decomposition.

A similar approach may be used when discussing the effect of Ca on lignin degradation by the microbial community (cf. below). Calcium may influence the lignin-degrading microflora, and thus, through lignin-degradation rates, the litter decomposition rates. The higher the Ca concentration, the steeper the slope for lignin concentration vs. mass-loss rate ($R^2 = 0.895$, Table 7.10). This is possibly due to a higher lignin degradation rate when Ca is not limiting, leading to less lignin regulation of litter mass loss. Early work on this relationship demonstrated that Ca concentration affects lignin decay (Lindeberg 1944).

7.8 Climate, and the Decomposition of Humus and Litter in Humus-Near Stages

The idea of a low climatic influence on respiration from humus is in part supported by a study by Bringmark and Bringmark (1991), who made respiration measurements on humus in a climate transect along Sweden from the latitude of the Arctic Circle to that of the city of Copenhagen (66°08′N to 55°39′N). Incubating their samples at a standard temperature, they found higher respiration rates for the northern humus samples, compared to the southern ones. The relationship between latitude and respiration was highly significant ($R^2 = 0.41$, $n = 166$), with respiration expressed as mg CO_2 g^{-1} ash-free humus under standardized temperature and moisture conditions. Although this measurement was made on humus, the results have a clear similarity to those of Dalias et al. (2001) described in Section 7.4.2.

Respiration rates from humus samples are sometimes negatively correlated with the N concentration of decomposing humus (Bringmark and Bringmark 1991; L. Bringmark, pers. comm.). Thus, respiration rates of humus samples collected along a transect over Sweden, and kept under standard climatic conditions showed a significant negative relationship to N concentrations in the humus ($R = -0.650$, $n = 15$, $p < 0.01$; Fig. 7.8; Berg and Matzner 1997). Nitrogen concentrations were in the range of 1.0–1.9%, and such a variation in N concentrations in humus could be a natural phenomenon (Berg et al. 1999b), rather than being pollution-related. In another study in which humus was collected from sites across Europe, from the Arctic Circle to the Mediterranean, a highly significant, negative relationship between respiration and N concentration was found (R. Laskowski, pers. comm.).

When investigating the literature on laboratory measurements of respiration from humus that has been equilibrated, we found these to be very high (B. Berg, unpubl. data). Thus, when converting the amounts of CO_2 developed per hour or per day from a given ash-free sample into annual mass loss, the respiration rates often correspond to between 10 and 100% of the total humus mass per year (e.g., Persson et al. 2000a), values that do not agree with an accumulation of humus. We must conclude that such rates are not to be regarded as a quantitative measure of humus decomposition, and cannot exclude that in some cases the reported effects of rate-regulating factors may be in doubt.

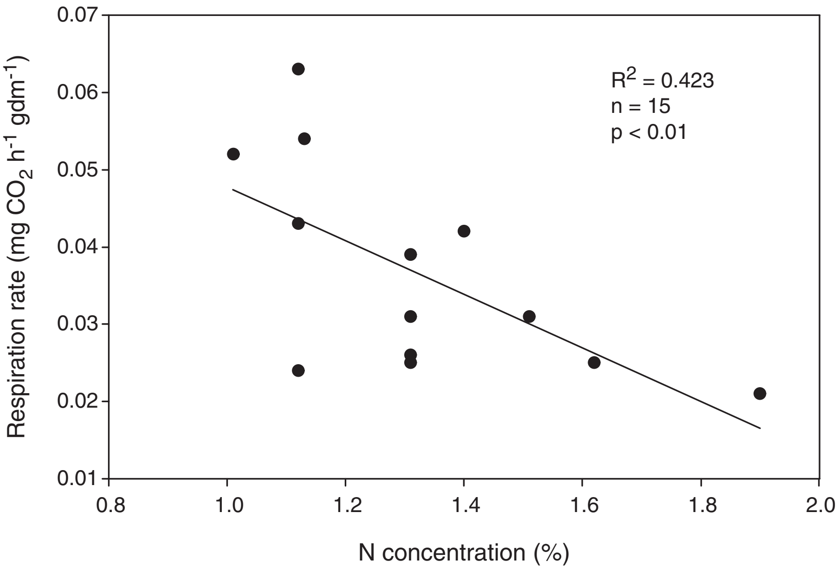

Fig. 7.8 A comparison between N concentration in humus (F and H layers), and CO_2 release rate from the same samples incubated under standard temperature and moisture conditions. Samples were collected in a transect along Sweden (Berg and Matzner 1997, based on L. Bringmark, pers. comm.)

Chapter 8

Influence of Soil and Plant Community Factors

8.1 Introduction

Although litter chemical composition and climate appear to dominate as regulating factors in decomposition over a regional scale (cf. Chaps. 4–7), there are numerous factors that are important in regulating decomposition at the local, or even microscale. These are related to soil characteristics, nutrient availability and cycling, plant community composition and structure, and soil fauna. Some of these factors exert their influence by modifying the microclimate. Other factors operate primarily through biochemical or nutritional influences on microbial metabolism. Not only can these site-specific factors influence microbial metabolism, but they can also alter the composition of the microbial community, as was discussed in Chapter 3.

As is the case for many ecological processes, scale is a key issue. It is often possible to describe a process on a large scale with reasonable accuracy, and a good understanding of the underlying mechanisms and regulating factors (e.g., climate). On a smaller scale, however, the impact of these same factors may be more subdued, and other, more subtle factors emerge as being more important.

The choice of appropriate measurement methods is another key issue in studies of decomposition. We mentioned (Chap. 2) that traditional quantitative measurements of decomposition rate often encompass mass-loss determinations using, e.g., litterbags, and are carried out during those decomposition stages when a mass loss is large enough to be readily recorded, namely, the early and late stages of decomposition, but not in the near-limit stage. The litterbag may in principle represent an undisturbed system, but to measure extremely low decomposition rates in undisturbed systems, we could include the concept accumulation of SOM in the humus layer on top of mineral soil. Although crude, at present this is arguably the only appropriate method available.

A method of measuring the decomposition of organic matter by sampling well-defined humus layers (see below) may also serve to indicate carbon sequestration, or a potential for carbon sequestration.

B. Berg and C. McClaugherty, *Plant Litter*.

8.2 Soil Factors

Soil factors include both physical and chemical properties. Texture is perhaps the most important physical property of soil, because it influences nutrient and water dynamics, porosity and permeability, and surface area. Chemical properties include pH, cation exchange capacity, and organic matter content, all of which can influence the mobility of nutrients, and the composition of the microbial community.

8.2.1 Soil Texture

Organic Matter on Top of the Mineral Soil

An experiment that may give a new view on the effect of nutrients and/or mineral soil structure on the long-term decomposition process, as well as on storage or sequestration of humus on top of the mineral soil was made by Vesterdal and Raulund-Rasmussen (1998). They used a tree trial experiment started ca. 30 years earlier. That experiment investigated the growth and humus formation of ca. 16 tree species at 14 locations throughout Denmark. Each plot had a monoculture, and measured at least 0.25 ha. All tree species at all locations were planted in the same year (Holmgaard and Bang 1977). One difference between the sites was the soil types, and their richness in weatherable nutrients. Denmark is a rather flat land, and all sites were located within a circle of radius less than 150 km, which means that any climatic differences would have had only minimal impact. The climate imprint, expressed as annual average temperature and annual precipitation, ranged between 7.5 and 8.4 °C, and 610 and 890 mm, respectively. The mineral soil was bare at time for planting meaning that the humus layer on top of the mineral soil, had thus been formed at all sites after the stands were planted. Furthermore, all the organic material accumulated had formed a clearly distinguishable layer on top of the mineral soil. This means that sampling of the O-horizon in a set of stands would have yielded data that could be compared in terms of similarities/differences in the character of humus horizons. Moreover, the similarities in the design of the experiment, and in climate among the stands enabled the data to be evaluated statistically as a block experiment.

Using humus samplers of 25 × 25 cm and with ten replicates per stand, Vesterdal and Raulund-Rasmussen (1998) measured the amount of humus (and carbon) accumulated at seven sites. They selected seven tree species, namely, lodgepole pine, Norway spruce, Sitka spruce, Douglas-fir, grand fir, common oak, and common beech. They found distinct differences among sites and among species, in terms of both the chemical composition of the remaining organic material (humus), and the amounts of sequestered carbon on top of the mineral soil.

The amounts of humus in the forest floor, expressed as carbon, varied among species at a given site, as did the average amounts for the seven sites, expressed as average values for each species over the seven sites (Fig. 8.1A). Lodgepole pine

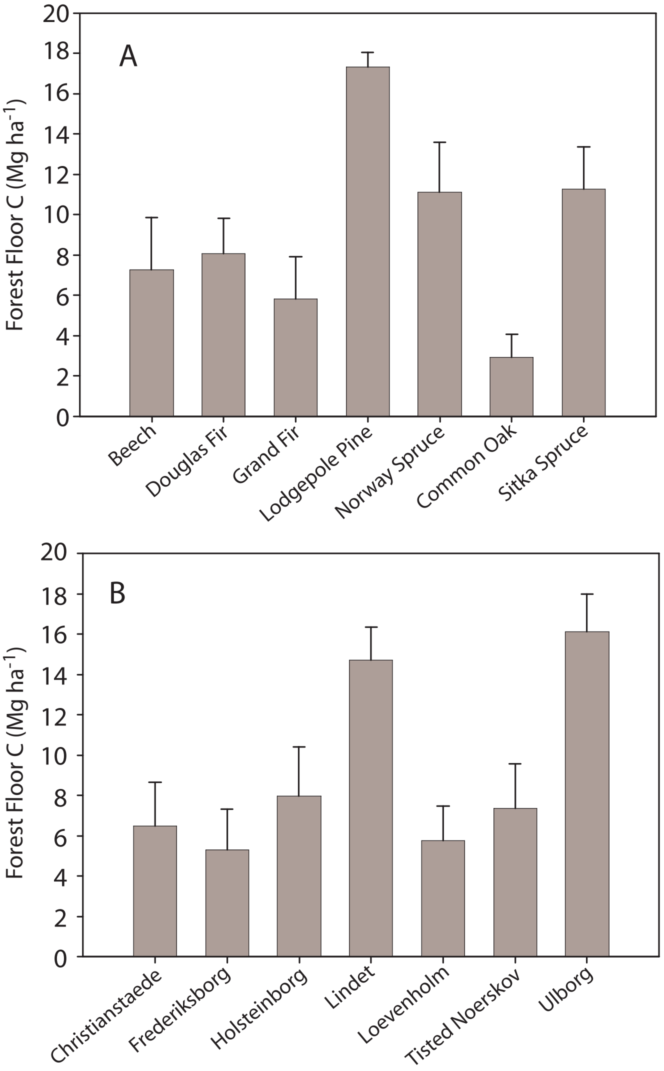

Fig. 8.1 Average amount of carbon stored in humus layers formed in stands of seven monocultures of different tree species. The same tree species were planted at seven different sites with soils of different richness. **A** Average values for tree species over the seven sites. **B** Average values for all tree species within each site. The data suggest an effect of both tree species and site (from Vesterdal and Raulund-Rasmussen 1998)

forests stored the highest amounts, and significantly more than the two spruce species. In turn, these stored significantly more carbon than did beech, which in turn stored more than did common oak. Douglas-fir and grand fir were in-between. Thus, there was a clear effect of species on the sequestered amounts. However, Vesterdal and Raulund-Rasmussen (1998) also found an effect related to site (Fig. 8.1B). Taking the average values of all tree species at the different sites, they obtained average amounts that were significantly different among sites.

Carbon content in the O-horizon was negatively correlated to mineral soil pH and to soil clay content; the coarser the soil structure, the more C was stored. Thus, carbon content in the humus layer was related to properties of the underlying mineral soil. This amount decreased with increasing concentrations of clay and silt, and increased with increasing concentrations of coarse sand.

Organic Matter Mixed into the Mineral Soil

One of the first long-term studies to examine the effects of soil properties on decomposition was that by Jenkinson (1977). He examined the decomposition of ^{14}C-labeled ryegrass in a variety of soils. In these soils, clay content ranged from 5 to 21%, pH from 3.7 to 8.1, and organic C from 0.97 to 4.57%. He found that neither organic matter content nor pH had much impact, except that decay was initially slower in the most acidic (pH 3.7) soil. On the other hand, soil texture was an important factor, with more litter-derived C retained in soils with higher clay content. Similarly, the total soil organic matter levels were less in sandy soils (14%) than in soils with more clay (up to 29%). This suggests that soils with clay are able to store more biologically degradable SOM than are sandier soils. Several mechanisms could account for the influence of soil texture on decomposition.

Using very short-term laboratory studies of cellulose degradation, Schmidt and Ruschmeyer (1958) evaluated 11 different soil factors among 21 different soils, by correlating these with cellulolytic activity. With regard to soil texture, they found that sand content was negatively correlated with cellulolytic activity ($R = -0.47$, $p < 0.05$). In their study, pH, ranging from 4.0 to 7.6, showed the most highly significant correlation with cellulolytic activity ($R = 0.76$, $p < 0.01$), and total N and nitrate-N were also positively correlated. This study is not directly applicable to field conditions, but serves to illustrate the importance of soil factors including texture, pH, and nutrients in decomposition processes – in this case, cellulolytic activity, as an index for the potential to degrade litter.

Because soil texture is so closely related to soil water dynamics, Scott et al. (1996) undertook a study to examine the effects of both soil texture and soil water potential. They made artificial soils by blending soils collected from the field. Their soils had sand contents of 40, 55, and 73%. In each of these soils, they regulated water at −0.012, −0.033, and −0.30 MPa. This combination of treatments yielded a continuum in water content that they described as a single variable, percentage water-filled pore space. Soil texture had no effect on the decomposition of wheat litter. However, there was an interaction between soil texture and water potential, such that the effect of water potential was negligible in the sandy soil, and was greatest in the loam soils. Also noteworthy was that the effects of soil texture and water potential on litter decomposition were very

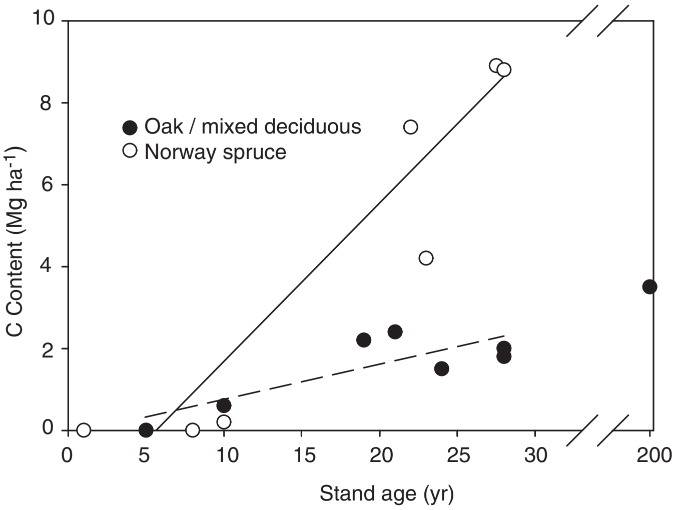

Fig. 8.2 Absolute amount of soil carbon in the organic layers in chronosequences of Norway spruce (○) and common oak (●) up to 29 years of age. All studies were carried out on the same soil, and under the same climate (redrawn from Vesterdal et al. 2002)

much less than their effects on the decomposition of the older C that was already in the soil.

A very direct and convincing investigation is one by Vesterdal et al. (2002) in different soil layers. Their study was carried out in stands of Norway spruce and common oak, and the authors investigated soil organic matter in a chronosequence. They separated different soil layers and monitored the amount of carbon in the organic layer, and in three layers of mineral soil, namely, at 0–5, 5–15, and 15–25 cm (Figs. 8.2 and 8.3). In the case studied, the amount of newly stabilized carbon increased over a period of 29 years in the organic layer. The increase rate was considerably higher for Norway spruce than for common oak (Fig. 8.2), with 9 and 2 Mg C ha^{-1}, respectively over a 30-year period. It may be noted that the stands differed in the kind of material that accumulated in the organic layer. Whereas the spruce stand accumulated organic matter that originated mainly from foliar material (>75%), the stored matter in the oak stands had a considerable fraction (<50%) of wood litter, such as twigs and branch material (Vesterdal et al. 2002). Organic carbon also increased in the top mineral soil, and both the concentration (Fig. 8.3) and amount increased significantly ($p<0.01$). In the two lower layers (5–15 and 15–25 cm), however, there was a statistically significant decrease in amount, in the order of 250 to 290 kg carbon per hectare and year in each lower layer. We may emphasize (Fig. 8.3) that even concentrations decreased. The soil had been plowed before the stands were planted, and it is highly likely that this explains the decrease in the amount of carbon in the mineral soil. That a disturbance of soil activates the soil microorganisms is well known to soil microbiologists, and Fig. 8.3 gives a quantification of this effect, resulting in a clear decrease

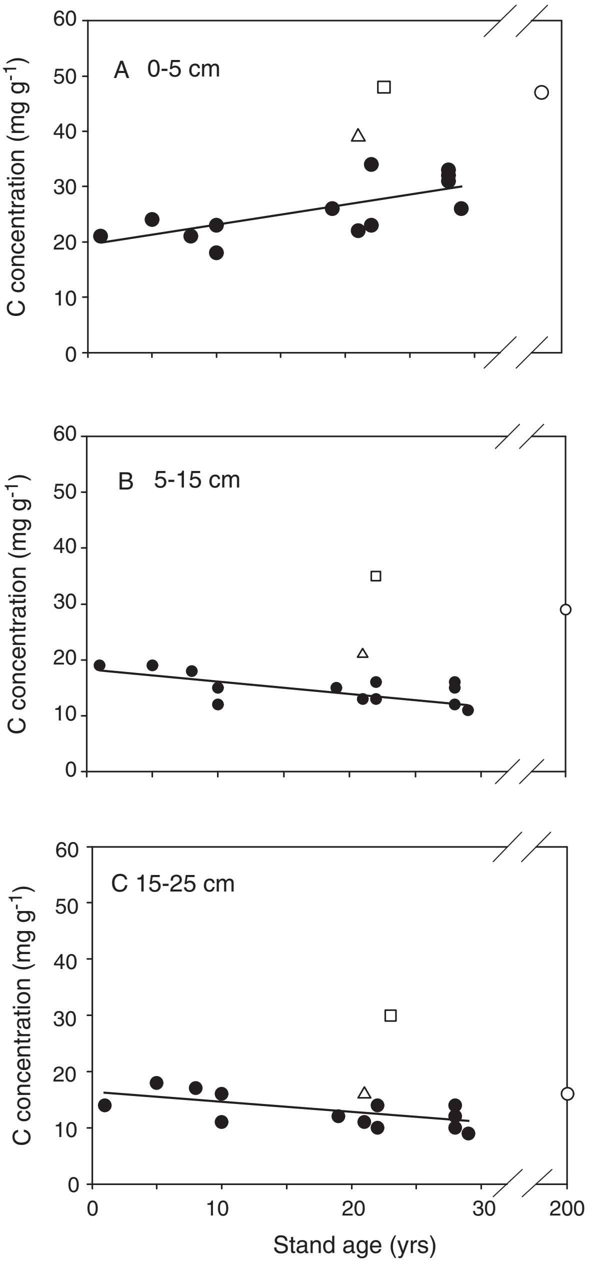

Fig. 8.3 Carbon concentration in three different mineral soil layers in chronosequences of Norway spruce and common oak up to 29 years of age: **A** 0–5, **B** 5–15, and **C** 15–25 cm layers. The initial concentrations, and the concentrations in the chronosequence were similar for both species, and the data were combined in linear regression analysis. All studies were carried out on the same soil, and under the same climate (redrawn from Vesterdal et al. 2002)

over at least 28 years since the disturbance. We have selected this study to illustrate this kind of effect, which also is likely after, e.g., ditching or site preparation of a forest soil, enabling air (e.g. oxygen) to penetrate deeper soil layers. We do not know the limitations of this effect, and the question remains whether a similar decrease in carbon in even deeper soil layers is found after a clear cut or a forest fire. One consequence may be that under disturbed conditions, there is new formation of stable matter in surface soil layers, whereas degradation of old organic matter takes place in deeper layers.

We conclude that soil texture is more important for long-term organic matter dynamics than for initial phases of decay. Not surprisingly, finer-textured soils will interact with water more than do coarser-textured ones. As a result, water levels generally influence decay relatively little on sandy soils, but have a significant effect on loams or finer-textured soils.

8.2.2 Site's Natural Nutrient Availability

Organic Matter on Top of the Mineral Soil

Nutrients, especially N and P, have received considerable attention in decomposition studies. The nutrient content of litter, the so-called endogenous nutrients, can be a major factor in regulating the patterns and rates of decomposition (cf. Chaps. 4–6). Somewhat less well understood is the role of nutrient availability in the environment, or exogenous nutrients. Nutrients are available to the community of decomposer organisms from natural biological and physical mineralization, from atmospheric input, and from fertilization. Most of the studies on the relationship between nutrient availability and litter decay have relied on fertilization, or other artificial additions. Although this approach can alter nutrient availability, there may be some impact of the pulsed nature, and the timing of nutrient addition. The relationships between the main nutrients used by decomposing microorganisms are rather strict (cf. Chaps. 2 and 5), and an excess of a single nutrient – for example, N added from an external source via, e.g., deposition – should not necessarily be expected to have an effect on, e.g., initial decomposition rate.

In the experiment mentioned above, Vesterdal and Raulund-Rasmussen (1998) compared the amount of carbon accumulated on top of the mineral soil, and soil properties (Fig. 8.1A, B). There was a clear effect of species on the sequestered amounts. Vesterdal and Raulund-Rasmussen (1998) also found an effect related to site. Taking the average values of all tree species at the different sites, they obtained average amounts that were significantly different among sites. Thus, at two sites with very low levels of extractable phosphorus, calcium, and magnesium in the mineral soil, the stored amounts of carbon (humus) on top of the mineral soil were higher than at sites with higher levels. Intuitively, we may expect that such higher carbon storage at nutrient-poor sites would be a regulating mechanism to

Table 8.1 Average values for soil nutrients as related to the organic fraction of the forest floor, formed under seven tree species in a tree trial experiment on different soils but under very similar climate conditions (from Vesterdal and Raulund-Rasmussen 1998)

Tree species	C/N	C/P	C/Ca	C/K	C/Mg
Lodgepole pine	35.2	674	264	805	753
Sitka spruce	28.7	530	94	533	648
Norway spruce	26.4	462	77	412	480
Douglas-fir	31.4	434	114	462	546
Grand fir	26.8	465	58	438	482
Common beech	26.8	465	48	337	396
Common oak	27.5	440	55	315	398

store more nutrients under nutrient-limited conditions, the reverse being the case at nutrient-rich sites.

Of the single species, lodgepole pine had formed an O-horizon that was clearly more nutrient-poor than that of the other species. In general, grand fir, common oak, and common beech had the most nutrient-rich organic layers (Table 8.1). Also worth noting is that lodgepole pine had the most C accumulated in the forest floor, and the three latter species the least.

Although nitrogen is a nutrient that often is limiting, it is one that originates from the air, like carbon. Also like carbon, N is taken up by fixation processes in plants, except for the N cycled via natural background deposition. Thus, an index for a soil's ability to store carbon would also serve as index for its ability to store nitrogen, as these two compounds are largely sequestered together.

In their approach, Vesterdal and Raulund-Rasmussen (1998) related concentrations of extractable (plant-available) mineral nutrients, originating from the mineral soil, to the amounts of carbon sequestered. They found that carbon amounts on top of the mineral soil decreased with increasing concentrations of extractable P, Ca, K, and Mg, and concluded that soil texture (see above), Ca, and P concentrations appeared to be the most important variables explaining the amounts of C in the forest floor soil organic matter. When comparing concentrations of P with forest floor C mass, clearly negative relationships were seen between the amount of carbon sequestered in the O-horizon and the mineral soil concentration of extractable P (Fig. 8.4).

The findings of Vesterdal and Raulund-Rasmussen (1998) relate to a period that may correspond to a certain stand age (30 years). Assuming that soil properties affect the soil microorganisms, such effects may decrease as a humus layer develops, and the immediate environment of the microorganisms changes. Although this may take some time, it may mean that we can not exclude the possibility of finding well-developed humus layers under deciduous stands also on nutrient-rich soils.

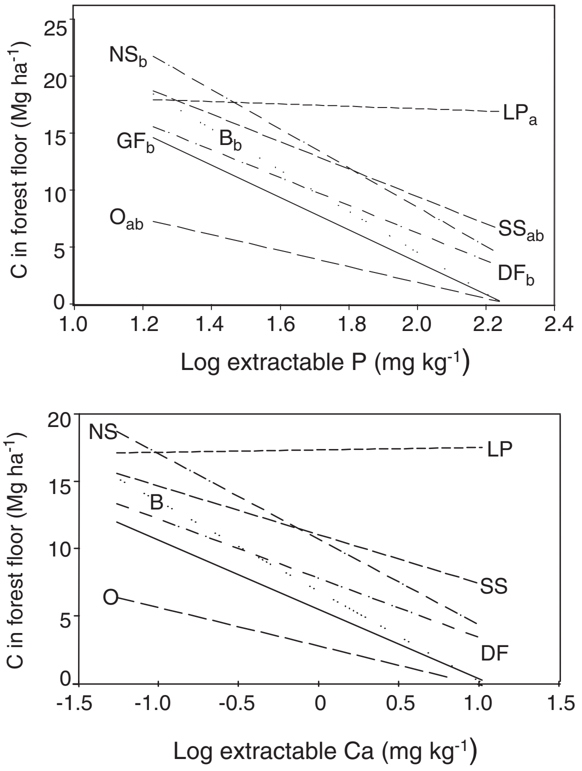

Fig. 8.4 *Top* Linear relationships between average concentrations of extractable P in the mineral soil (0–50 cm), and amounts of carbon in the forest floor SOM for seven tree species. Lines with the same *lowercase letters* do not have significantly different slopes ($p < 0.05$). *Bottom* Linear relationships between average concentrations of extractable Ca in the mineral soil (0–50 cm), and amounts of carbon in the forest floor for seven tree species. Abbreviations: *O* common oak, *B* common beech, *DF* Douglas-fir, *SS* Sitka spruce, *NS* Norway spruce, *LP* lodgepole pine (from Vesterdal and Raulund-Rasmussen 1998)

8.2.3 Artificially Added Nitrogen

Organic Matter on Top of the Mineral Soil

Nitrogen is traditionally considered the most commonly limiting factor for litter decomposition, and has received the most study. Adding N to decomposing substrates has been observed to increase the initial rate of decay (Tenney and Waksman 1929). Other studies with agricultural residues have found little effect of added N, except occasionally during the initial stages of decay (Lueken et al. 1962; Knapp et al. 1983; Bremer et al. 1991). However, when considering a longer period of decay, the effects of added N on decay rate appear to be negligible, and may even become negative (Fog 1988). We described mechanisms for this in Chapter 6.

Table 8.2 Rate constants (*k*, cf. Eq. 10.1) and limit values (cf. Eq. 10.4) calculated using the single exponential function (cf. Eq. 10.2) for Scots pine needle litter and Scots pine green needles incubated in a nutrient-poor Scots pine forest (Norrliden, Tamm 1991). Litter was incubated for 4 years (in duplicate), partly in control plots, and partly in plots fertilized with N (80 kg ha^{-1} year^{-1}) and P (40 kg ha^{-1} every 4th year; B. Berg, unpubl. data)

Concentration (mg g^{-1}) Wsol[a]	Lignin	N	P	Ca	Mn	Rate constant (year^{-1})	Limit value (%, ±SE)	NCIR
Control plots								
178.4	228.6	3.8	0.310	5.93	1.08	0.2831	71.5 (7.7)	0.0831
178.4	228.6	3.8	0.30	5.93	1.08	0.2825	74.2 (11.7)	0.1047
Fertilized plots								
178.4	228.6	3.8	0.30	5.93	1.08	0.2903	59.6 (2.4)	0.1467
178.4	228.6	3.8	0.30	5.93	1.08	0.3146	59.6 (6.1)	n.d.

[a] *Wsol* Water-soluble substances, *n.d.* not determined

There was a clear effect of N plus P fertilizer on the decomposition pattern, or extent of decomposition of Scots pine needle litter. The mass-loss data fitted well to both a single exponential (cf. Eq. 10.1) and an asymptotic function (cf. Eq. 10.4; Table 8.2). When comparing the data for fertilized and control plots, we may see that there was no real difference in the single exponential *k*. On the other hand, a distinct difference in limit values was seen, with a lower limit value in the fertilized plots (Table 8.2), thus reflecting a long-term effect of N and P. We may also see that the NCIR (cf. Chap. 5) is clearly higher for litter from the fertilized plot, indicating a higher N concentration at the same mass-loss value. In this case, we see that the addition of N and P supported an accumulation of humus.

To examine the influence of N availability on rates of litter decomposition, Prescott (1995) incubated lodgepole pine needle litter in forest plots that had received various fertilization treatments. These plots had significantly different amounts of available N in their soils, but there was no difference in cumulative mass loss after 33 months, regardless of the N available. Prescott reported similar results (i.e., no difference in decay rates) for litters of other forest species in response to addition of N-rich sewage sludge, and in laboratory microcosms.

In another approach to the question that relies on a naturally occurring N-availability gradient, McClaugherty et al. (1985; Table 8.3) incubated six foliar litter types in a reciprocal transplant study among five forest stands on Black Hawk Island, Wisconsin (Appendix III). Annual net N mineralization among the five study stands ranged from 2.9 to 12.5 g N m^{-2} year^{-1} (Pastor et al. 1984). After 2 years of decay, the only significant differences ($p<0.05$) found were with bigtooth aspen leaves and white pine needles, both of which decomposed slower in the sugar maple stand – which had the highest N availability – than in their own stands. After 5 years of decay (McClaugherty, unpubl. data), white pine needles had still decomposed less in the sugar maple stand than in the white pine stand. The only other difference after 5 years was with sugar maple leaves, which had decomposed more slowly in

Table 8.3 Mass lost as percent of initial after 2 and 5 years for six litter species incubated in forests with different levels of N mineralization (McClaugherty et al. 1985; C. McClaugherty, unpubl. data)

	NMIN[a]	Litter species					
	(g m^{-2} year^{-1})	RMW	WOL	WPN	ASL	HMN	SML
2 Years							
Sugar maple	12.5	55.6	64.8	53.2	55.3	45.1	75.4
White oak	8.4	55.2	72.7				69.9
White pine	5.2	54.6		67.5			75.5
Bigtooth aspen	4.8	44.7			62.4		66.8
Canadian hemlock	2.9	38.6				47.5	66.9
5 Years							
Sugar maple	12.5	83.2	79.8	72.1	72.8	64.1	81.4
White oak	8.4	79.1	82.6				83.2
White pine	5.2	81.8		80.7			84.5
Bigtooth aspen	4.8	82.8			83.9		82.4
Canadian hemlock	2.9	82.8				64.3	74.5

[a] *NMIN* N mineralization rate, *RMW* red maple wood chips, *WOL* white oak leaves, *WPN* white pine needles, *ASL* bigtooth aspen leaves, *HMN* Canadian hemlock needles, *SML* sugar maple leaves

the hemlock stand than in the other stands. The hemlock stand had the lowest N mineralization. Thus, N availability does influence the decay of litters under some, but not all circumstances.

In contrast to mass loss, N availability does seem to have an impact on the amount of N retained (immobilized) in decaying substrates. Magill and Aber (1998), in an N-enrichment study described in more detail in Chapter 12, found much more N remaining in litter on high N-treated plots. Similarly, McClaugherty (unpubl. data) incubated low-N red maple wood chips and high-N sugar maple leaves along the N mineralization gradient described above (Pastor et al. 1984; Fig. 8.5). After 5 years of incubation, the concentration of N in the remaining litter was weakly ($p=0.08$) correlated with the N mineralization rate at the site of incubation. We may compare this finding to the observation (cf. above) that in the fertilized plot (Table 8.2), there was a faster increase of N in the decomposing litter.

We conclude that external N availability is not of general significance in determining the rate of mass loss when considered over the continuum of litter to humus. Nitrogen availability may indirectly regulate initial decay rates by influencing the nutrient content of litter, or by influencing plant community composition, and hence the quality of the litter. However, during early stages of decay, it seems that the internal nutrient composition is more important than the external. As decay progresses to later stages, the external N concentration may have a positive influence

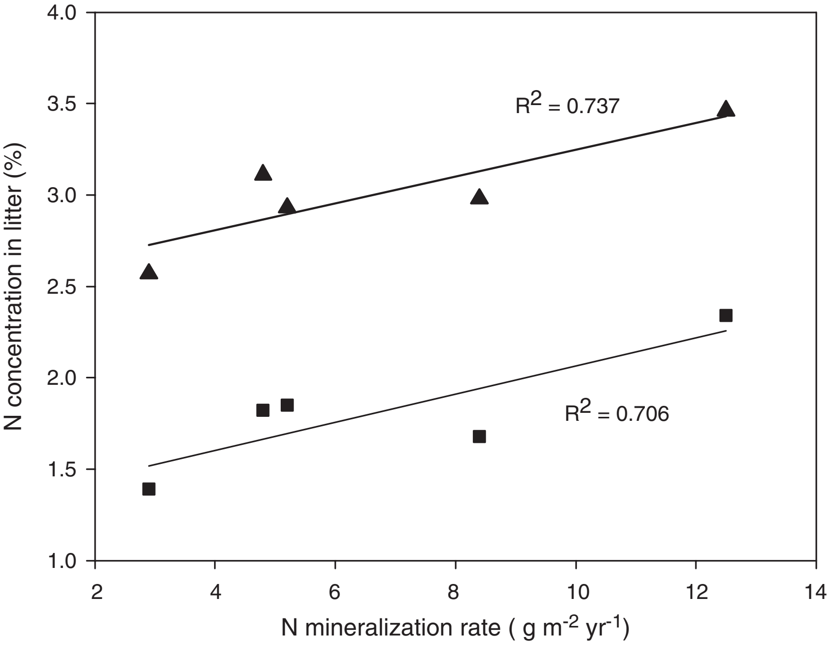

Fig. 8.5 Nitrogen concentration in sugar maple leaves (▲) and red maple wood chips (■) after 5 years of incubation in five different forests with differing N mineralization rates. All forests were located within 2 km of one another on Black Hawk Island, Wisconsin (Appendix III; from McClaugherty, unpubl. data)

on the general activity of the microbial community, but it may have a negative influence on the decay rate of the litter, due to mechanisms we have described earlier (cf. Sect. 2.4.3), and a negative influence on the extent of decomposition. The external N concentration may be of importance in determining the amount of N retained by decomposing litter in some systems, and hence the N storage in humus.

8.2.4 Forest Floor Type

The effect of forest floor type (humus types: mull, moder, or mor) is perhaps an obvious line of inquiry. The results, however, are not as clear as might be expected. Bocock et al. (1960) incubated European ash and Durmast oak leaf litter in hairnets with 1-cm openings at mull and moder sites. Oak litter decay rates were independent of forest floor type, but ash leaves disappeared much more rapidly at mull sites (Fig. 8.6). It is important to note that there was significant earthworm (*Lumbricus terrestris* L.) activity at the mull sites, and that disappearance may have been greater than actual decomposition, because material could have been easily moved out of

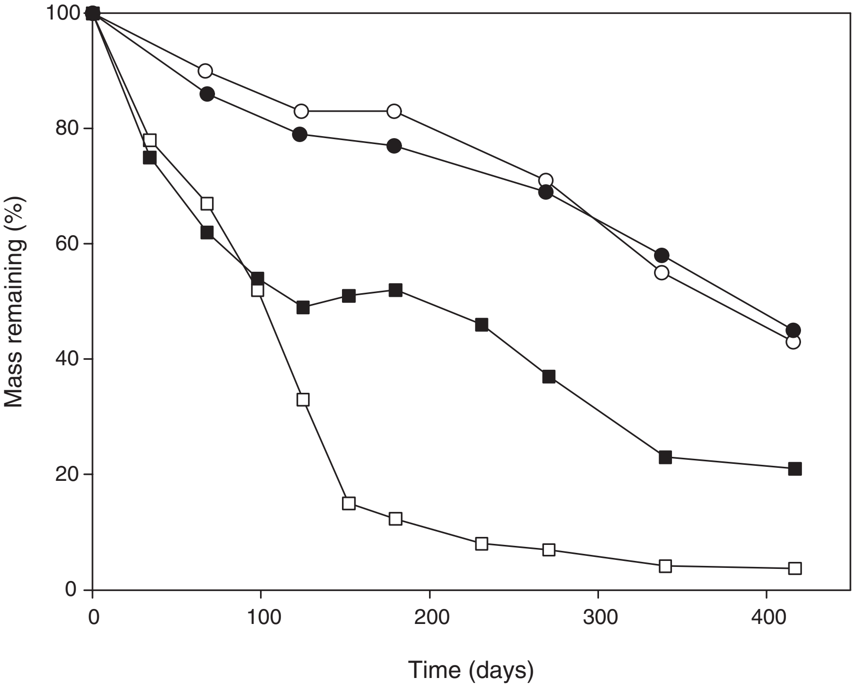

Fig. 8.6 Decomposition of deciduous leaf litters on mull, and moder forest floors. (○) oak on mull, (●) oak on moder, (□) ash on mull, and (■) ash on moder (Bocock et al. 1960)

the coarse-mesh nets. A similar study compared mull and mor sites (Howard and Howard 1980). Using reciprocal transplants of hybrid oak and silver birch leaf litters, Howard and Howard (1980) were able to distinguish between effects of species and soil types over a 2-year decay period. They incubated litter in glass tubes that were open to microorganisms, but closed to mesofauna, including earthworms. Birch leaf litter decomposed more rapidly than that of oak, a fact attributed to the ability of birch leaf litter to retain more moisture. The impact of site (mor versus mull) was not consistent in their study, with birch leaf litter decomposing more slowly at mor sites, but oak leaves decomposing at the same rate at all sites.

A study on leaf litter of common beech in southernmost Sweden (Staaf 1987) showed similar results to those of Bocock et al. (1960). The study was performed at three stands with different humus types, namely, mor, a nutrient-poor mull, and a nutrient-rich mull. Fertility, pH, and base saturation each increased from mor to mull (Table 8.4). The chemical composition of the litter was different among sites, the litter from the richer sites having higher concentrations of Ca, Mg, and S, and lower concentration of Mn. Decomposition rates of local litter measured as first-year mass loss increased with increasing site fertility when 6-mm mesh litterbags were used. Both numbers of earthworms and their biomass increased with increasing

Table 8.4 Some data for litter chemical composition, climate, and soil properties in an experiment carried out at three stands of common beech of different fertility, as reflected by humus type, viz. a mor humus, a nutrient-poor mull, and a nutrient-rich mull. The sites were climatically very similar (from Staaf 1987)

	Nutrient-poor mor	Nutrient-poor mull	Nutrient-rich mull
Litter properties			
Lignin conc. (%)	39.0	38.7	39.9
Water solubles (%)	7.6	7.8	5.5
pH (H_2O)	3.9	4.1	4.5
N (mg g^{-1})	0.92	0.93	0.81
P (mg g^{-1})	1.04	0.59	0.62
S (mg g^{-1})	1.0	1.4	1.7
K (mg g^{-1})	2.8	2.8	2.6
Ca (mg g^{-1})	7.2	10.1	15.1
Mg (mg g^{-1})	1.1	1.8	1.9
Mn (mg g^{-1})	1.9	1.6	1.0
Climate properties			
Annual avg. temp. (°C)	6.5	7.0	7.0
Annual precip. (mm)	800	650	650
Soil properties			
Bedrock	Gneiss	Silurian slates	Silurian slates
Soil type	Iron podsol (Orthic podsol)	Brown forest soil (Gleyic cambisol)	Brown forest soil (Gleyic cambisol)
Base saturation (%)	12	22	60
pH	3.5–3.8	4.1–4.4	5.0–5.4
Clay content (%)	<1	10–20	>25
Earthworms			
Numbers	2.5	39.8	219.7
Biomass (g m^{-2})	0.3	10.2	11

site fertility (Table 8.4). There was a relative effect of earthworms on decomposition (Fig. 8.7 bottom), as measured by incubating litter from the three sites at the site most rich in nutrients and with the highest earthworm population. We can also see that the effect of litter quality on first-year mass loss can be distinguished when decomposition was measured in 1-mm mesh bags to which the earthworms did not have access. We interpret the data shown in Fig. 8.7 bottom as that the increasing first-year mass loss is due exclusively, or at least largely to microbial activity. The filled bars show first-year mass loss as measured using 6-mm mesh bags, and as we can see the mass loss in the first year was doubled for leaf litter from the nutrient-poor site. Furthermore, in all three cases the mass loss was similar; we interpret this as indicating that the effect of earthworm activity on decomposition was simply less sensitive to litter quality, at least for the given species, and within the given range in chemical composition.

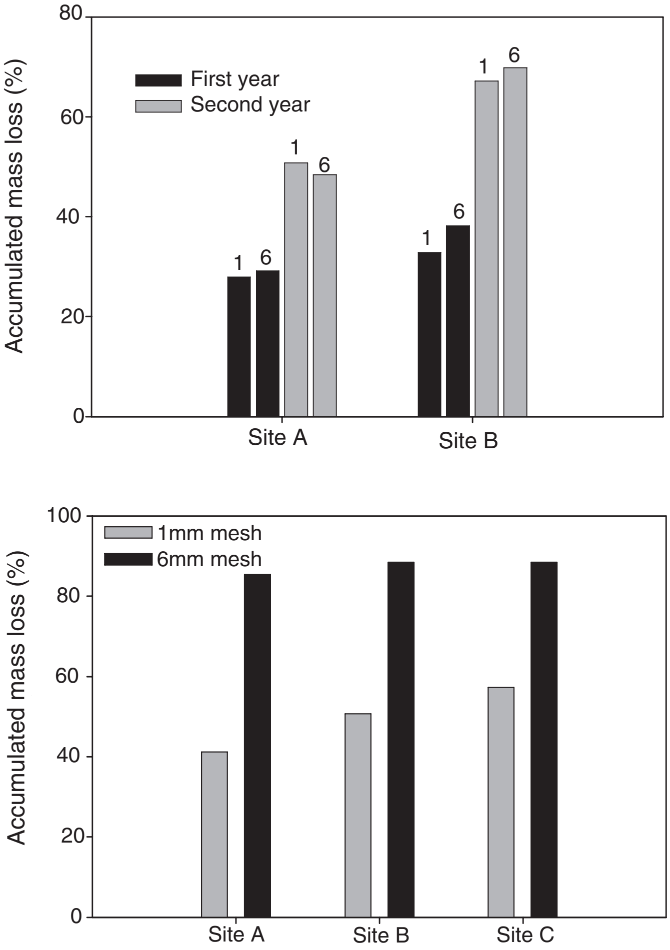

Fig. 8.7 *Top* Accumulated mass loss after 1 and 2 years of decomposition of common beech leaf litter incubated at a mor site (*A*), and a mull site (*B*). Incubations were made using 1-mm mesh allowing only microbial decomposition, and 6-mm mesh allowing access of worms to the litter. *Bottom* Mass loss after 1 year's incubation of leaf litter of common beech. Leaf litters from three neighboring sites of different nutrient status were incubated at the site most enriched in nutrients, which also had the highest abundance of worms. Incubation was made in 1-mm litterbags allowing only microbial decomposition, and in 6-mm mesh bags allowing access of worms (redrawn from Staaf 1987)

8.3 Plant Community Composition and Structure

The floristic composition of a community could influence decomposition due to either synergistic or antagonistic interactions among litter types. Furthermore, the physical structure of a community could influence microclimate, with canopy cover being an obvious structural consideration. Human activities including thinning and clear cutting can be important site factors, and these will be discussed in Chapter 12.

8.3.1 Effect of Litter Species Composition

Most studies of decomposition have followed the decay of a single species of litter. A few studies have deliberately mixed litters to investigate the possibility that a mixture reflecting the natural heterogeneity of litter fall would behave differently than a single species. Blair et al. (1990) used both single and mixed species of foliar litter in a 1-year litterbag study. They used three common co-occurring species that differ greatly in potential decay rates. In order of increasing resistance to decay, these were leaves of flowering dogwood, red maple, and chestnut oak. The individual litters decayed at rates that were expected, based on their initial chemical composition, and there was no significant effect of mixing on the decay rate. However, mixing did influence N dynamics. Addition of dogwood litter to a mixture resulted in a greater loss of N from the mixture during the first 6 months than that predicted based on the N dynamics of individual (unmixed) litters. However, after 1 year there were no significant differences in net immobilization of N in the litter mixtures containing dogwood and the other litters. Unfortunately, the study did not last into the late stage of decay, but we predict that any impacts of mixing will diminish as decomposition proceeds.

Using a somewhat different approach, Chadwick et al. (1998) incubated Scots pine needle litter in laboratory microcosms containing native litters from six different coniferous forests in Europe. The standard Scots pine needle litter that was used is the same as that used by Berg et al. (1993b) in a climatic transect study. Four of the underlying litters were Norway spruce, and two were Scots pine. The litters had a wide range of nutrient and organic-chemical composition. Mass loss of the standard Scots pine needle litter after 203 days ranged from 20 to 38%. Decay rate did not depend upon the type (pine versus spruce) of litter underlying the litterbags, but did appear to depend on the N and Ca contents of the underlying litter. The most rapid decay rates were found when the underlying litter had high N and Ca contents.

8.3.2 Community Structure and Development

Relatively few studies have examined the importance of stand development, age, or physical structure on decomposition. Some studies have examined the role of silvicultural practices such as thinning and clear cutting, which will be discussed in Chapter 12.

Many ecosystem properties change during forest succession. Turner and Long (1975) suggested that rates of litter decomposition would change as stands develop. To test this idea, Edmonds (1979) incubated needle litter for 2 years in a chronosequence of Douglas-fir stands ranging from 11 to 97 years of age. He also measured air temperature, litter temperature, and litter moisture periodically throughout the study. The youngest stand had not achieved canopy closure, but by 24 years of age the canopy was closed. The highest decomposition rate occurred in the 24-year-old stand, where temperature and moisture conditions were most favorable for decay. The lowest decomposition rates were found in the 11-year-old stand, where the lack of canopy closure created unfavorable microclimatic conditions for decay.

In mature forests, gaps of various sizes may occur. These can have microclimatological effects that influence decomposition. In a subtropical forest in China, Zhang and Liang (1995) demonstrated that gap size could have a large effect on the rate of mass loss in leaf, bark, and branch litter. They were able to demonstrate that gap size was a proximate factor, the ultimate factor being primarily soil moisture. Naturally occurring gaps ranged from 5 to 40 m in diameter. As the gap sizes increased, leaf litter annual mass-loss rates decreased from 57 to 44%. Mean gravimetric soil moisture decreased from 19.2% in the closed forest to 11.4% in the largest gaps. This factor alone gives a highly significant correlation between decay rate and soil moisture ($R^2 = 0.922$, $p < 0.001$). It is important to note that this study was done in a subtropical forest, and that the effects of gap size may change as latitude increases, as suggested by Yin et al. (1989).

Lockaby et al. (1995) superimposed a decomposition study onto a community manipulation study in loblolly pine stands. Vegetation suppression created four different communities. The treatments were (1) no suppression (control), (2) deciduous woody suppression, (3) herbaceous suppression, and (4) pine only, with both woody and herbaceous suppression. After 20 months, mass loss was highest in treatment plots where herbaceous vegetation had been removed, and lowest in the pine-only treatment (no. 4). The mechanism for this difference is not known.

8.4 Carbon Dioxide Levels

Atmospheric CO_2 continues to increase, and may double by the year 2100 (Watson et al. 1992). Considerable scientific attention has been directed toward understanding how increased CO_2 might influence ecosystems. Accordingly, several studies have examined the influence of CO_2 concentrations on decomposition. These influences can be direct or indirect. Direct influences would occur if changing CO_2 levels impacted microbial communities, or the biochemistry of decomposition. Direct effects are unlikely, or at least difficult to document, because by its very nature, decomposition takes place in a CO_2-enriched environment. One type of indirect effect would occur if changing CO_2 levels altered the chemistry of the litter. Another type of indirect effect would be linked to any climate changes. The latter effects are discussed in Chapters 7 and 12.

Franck et al. (1997) hypothesized that increased atmospheric CO_2 would cause plants to produce lower-quality litter that would decompose and release nutrients more slowly. They tested this by growing four grass species at ambient and twice-ambient levels of CO_2, and following the C and N dynamics of the litter. The results showed several interactions. The litter of species grown under enriched CO_2 had higher decay rates for three species (perennial ryegrass, soft chess, and wild oats), and a lower rate for the only native grass in the study (small six-weeks grass). Though not examined in the study, it is possible that the higher initial decay rates in the litter grown with CO_2 enrichment were due to increased production, and storage in litter, of labile C compounds.

Cotrufo and Ineson (1995) conducted a similar laboratory microcosm study with tree roots. They grew birch and Sitka spruce at 350 and 600 ppm CO_2, and under two nutrient regimes. Spruce root litters had the same mass loss, regardless of treatment, but birch roots grown under elevated CO_2 had slightly (albeit significantly) lower mass losses. This may be due to changes in litter chemistry, as the authors reported an increase in C/N ratio in roots grown under CO_2 enrichment. In a subsequent field study (Cotrufo and Ineson 1996), birch was grown under both ambient and elevated levels of CO_2. Cotrufo and Ineson (1996) examined both the litter chemical composition and its decomposition, and found that the lignin content of birch leaf litter increased from 17.7 to 28.7% when the atmospheric CO_2 concentration during growth increased from 350 to 600 ppm. Adding a slow-release mixed fertilizer containing N, P, and K decreased lignin concentrations to 13.3 and 17% at low and high CO_2, respectively. As a result, initial decay rates increased. Remarkably, unfertilized litter grown under 600 ppm CO_2 had nearly three times as much mass remaining after 1 year in the field as did fertilized and low-CO_2 litters.

In a review on the effects of increased atmospheric CO_2 on litter quality and decomposition, Cotrufo et al. (1998) suggest that the major effect is an increased C/N ratio, though relatively few species have been studied. This decrease in N concentration may have different effects on the successive stages of decay (cf. Chap. 2), possibly slowing decay during early stages, but actually increasing the total amount of mass lost by the time the litter enters the humus-near stage. Elevated CO_2 may influence the composition of the plant community in ways that would also cause changes in patterns of decomposition. For example, the relative abundance of N_2-fixing plants, or the ratio of C3 to C4 plants, could change if atmospheric CO_2 levels increase, or climate changes (Zanetti and Hartwig 1997; Huang et al. 2001).

Chapter 9
Decomposition of Fine Root and Woody Litter

9.1 Introduction

Most studies of litter decomposition in forests have focused on foliar litters because of their large amounts, and relatively high nutrient contents. Foliar litter provides an important transfer of organic matter and nutrients to the soil, and the patterns of its deposition are temporally regular and spatially rather uniform. Woody and fine (small diameter) root litter can also contribute large amounts of organic matter to forest soils. Fine root litter inputs are highly variable across ecosystems, but in at least some ecosystems, they represent a transfer of organic matter and nutrients to the soil of the same magnitude as that of foliar litter. Woody litter is deposited sporadically in time and space. Its deposition may be negligible in managed forests.

Fine roots are variably defined, usually based on diameter, and represent a rapidly changing component of forest biomass. Fine root litter differs from woody litter in several key respects. It may comprise less than 2% of the biomass present in a forest ecosystem, but it may contribute as much as 40% of the annual production (Vogt et al. 1990). Fine roots and green leaves are among the most nutrient-rich of plant tissues (Table 9.1). Furthermore, they have one of the highest surface area-to-volume ratios of any litter type. With all these characteristics, we would expect fine roots to decay very rapidly, but that is not the case, as will be discussed below.

According to Harmon et al. (1986), woody litter plays important, but poorly studied roles in forest ecosystems. Woody litter includes stems, stumps, branches, twigs, and most roots, i.e., excluding those with a small diameter. These litter components enter the soil very erratically in space and time, often as a result of sporadic events such as strong wind, heavy snowfall, or freezing rain. Furthermore, the tendency for the amount of woody litter fall to increase with stand age gives it a pattern different to that of foliar litter. A single tree may fall as a result of a storm, or death. The bulk of its biomass is concentrated along the bole and branches. The chemical and physical quality of this woody litter is quite different from that of foliar litters.

The amount of woody litter present in forests varies by two orders of magnitude from about 1 Mg ha^{-1} in dry tropical forests, to 500 Mg ha^{-1} in old-growth coniferous forests in the Olympic Mountains in the Pacific Northwest of the USA (Agee

B. Berg and C. McClaugherty, *Plant Litter*,

Table 9.1 Representative concentrations of nutrients in living leaves, wood, and fine roots. For leaves and wood, values are averages for four species groups: European white birch, common oak, filbert, and European ash. For fine roots, values are taken from a northern hardwood forest containing sugar maple, yellow birch, American beech, and red spruce

	Concentrations as % of dry matter				
	N	P	K	Ca	Mg
Leaves[a]	2.28	0.19	1.45	1.26	0.29
Wood[a]	0.30	0.03	0.21	0.32	0.046
Fine roots (0.6 mm)[b]	2.00	0.10	0.23	0.21	0.05

[a] Swift (1977)
[b] Fahey et al. (1988)

and Huff 1987). However, most ecosystems fall into the range of 5 to 50 Mg ha^{-1} (Table 9.2). Woody litter often increases immediately after a harvest, due to logging slash (McCarthy and Bailey 1997; Table 9.2). However, older managed stands can have less woody litter than do corresponding old-growth stands (Goodburn and Lorimer 1998; Table 9.2). Estimates have been made of the proportion of woody litter fall relative to foliar litter. Using foliar litter fall as reference in a mature Scots pine forest, the woody litter fall (cones excluded) made up ca. 10%, and cones separately ca. 25% (Berg et al. 1993d).

Not only is woody litter deposited unevenly, but it also occurs in a huge array of sizes and conditions. Clearly, the diameter of the woody debris will influence surface area-to-volume relationships in a way that results in more rapid decay of smaller-diameter pieces. Furthermore, wood can undergo extensive decay before falling to the ground. This could be due to pathogens on living trees, or saprophytic organisms on snags. In contrast, a storm may blow over, or break limbs from a living tree.

One of the most important aspects of woody litter in terms of its decomposition is its extremely low nutrient content. This means that organisms must either consume very large quantities in order to extract sufficient nutrients, or that the nutrients must be supplemented from outside the substrate. Such a low-nutrient environment would be most suitable for organisms with low nutrient demands. A comparison of initial nutrient concentrations in wood, fine roots, and leaves is shown in Table 9.1.

9.2 Woody Litter Decomposition

9.2.1 Methods

Decay Classes for Coarse Wood (logs)

The state of decay of logs is often categorized using decay classes. Decay classes are based on visual and physical properties of wood. Although different investigators have given somewhat different definitions to each decay class, this approach is

Table 9.2 Mass of dead wood on the ground in selected types of forest stands

Forest type	Location	Mass (Mg ha^{-1})
Coniferous stands – boreal and temperate		
Douglas-fir–hemlock[a]	Oregon/Washington, USA	500
Boreal fir–spruce[b]	Newfoundland, Canada	4–22
Rocky Mt. spruce–fir[c]	Colorado, USA	52
Ponderosa pine[d]	Colorado, USA	3–5
Deciduous stands – boreal and temperate		
Aspen[e]	Alberta, Canada	15–25
Southern maple[f]	Tennessee, USA	14
Northern hardwood[g]	New Hampshire, USA	21–30
Hemlock–hardwoods[h]	Wisconsin/Michigan, USA	16
Mixed oak[i]	Kentucky, USA	16–22
Southern beech[j]	New Zealand	300
Managed temperate stands		
Northern hardwood – even-aged[k]	Wisconsin/Michigan, USA	6
Northern hardwood – selection[k]	Wisconsin/Michigan, USA	15
Northern hardwood – old-growth[k]	Wisconsin/Michigan, USA	29
Appalachian hardwood 2 years[l]	Maryland, USA	55
Appalachian hardwood 25 years[l]	Maryland, USA	17
Appalachian hardwood 80 years[l]	Maryland, USA	19
Appalachian hardwood >100 years[l]	Maryland, USA	33
Tropical stands		
Tropical thorn woodland[m]	Venezuela	1
Tropical very dry[m]	Venezuela	1
Tropical transition[m]	Venezuela	3
Tropical moist[m]	Venezuela	18
Tropical low montane moist[m]	Venezuela	21
Tropical montane wet[m]	Venezuela	18

[a] Agee and Huff (1987)
[b] Sturtevant et al. (1997)
[c] Arthur and Fahey (1990)
[d] Robertson and Bowser (1999)
[e] Lee et al. (1997)
[f] Onega and Eickmeier (1991)
[g] Gore and Patterson (1986)
[h] Goodburn and Lorimer (1998)
[i] Tyrell and Crow (1994)
[j] McCarthy and Bailey (1997)
[k] Muller and Liu (1991)
[l] Stewart and Burrows (1994)
[m] Delaney et al. (1998)

widely used, and a general scheme for decay classes is given in Table 9.3. Much of the recent literature has used a five-stage progression of decay, designated as decay classes I through V. This concept was first articulated by Maser et al. (1979) for coniferous trees, and has been more recently adapted to deciduous trees by Pyle and Brown (1998). One of the problems with this system is that objects as large as logs

Table 9.3 System of decay classes used in wood decay studies (modified from Maser et al. 1979, and Pyle and Brown 1999)[a]

	Decay class				
Characteristic	I	II	III	IV	V
Bark attached tightly	+	−	−	−	−
Wood not stained	+	−	−	−	−
Bark present, perhaps loose	+	±	−	−	−
Twigs retained	+	±	−	−	−
Wood solid, resistant	−	+	±	−	−
Log surface may flake, fall into shreds	−	−	+	−	−
Log solid, but decay clearly evident	−	−	±	+	−
Logs easily broken into large pieces	−	−	−	+	−
Log easily crushed	−	−	−	+	±
Log more than 85% powdery	−	−	−	±	+
Log shape oval to nearly flat	−	−	−	±	+

[a]+, Present; ±, present or absent; −, absent

do not decay uniformly. For one, logs are composed of substrates of different quality (e.g., inner and outer bark, sapwood, heartwood), each of which decays at a different rate, and begins to decay after different lag periods (Schowalter 1992). Furthermore, a particular log may be invaded by fungi with different mechanisms for decomposing wood (Boddy et al. 1989), and thus may contain parts in several different decay classes (Pyle and Brown 1999).

Mass-Loss Rates: Percent Loss and Decay Constants (k)

Many reports of wood decay use a decay constant, calculated in the sense of Olson (1963; see Eq. 10.1). It can be calculated based on a single point, using Eq. (9.1).

$$k = \frac{-\ln\left(\frac{M_t}{M_0}\right)}{t} \tag{9.1}$$

where M_t is mass at time t, and M_0 is initial mass ($t=0$).

The decay rate constant, k, can also be calculated using multiple points over time, and fitting a linear regression to the line formed by the natural log of mass versus time. The slope of this regression line is $-k$. This latter approach is better than the single-point approach, because it includes data taken over the course of decay. However, most litters, and especially wood, seldom decay at a constant rate, and the use of k can thus be misleading. For example, Fig. 9.1 shows both percentage mass loss and the changing value of k during decomposition of logs. Whenever available,

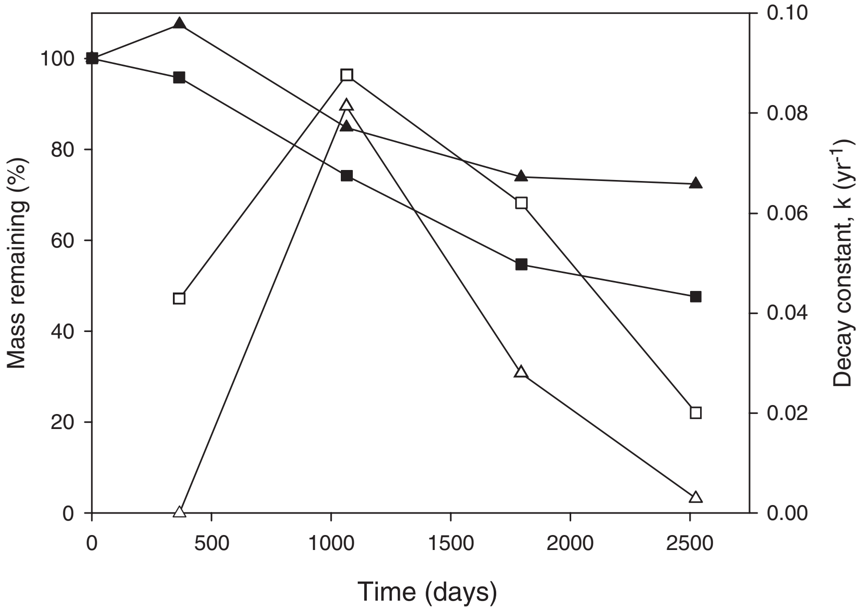

Fig. 9.1 Percentage of initial mass remaining, and decay rate constants (*k*, sensu Olson 1963) during each measured period for red pine and red maple logs incubated under a temperate climate in a red pine plantation, and an adjacent mixed hardwood forest at Harvard Forest, Massachusetts, USA. *k* values were calculated for each interval of the study. ■ Red maple % mass remaining, ▲ red pine % mass remaining, □ red maple *k*, and △ red pine *k* (C. McClaugherty, unpubl. data)

we present decomposition data as a percentage of the initial mass that is lost; however, many studies present only *k* values, and therefore we report those also.

Estimating Mass Loss in Coarse Woody Litter

Litterbags have been the dominant technique for studying foliar litter decomposition. For coarse wood, the sheer size, and the long life expectancy of the log make litterbags inappropriate. Most studies have relied on density changes to estimate mass loss, though this approach is not without its own problems. Volume displacement in water as a means of determining bulk density is commonly used, but it becomes less accurate as wood enters later stages of decay, and loses its structural integrity. Furthermore, bulk density measurements do not account for losses due to fragmentation and removal by tunneling arthropods. The methods for studying woody detritus have been well summarized by Harmon and Sexton (1996).

Litterbags have been used to study the decay of wood chips (see below). This technique enables a more direct comparison of wood with foliar litter, as a substrate, by eliminating the differences caused by the volume of the log.

Table 9.4 Representative decomposition rate constants (k, year^{-1}, see Eq. 9.1) for large woody debris

Ecosystem	Location	k
Boreal coniferous[a]	S Norway	0.033
Boreal coniferous[b]	NW Russia	0.019–0.108
Temperate deciduous[c]	Tennessee, USA	0.086
Temperate deciduous[d]	Indiana, USA	0.018–0.045
Temperate deciduous[e]	New Hampshire, USA	0.096
Temperate mixed[f]	Minnesota, USA	0.042–0.080
Temperate mixed[g]	Michigan/Wisconsin, USA	0.021
Temperate coniferous[h]	British Columbia, Canada	0.022
Tropical evergreen[i]	Brazil	0.015–0.67
Tropical dry[j]	Mexico	0.008–0.615

[a] Næsset (1999)
[b] Harmon et al. (2000)
[c] Onega and Eickmeier (1991)
[d] MacMillan (1988)
[e] Arthur et al. (1993)
[f] Alban and Pastor (1993)
[g] Tyrell and Crow (1994)
[h] Stone et al. (1998)
[i] Chambers et al. (2000)
[j] Harmon et al. (1995)

9.2.2 *Decomposition Rates Versus Climate*

Mass-loss rates of woody litter vary dramatically among climatic zones (Table 9.4), and among litter species. Yin (1999) has presented a very thorough compilation of woody debris decay studies. Temperature appears to be the most important climatic variable for large logs, at least in a wide range of tropical systems (Chambers et al. 2000), perhaps because the volume of the logs enables them to buffer changes in moisture. In fact, excessive moisture could suppress log decay by creating zones of low oxygen availability. However, the variation in decay rates among species within a single climate type can be greater than the variation of a single species across a range of different climates. This can generally be attributed to substrate quality, though this term is somewhat difficult to define for wood.

It is possible that physical factors relating to wood structure, such as porosity, play a more important role in regulating decomposition than do different nutrient levels. Thus, in an experiment with aspen and European beech wood sticks incubated for 1 year in the forest floor, the more porous aspen wood lost more than 50% of its initial mass, while the less porous beech had a barely measurable mass loss (B. Berg, unpubl. data).

Mass-loss rates change over time as logs become more decayed. McClaugherty (unpubl. data) has followed the decay of red maple and red pine logs for 7 years in a temperate deciduous forest, and an adjacent red pine plantation in Harvard Forest, Massachusetts, USA (Appendix III, Fig. 9.1). The species decay at different rates, but both have similar patterns of decay. The decay during the first year was very slow (not measurable in red pine). The highest decay rates occurred in the interval between years 1 and 3. The decay rate then slowed in the subsequent periods. Schowalter et al. (1998) observed a similar phenomenon in oak logs, describing their decay with a two-phase exponential decay model. They suggested that a slower, third exponential decay phase would likely emerge as decomposition proceeded.

The kinetics of decay in coarse woody debris is complicated because different parts of the log may be undergoing attack by microbial species or communities with very different metabolic abilities. In the simplest sense, an entire log could be invaded by either white-rot, or brown-rot fungi.

Smaller-diameter woody debris has been less well studied. Erickson et al. (1985) compared the decay of logging residue in two diameter classes in a variety of temperate coniferous forest ecosystems in Washington State, USA. They found that smaller-diameter (1–2 cm) twigs decayed much slower than did the larger-diameter (8–12 cm) pieces, and attributed this to the fact that smaller-diameter fragments dried more quickly, thereby suppressing decay. In their study, decay rate constants (*k*) for small-diameter slash ranged from 0.004 to 0.011, much lower than for most large or coarse woody debris (Table 9.4).

Twigs (< 5 cm diameter) of red pine and red maple, tethered to nylon strings on the forest floors of a red pine plantation and a red maple–red oak forest, respectively, in Massachusetts, USA, exhibited highly variable mass loss (Fig. 9.2; McClaugherty,

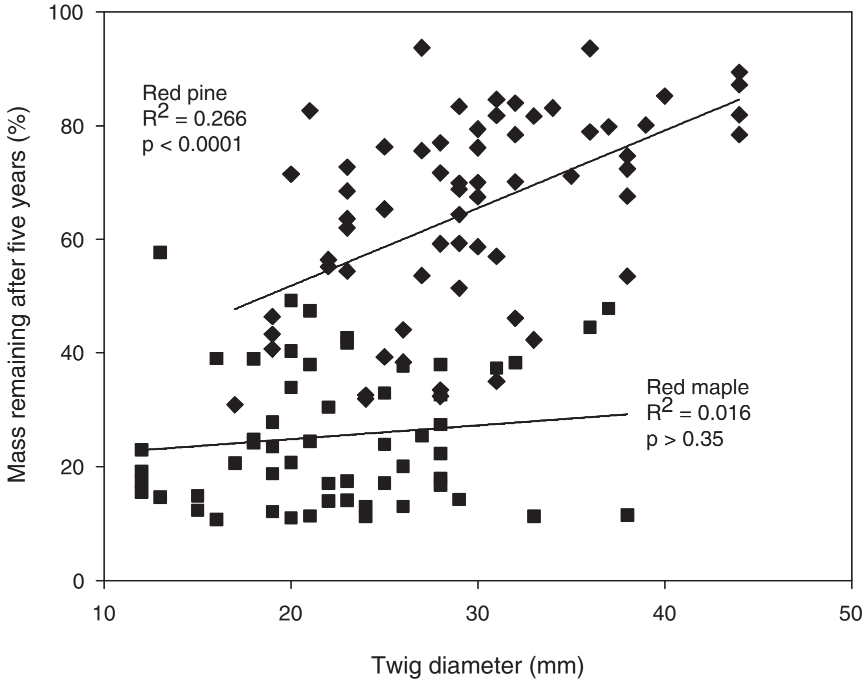

Fig. 9.2 Mass remaining after 5 years of field incubation of twigs (< 5.0 cm diameter). Twigs were incubated in a mature red pine plantation, or in a mixed mesophytic forest dominated by red oak and red maple. The study was conducted in Harvard Forest (see Appendix III). ◆ Red pine, ■ red maple (C. McClaugherty, unpubl. data)

unpubl. data). After 5 years, red pine twigs had lost considerably less mass (35.0%) than had those of red maple (74.6%). Diameter had no effect on mass loss in red maple twigs. A linear regression for pine twig mass loss versus diameter was significant ($p<0.001$), but the R^2 was only 0.266.

9.2.3 Carbon Dioxide Release

Decomposition of wood has also been measured as CO_2 release or respiration. This method enables more instantaneous assessment of C flux, compared to periodic mass-loss measurements. In a pair of studies, Marra and Edmonds (1994, 1996) measured respiration from logs in decay classes I through III and V (they did not measure decay class IV), in a clear-cut and an old-growth forest on the Olympic Peninsula of Washington State, USA. As expected in this seasonal environment, respiration reached a maximum in summer, and a minimum in winter. Variability was greater in the clear cut, but overall there was no difference between the clear-cut and the old-growth forest. Species did differ, however, western hemlock logs having higher respiration rates than those of Douglas-fir. This reflects the greater amount of inhibitory secondary compounds such as tannins and extractable phenols found in the wood of Douglas-fir (Kelsey and Harmon 1989). The results are similar to those of other studies that have compared the decay of these two species (Graham and Cromack 1982).

9.2.4 Organic-Chemical Changes

Studies of chemical changes during litter decay began in the early 20th century. Among the early studies, Rose and Lisse (1916) described the chemical composition of fresh, partially decayed, and “completely” decayed Douglas-fir wood. “Completely” decayed means that the wood has lost its structural integrity, and would correspond to decay class V (Table 9.3). They noted the resistance of lignin to decomposition, and suggested the possibility of connecting decayed organic matter and lignin residues to humic substances in the soil. Bray and Andrews (1924) demonstrated that various fungi acted differently on the cellulose and lignin of wood (cf. Chap. 3), with brown-rots acting only on cellulose. Using more recent technology, namely, ^{13}C nuclear magnetic resonance, Preston et al. (1990) characterized the chemical changes in decaying heartwood of Douglas-fir, western hemlock, and western red cedar. They distinguished changes in the relative amounts of C in carbohydrates, lignin, aliphatic groups, and the sum of carboxyl plus carbonyl groups. Douglas-fir and hemlock wood followed the more classic pattern, with a rapid decline in carbohydrate C to less than 10% of the original amount, and an increase in the relative amount of lignin C. In contrast, western red cedar wood showed little change in organic-chemical composition, even though density had declined, and the physical structure had collapsed.

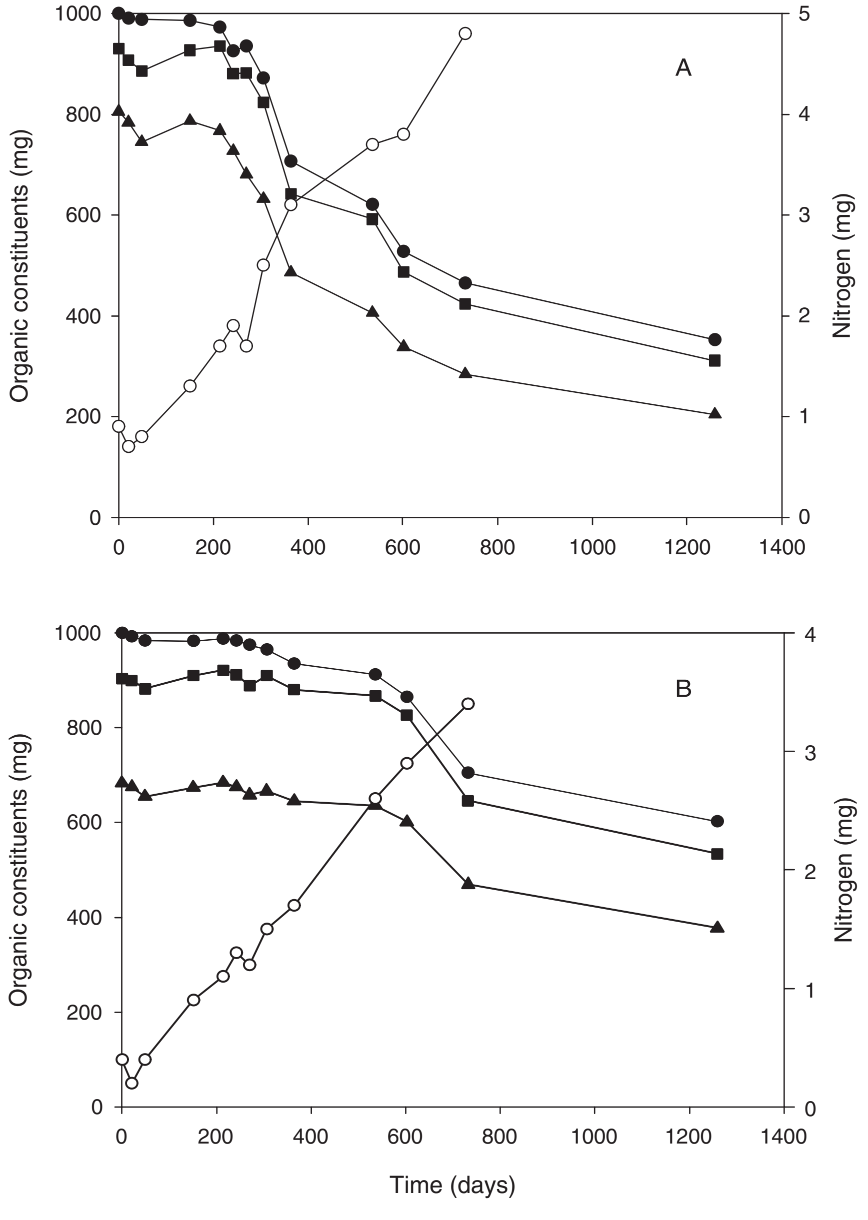

Fig. 9.3 Changes in amounts of some organic constituents and N over time in wood chips incubated in litterbags on the forest floor of a sugar maple forest on Black Hawk Island (see Appendix III). Organic constituents and N are each expressed as mg g^{-1} initial material. **A** Red maple wood. **B** White pine wood. ● Total organic matter, ■ lignocellulose, ▲ lignin, ❍ total N (C. McClaugherty, unpubl. data)

The loss of holocellulose dominates mass loss, at least during the initial stages of wood decay. Figure 9.3 shows the amounts of lignocellulose, lignin, and extractives remaining in wood chips of red maple and white pine during 42 months of decay on the forest floor of Black Hawk Island, Wisconsin (Appendix III). Although red maple wood lost considerably more mass than that of white pine, both species exhibited similar patterns of mass loss and change in chemical composition. Mass-loss patterns were similar to those observed in earlier studies: slow during the first year, faster during the second year, and then slower again in the third year.

9.2.5 Changes in Nutrient Concentrations

Woody litter contains relatively small amounts of nutrients, especially compared to foliar and root litter (Table 9.1). However, there is no clear agreement on the nature of nutrient dynamics in woody debris. Most investigators have found that decomposing wood accumulates some elements (e.g., N, P), retains some, and releases still others (e.g., K). Alban and Pastor (1993) studied logs of aspen, spruce, red pine, and jack pine that had decayed for 11 to 17 years, and compared the amounts and concentrations of nutrients in the original logs with those in the decayed logs. The concentration of N increased by an average factor of 4.3, from 1,090 to 4,698 ppm. Concentrations of P also increased in all four species, the average increase being from 120 to 348 ppm, a factor of 2.9. Potassium concentrations remained about the same, the average concentration increasing from 731 to 784 ppm. Concentrations of Ca increased from 2,225 to 5,784 ppm, and of Mg from 206 to 504 ppm. Initial concentrations of all nutrients were higher in aspen wood than in that of the conifers, but the nutrient concentrations increased by a larger factor in the three conifer species. In a study of Sitka spruce and western hemlock, Graham and Cromack (1982) found that N accumulated (net transport into the wood) in western hemlock, but not in Sitka spruce, though the concentration of N increased in both species. Concentrations of other elements (P, Ca, Mg, K, Na) did increase, but their (absolute) amounts did not.

When comparing net movement of nutrients over the entire span of decomposition (all five decay classes) for Douglas-fir wood, Means et al. (1992) observed that N and K were lost, Ca and Mg were accumulated, and P and Na were accumulated and then released, with no overall net change. In a northern hardwood forest, Arthur et al. (1993) examined the change in nutrients in logs that had been on the ground for 23 years following a clear cut. They estimated that during that time the logs had released, as a percentage of initial content, 31% of N, 68% of P, 77% of Mn, and between 86 and 93% of Ca, K, Mg, and Na. At different stages of decay, and for different nutrients, logs may be either net sinks or net sources of nutrients for the soil.

Krankina et al. (1999) measured the concentrations of 12 nutrients (N, P, K, Ca, Mg, Al, Cu, Fe, Zn, Na, B, Mn) in decaying logs of Scots pine, Norway spruce, and birch in northwestern Russia. They found that nearly all nutrients showed an increase in concentration as logs passed through decay classes III, IV, and V. The exceptions were K, which did not increase in pine and birch logs, and B, which did not increase in spruce and pine logs. Although concentrations of many of these elements increased, there was no net accumulation of nutrients over the course of decay, except for Al, which accumulated in wood of pine and birch, and Na, which was retained throughout decay.

N_2 fixation. With the low N concentration in wood, even low N_2-fixation rates could be important in influencing the N concentration of the wood during its decay. N_2 fixation has been noted in decaying logs, and may be of importance in the N dynamics of wood decay. Using acetylene reduction to estimate the potential for N_2 fixation, Larsen et al. (1978) found that brown-rotted wood was more likely than white-rotted wood to support N_2 fixation, and that there were differences between species, with Douglas-fir wood having higher rates. Jurgensen et al. (1984), and Griffiths et al. (1993) found that the N_2-fixation potential increased as decay proceeded. The rate of N_2 fixation in rotting wood is generally low, but potentially important to the N dynamics of the log (Larsen et al. 1982).

Fungal transport. Fungi that decompose wood can be important in transporting nutrients into, or out of the decaying wood. Although the actual work of decay is done by hyphae penetrating the wood, nutrients are transferred to, and accumulated by, two particular fungal structures that are on, or above the surface of the wood: rhizomorphs and sporocarps. Sporocarps are the fruiting bodies, or reproductive structures, of fungi, and they often appear on wood during the first decade of its decay. Their tissues are greatly enriched in nutrients, in contrast to the woody substrate. Harmon et al. (1994) found that fungi had concentrations of N, P, and K that were 38, 136, and 115 times, respectively, as high as the concentrations in the logs on which the fungi were growing. This enrichment occurs largely by mycelial transport from the log and the surrounding environment into the sporocarp. Although small in mass, the fungi transferred measurable amounts of nutrients out of the logs and into the sporocarps, clearly against the nutrient gradient. The amounts of nutrients found in the sporocarps, expressed as percentage of the total amounts initially present in the logs, were 0.9–2.9% for N, 1.9–6.6% for P, and 1.8–4.5% for K.

After fungi have decayed a substrate, they must eventually forage for new substrates, reproduce sexually, or perish. In many basidiomycetes, fungal hyphae can aggregate into cords or rhizomorphs, and grow until they encounter suitable substrate. The cords can form long-lived networks that have the ability to transport, e.g., C and P over one meter (Boddy and Watkinson 1995). For both fruiting bodies and rhizomorphs, nutrients are moved and concentrated.

Although wood is low in nutrients, it demonstrates a wide variety of decomposition patterns. Because of its low nutrient status, its decay may be more dependent on an exogenous supply of nutrients. Given this wide diversity of nutrient dynamics, it is not at present possible to define a general conceptual model for changes in nutrient concentrations during wood decay. The variability among the example studies given above may be due to species, environmental, and methodological differences.

9.3 Fine Root Decomposition

Estimates of root litter input are highly variable. Because of the difficulty of measuring root processes, few studies on fine root litter production have been done. Similarly, root decomposition occurs below ground, and is difficult to examine without significantly disturbing the system. Nevertheless, fine root litter may represent a large input of organic matter into ecosystems, and the decay of roots has implications for organic matter and nutrient dynamics in ecosystems.

It is important to note that fine roots are markedly different from larger-diameter roots. The definition of fine roots cannot be made solely on the basis of diameter, because species differ. Fine roots can be defined to include root tips and small-diameter roots without secondary growth. Thus, fine roots have, in general, about the same diameter, or less, as root tips. In fact, root tips may be slightly larger in diameter, due to mycorrhizal coverings.

9.3.1 Fine Root Litter

Amounts of Litter

In contrast to aboveground litter, it is not possible to directly measure fine root litter production. A variety of methods have been used to approach this problem. Several investigators have used sequential measurements of live and dead roots to develop estimates of production, mortality, and decomposition (Persson 1980; McClaugherty et al. 1982; Santantonio and Hermann 1985). This mass-balance approach assumes that decreases in living biomass are due to death, which is therefore equivalent to litter production. Timing and frequency of sampling are important in this technique. Kurz and Kimmins (1987) analyzed this method using a computer simulation, and found that the estimates were very sensitive to violations of the assumptions, and that estimates could be either too high or too low.

Rhizotrons (direct viewing through underground windows or tubes; Hendrick and Pregitzer 1992; Burke and Raynal 1994) enable direct observation, but some disturbance of the rooting environment is inevitable. Another method involving elemental budgets was proposed by Nadelhoffer et al. (1985), and developed further by Raich and Nadelhoffer (1989). In this technique, fine root production is estimated by using fine roots to “balance” the nutrient budget.

With all these techniques (see review by Hendricks et al. 1993), we are still not able to precisely measure the transfer of fine root litter to the soil. Vogt et al. (1996) reviewed the literature, and found 41 datasets that included estimates on belowground litter transfer. The values were derived from different investigations, and the methods were not comparable. Nevertheless, the estimates for belowground litter input, which is predominantly from fine roots, ranged from 100 g m^{-2} year^{-1} in a northern hardwood forest in New Hampshire, USA, to 1,262 g m^{-2} year^{-1} in a Pacific silver fir forest in Washington State, USA, with a mean of 436 g m^{-2} year^{-1}. These values are similar to the amounts of foliar litter fall.

Chemical Composition of Fine Roots

Fine roots have rather high "lignin" concentrations, compared to wood and foliage (cf. Table 4.8), in the range of 25 to 50% (Vogt et al. 1991). Nitrogen concentrations also tend to be relatively high, generally in the range of 1 to 2%, especially compared to wood (Table 9.1), but other nutrients are less predictable. Because of their location in the soil, fine roots may accumulate elements such as aluminum (Dahlgren et al. 1991). Furthermore, the tips of many, if not most, fine roots in forests are mycorrhizal. The mycorrhizal association may have a direct influence on chemical composition, due to the presence of fungal biomass, as well as indirectly by influencing nutrient concentrations in the root environment, and possibly by influencing the decay resistance of the root (Harley and Smith 1983).

9.3.2 Mass-Loss Rates

Researchers have had considerable difficulty reconciling the apparent high productivity of fine roots in forest ecosystems with the apparent low decomposition rate of fine root litter in forests (Fahey and Hughes 1994). It is unclear whether the problem is due to errors in the production estimates, or in the decomposition estimates, or both.

Litterbag methodology. Most studies of mass loss in fine roots have utilized a litterbag approach, though some have used sequential measures of dead and live root mass (see above). Litterbags are generally filled with excised live roots that are dried, killing at least a proportion of the attached mycelia. For foliar litter, the bags are generally filled with newly and naturally senesced material. Another difference in comparison with foliar litter is that fine root litter remains in the place where the roots die, possibly already attached to, or at least closely surrounded by saprophytic microorganisms. Removing fine roots from this environment, placing them into a litterbag, and then reburying them is much more "drastic" than placing leaves or needles into litterbags. Nevertheless, litterbags continue to be used, and so far, there have been no definitive studies that show if, or how seriously litterbags modify the decay of fine roots. Accepting that fine root decay studies are subject to a rather large and uncertain amount of error, we will nevertheless proceed to summarize some of these studies.

Studies on fine root mass loss. Selected first-year mass losses (%) for a variety of fine roots are given in Table 9.5. In boreal forests, first-year mass loss ranged from 19 to 40%, much of this variability being due to climate (Berg et al. 1998). One

Table 9.5 First-year mass loss of fine roots in a variety of ecosystems

Species/system	Diameter (mm)	Mass loss 1st year (%)	Comments
Boreal			
Scots pine[a]	2–3	19.3–40.9	Sweden, latitudinal climatic transect, 18 sites
Norway spruce[a]	2–3	27.4–39.7	Sweden, latitudinal climatic transect, 12 sites
Lodgepole pine[a]	2–3	29.8–35.3	Sweden, four sites
Norway spruce[b]	<1	23.5	Estonia
Norway spruce[b]	1–2	21.6	Estonia
Temperate			
N. hardwoods[c]	<1	17	White Mountains, New Hampshire, USA
N. hardwoods[d]	<0.5	30	Adirondacks, New York, USA
N. hardwoods[d]	0.5–1.5	17.4	Adirondacks, New York, USA
N. hardwoods[d]	1.5–3.0	20.9	Adirondacks, New York, USA
White pine[e]	<3	21.5	Sugar maple forest, Black Hawk Island
Sugar maple[e]	<3	15.4	Sugar maple forest, Black Hawk Island
Tropical			
Tabonuco[f]	<2	99.8–99.9	Puerto Rico, tropical montane rain forest
Sierra palm[f]	<2	36.7–43.4	Puerto Rico, tropical montane rain forest

[a] Berg et al. (1998)
[b] Lõhmus and Ivask (1995)
[c] Fahey et al. (1988); northern hardwoods refers to sugar maple, American beech, yellow birch, and red spruce
[d] Burke and Raynal (1994); northern hardwoods sample from forest dominated by sugar maple, American beech, yellow birch, and red maple
[e] Aber et al. (1984); cf. site description in Appendix III
[f] Bloomfield et al. (1993)

study from Puerto Rico compared two species, Sierra palm and Tabonuco, a tropical hardwood tree. The roots from the hardwood tree almost completely disappeared after 1 year, while the palm roots lost only 37 to 43% (Bloomfield et al. 1993). In this case, the sites had a similar climate, so the contrast between the two species is most likely due to differences in chemical composition.

Decomposition of fine roots of sugar maple and white pine roots was followed in a 10-year litterbag study in a temperate sugar maple forest on Black Hawk Island, Wisconsin (Appendix III; McClaugherty, unpubl. data; Fig. 9.4). After 10 years, sugar maple fine roots had lost 56.5% of their initial mass, and white pine fine roots had lost 66.4%. White pine roots lost more mass than did sugar maple roots during their first year of decay. After that, decay rates remained constant. This illustrates again that relying on first-year mass-loss rates to predict longer-term decomposition may be incorrect.

Factors that influence fine root decay rates. Silver and Miya (2001) collected and analyzed 176 datasets on root decomposition. Their analysis included broadleaf, coniferous, and graminoid roots, and sites with latitudes ranging from 4 to 66°N. Using stepwise multiple regression, they found that AET, root Ca concentrations, and C-to-N ratios accounted for 90% of the variability in early-stage root decay rates (*k* values). They concluded that, on a broad scale, root chemistry was

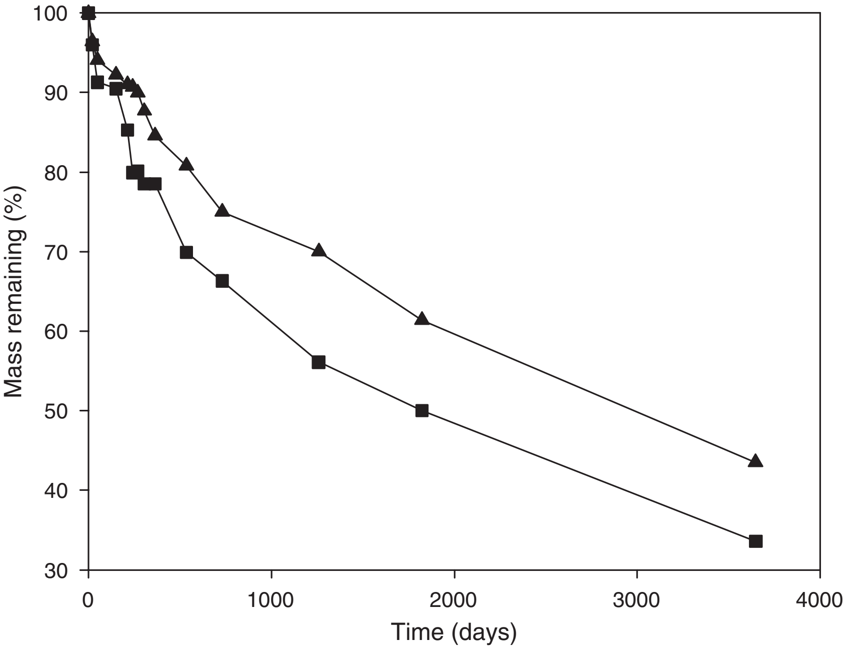

Fig. 9.4 Mass remaining in fine roots incubated in litterbags over a 10-year period in a sugar maple forest floor on Black Hawk Island (see Appendix III). ▲ Sugar maple, ■ white pine (C. McClaugherty, unpubl. data)

the primary determinant of root decomposition rates, with secondary roles for climate and environmental factors. Looking at fine roots only (defined here as <2 mm in diameter), conifer roots decayed much more slowly than broadleaf roots. It is noteworthy that their results show a greater importance of chemistry than of climate, which is in contrast to what has been observed for most foliar litter species (cf. Chap. 7). Silver and Miya (2001) suggest that because roots are buried in the soil, they are more buffered from climatic conditions.

Studies in boreal and temperate forests have also indicated that the chemical composition of fine roots influences their decay rates. For example, Camiré et al. (1991) noted that fine root decay rates appeared to be inversely related to their initial N concentrations. They based this on their own findings with black alder and hybrid poplar roots, and on comparison with the results of Berg (1984), and McClaugherty et al. (1984).

9.3.3 Changes in Chemical Composition

Fine roots are chemically similar to foliar litter, so one would expect that their organic-chemical composition would change during decay with a pattern similar to

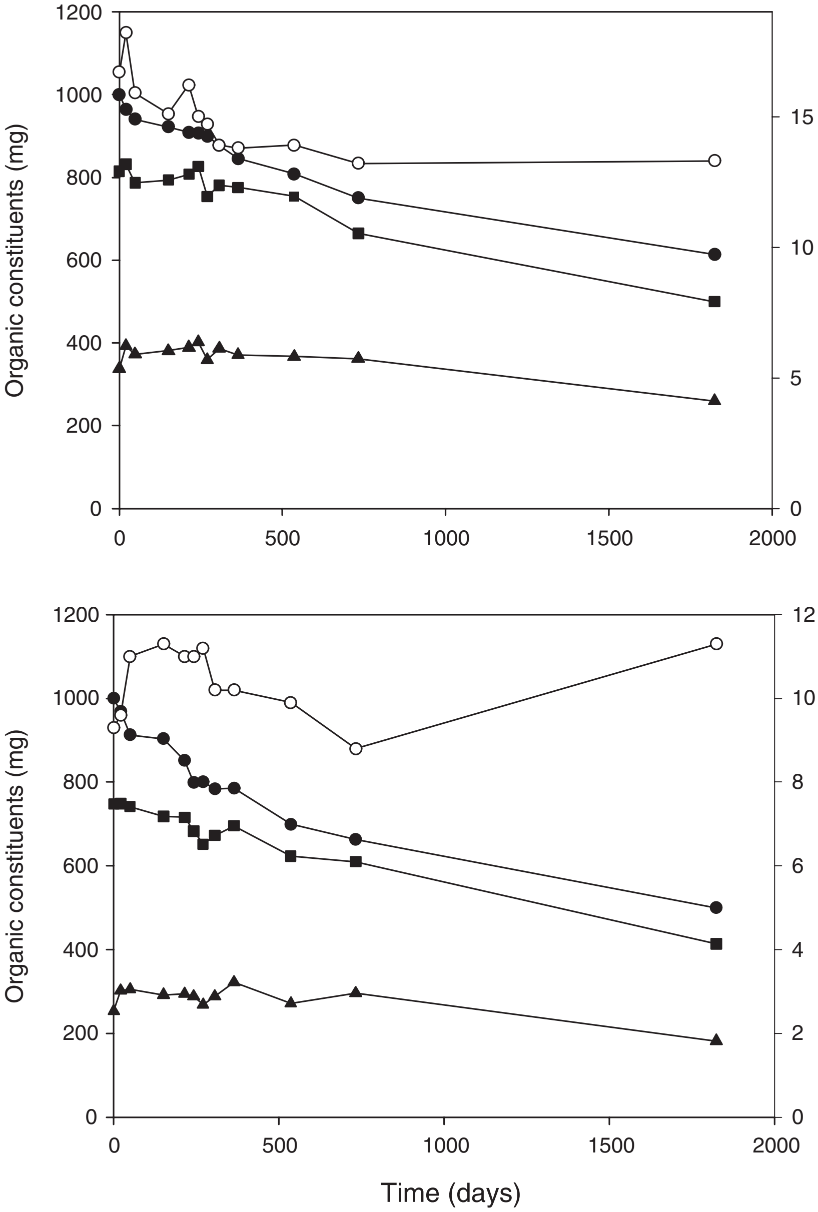

Fig. 9.5 Changes in amounts of some organic constituents and N over 5 years in fine roots incubated in litterbags on the forest floor of a sugar maple forest on Black Hawk Island (see Appendix III). Organic constituents and nitrogen are each expressed as mg g^{-1} initial material. *Top* Sugar maple fine roots. *Bottom* White pine fine roots. ● Total organic matter, ■ lignocellulose, ▲ lignin, ❍ total N (C. McClaugherty, unpubl. data)

that for foliage litter. Although many studies have reported initial chemical composition of fine roots, few have followed the chemical composition during decay.

The changes in chemical composition of fine roots during 5 years of decay in litterbags in a temperate sugar maple forest (Black Hawk Island, Appendix III) are shown in Fig. 9.5 (McClaugherty, unpubl. data). For white pine and sugar maple, most of the mass loss during the first year could be explained by the loss of soluble substances. Subsequent losses were largely due to a decline in polymer carbohydrates. Lignin declined rather slowly, beginning after the first year of decay.

The concentration of N in the root litters was initially high, 16.7 and 9.3 mg g^{-1} in sugar maple and white pine, respectively. Nitrogen contents varied during decay, but there was no clear pattern as is generally seen for foliar and wood litters (Fig. 9.5).

10
Models that Describe Litter Decomposition

10.1 Introduction

Models serve a variety of functions for ecologists, but all ecological models are abstract representations of biological systems expressed in either mathematical or symbolic terms. Models may serve as hypotheses to be tested, or as tools to predict the behavior of an ecosystem, or one of its subsystems. In a concise review, Moorehead et al. (1996) distinguished three groups of decomposition models.

Some models are empirical, and most of these are statistically based. For example, regression models relate parameters in a system. These models are useful for identifying, or indicating the strength of hypothesized relationships, but they cannot, by themselves, reveal causality. Empirical models are often useful for prediction, but they are – or at least, should be – limited to the range of data from which they were developed. Extrapolation, however tempting, can be misleading.

Mechanistic models are another general class of models. They are often analytical in nature, using a system of equations to describe complex processes. Such models have proven very useful for gaining insight into ecosystem behavior, and for developing and testing general theories.

A third group of models are simulation models. They are created to simulate the behavior of a system, in a way that allows researchers to manipulate initial conditions, or other aspects of the model, to investigate potential outcomes. Simulation models may use a combination of mechanistic and empirical components to achieve their goal. Ecosystem simulation models often include a decomposition submodel.

In reality, models are often hybrids of these types. Empirical or data-based models may be based on a mechanistic understanding of processes. From a different perspective, theoretical (theory-based) models can be made more specific by validation with experimental data, and by using data to determine parameters. Simulation models often use such hybrids to enhance their ability to predict.

One of the challenges facing those who model decomposition is the large number of factors that influence the rates and patterns of litter decomposition. Thus, a single model, or a relatively simple approach would not likely give a generally applicable description of the decomposition process. Factors that influence

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decomposition can be highly interactive, variable, and even hard to measure. These factors include microbial ingrowth, climate, variation in weather between years, and different levels of nutrients and lignin. Considering the complexity of the decomposition process, we should expect a set or system of functions, each specific for different litter types and conditions. Such a set of functions in relation to litter type and ecosystem remains to be established. In this chapter, we simply describe empirical functions that have been found to fit particular types of litters.

The concept of "kinetics" for litter decomposition is not used here in the same way as it is for enzymatic or chemical reactions, for which there are well-defined systems with, e.g., zero-, first-, or second-order reactions. Rather, the mathematical descriptions of the litter decomposition process have used functions that simply fit to, and describe, the process as well as possible. These fits are sometimes related to short-term decomposition, covering only part of the process, often to less than 50% mass loss. The models describe the decomposition as regulated by the sum of different effects on the decomposition process. Effects that are often used in these models are litter chemical composition, soil or site richness, and variation in climate over the period of incubation.

There are, of course, several mathematical functions that may be used to describe the litter mass-loss process (Howard and Howard 1974), but the models we present here have been the most commonly used. The most widely used mathematical model – the single exponential model (Jenny et al. 1949; Olson 1963) – is often used for very early stages of litter mass loss, but is frequently unable to fit observations from later phases of decomposition. A slightly more complex model uses a double exponential with two decay rate constants. These two decay constants can relate to two different components of litter, or to two different phases of decay (Lousier and Parkinson 1976). A further development of the idea that it is necessary to use differing rates for different substrate-quality compartments is the triple model (Couteaux et al. 1998). This model divides litter into three substrate-quality components, each with different decay rates, and estimates separate rate constants for each. With the different rate constants that are produced from this model, it has been possible to estimate the potential decomposition rates for the very late stages.

A different approach is represented by the model based on an asymptotic function that estimates the decomposition rate as the derivative of the function at each point of the graph, and ultimately reaches an asymptote, which is normally at a level between 50 and 100% mass loss.

Investigators working from a mechanistic perspective have proposed general models that could also lead to an asymptotic function. Among the first was Carpenter (1981). His model was based on the idea that litter constituents could be placed on a continuum of decomposability. Furthermore, the model allows that during the decay process, particular components could be transformed into substances of either higher or lower decomposability. Carpenter's model produced declining decay rates, and provided improved fits to the decay data for aquatic vegetation.

Ågren and Bosatta (1998) presented a mechanistic model that considers the continuing change in the quality of litter during its decomposition. The model has been validated with empirical data (Joffre et al. 2001), and has been used to predict temperature responses of organic matter in coniferous forest soils (Hyvönen et al. 2005). These models and their applications are helping to minimize the gap between empirical and theoretical studies in the ecology of decomposition.

In this chapter, we focus on empirical models, though as stated above, the best empirical models have a mechanistic foundation. In practice, different types of models may be used for the same dataset, and the fit of theoretical to observed data will give different levels of statistical significance. However, the utility of a given model as a predictor is dependent not only on a statistical significance of the fit, but also on the causal relationships that are behind the specific model.

10.2 Two Main Kinds of Empirical Models

The models found in the literature may be subdivided into two categories. The one group of models comprises those that describe the decomposition of the whole litter, specifically whole litter mass loss. The organic matter that is being degraded is thus regarded as one "unified" material. Sometimes, the ash is subtracted (for example, at high concentrations; cf. Sect. 5.3.2), and the model is applied to the organic matter only (Faituri 2002). We may call these unified-substrate-quality models.

Another group of models was developed from litter that had been analyzed for organic-chemical components of different stabilities. For example, if two main groups of organic matter are degraded at very different rates, then these degradation rates are estimated separately for each component. Similar models with three components have been developed (Lousier and Parkinson 1976; Couteaux et al. 1998). Mathematical formulae for examples of these models are given in Table 10.1.

With regards to the litter types for which these models are applicable, we can distinguish two main classes: foliar, and non-foliar litter. The above models have been applied primarily to foliar litter. The two major types of non-foliar litter are

Table 10.1 Some models used to describe the decomposition of litter

Formula	Comments	Characteristic	Reference[a]
Unified-substrate quality			
$M_t = A + Br^t$	Asymptotic	Leaves a residual	(1)
$L_t = m(1 - \mathrm{e}^{-kt/m})$	Asymptotic	Leaves a residual	(2)
$M_t = M_0\mathrm{e}^{-kt}$	Single exponential	Leaves no residual	(3), (4)
Two or three substrate-quality components			
$M_t = A\mathrm{e}^{-k_1 t} + B\mathrm{e}^{-k_2 t}$	Double exponential	Leaves no residual	(5), (6)
$M_t = A\mathrm{e}^{-k_1 t} + B\mathrm{e}^{-k_2 t} + C\mathrm{e}^{-k_3 t}$	Triple exponential	Leaves no residual	(7)

[a] (1) Howard and Howard (1974), (2) Berg and Ekbohm (1991), (3) Jenny et al. (1949), (4) Olson (1963), (5) Bunnel et al. (1977), (6) Lousier and Parkinson (1976), (7) Couteaux et al. (1998)

wood, and roots. For wood, a critical characteristic is the extremely low nutrient concentrations, especially that of N (see Chaps. 4 and 9), which changes the decomposition pattern. We give attention to wood and root decomposition in Chapter 9. In the present chapter, we intend to focus on models that describe decomposition of foliar litter.

10.3 Models Used to Describe Decomposition of Whole Litter as a Single or "Unified" Substrate

10.3.1 Single Exponential

This model, first proposed by Jenny et al. (1949), and elaborated by Olson (1963), is an equation for first-order kinetics, the same as for radioactive decay. A basic condition for applying this equation is that the process runs at the same rate (constant fractional rate), irrespective of the amount of material remaining at any given point in time, and that one component be considered as active in the process.

The formula may be written (Wieder and Lang 1982)

$$M_t = M_0 \mathrm{e}^{-kt} \tag{10.1}$$

and is often used in the form

$$\ln(M_t / M_0) = -kt \tag{10.2}$$

In these and subsequent equations, M_0 is the initial mass, M_t the mass at a certain time, *t*, and *k* the decay rate constant. The single exponential model is often used for predictive purposes, based on the assumption that the decomposition rate is constant, and that all material is decomposed. The "half time" and "mean residence time" of litter is also calculated, although the validity of this function in any specific case is open to question. Aber et al. (1990) suggested that this model works reasonably well for a variety of litters until only 20% of initial mass is remaining. Because of its relative simplicity, and its reasonably good fit for the early stage of decay, this model is widely used (Gholz et al. 2000).

10.3.2 Asymptotic Model

We have described (cf. Chaps. 2 and 6) that for several litter types, decomposition proceeds progressively more slowly, and may even approach zero, as decay progresses, which is most likely due to the retarded degradation of lignin. Howard and Howard (1974) found that the amounts remaining after decomposition of some litter types approached a minimum level. They found that the model that best described this process was an asymptotic nonlinear model with three parameters: A, B, and r.

$$M_t = A + Br^t \tag{10.3}$$

where M_t is the percentage of remaining litter mass, t time in days, A and B variable parameters, and r an expression for the decomposition rate. By definition, the sum of A and B should be equal to 100%, resulting in only two free parameters. By making a slight parameterization ($m=B$ and $k=B\ln r$), Berg and Ekbohm (1991) arrived at the following nonlinear model that they found more feasible to use (cf. Fig. 6.3):

$$L_t = m(1 - \mathrm{e}^{-kt/m}) \tag{10.4}$$

where L_t is the accumulated mass loss (in percent), t time in days, k the decomposition rate at the beginning of decay, and m the asymptotic level that the accumulated mass loss will ultimately reach, normally not 100% and often considerably less. The k of this function is the derivative of the function at $t=0$, and should not be directly compared to rate constants estimated with other models.

The asymptote should not be regarded as an asymptote in a strict mathematical sense, but rather as a practical limit for decomposition. The asymptote can be related negatively to, among other factors, initial litter N concentrations, and positively to litter Mn concentrations. These nutrients may regulate the microbial degradation of the litter's lignin, and N is an active participant in the formation of humic acids that may retard the decomposition (cf. Chap. 6).

10.4 Dominant Factors that Influence the Unified-substrate Models

Numerous factors, both internal and external to the litter, and related to the collection of data, can influence how well a unified-substrate model can be extended across litter types or ecosystems. For example, levels of lignin and macronutrients are not consistent within or across litter types. The quality of the collected data, and the duration and frequency of the measurements, can also influence the development of a model. Before applying a model, several questions must be answered. Given a model based on a particular litter type with a certain chemical composition, would the model be appropriate over a range of ecosystems? How much would a selected characteristic of the ecosystems – for example, nutrient availability in the humus layers – influence the fit of the model? Furthermore, how would climate influence the model?

To our knowledge, there are no consistent answers to these questions. In addition, the specific microbial population of a site, having developed in relation to the local environment, is a critical factor. Thus, for a given litter type and litter species, the decomposition pattern may vary between different systems and climates. Generally, we expect all factors that influence decomposition rates to also have a potential influence on the general decomposition pattern. We may give one example from a Scots pine forest, experimentally fertilized with N and P for ca. 10 years (also see below). For nutrient-poor Scots pine needle litter, the single exponential *k* normally fits rather well, and unified Scots pine litter was incubated for some consecutive years in both control and fertilized plots. We may see that for both types of plots, there is not much difference in the single exponential (Eq. 10.1) *k*, whereas the asymptotic one (Eq. 10.4) indicates a difference, both in initial rate and in limit values (Table 10.4, also see below).

Different models may be applied to the same datasets with varying degrees of fit. One point in choosing a model is how far the decomposition pattern is to be described. The technique of measuring litter decomposition as mass loss may allow the decomposition to be followed until ca. 60–70% mass loss, or until the process has come to a halt, which for some litter types may take place even earlier (see Chap. 6). The present basis for our discussion is that decomposition should have either reached a point where no further change can be measured, or be followed to at least 60–70% mass loss.

10.4.1 Extent and Quality of the Dataset

It is often the patterns in later stages of decay that are most difficult to describe with a model. As a rule, datasets that cover only low values of accumulated mass loss fit well to the single exponential model. Likewise, small datasets with a low number of measured values can almost always satisfy a single exponential equation. In contrast, datasets that are sufficient to test for asymptotic functions have a set of conditions imposed on them. Thus, a dataset with a low number of mass-loss values is not likely to give a significant limit value (asymptote). Since data often are collected over some years, annual and seasonal variation in weather will influence the mass-loss patterns. The best datasets tested so far have been those with a high number of samplings, ideally ten or more, and with some of the samples collected at exactly 1-year intervals to minimize the effect of short-term weather variations. The quality of a dataset is often determined by the number of replicates for each sampling relative to the inherent variability of the data. For example, in the case of litterbags, a low number of replicates normally results in scatter among the average values. Furthermore, the study should ideally follow the accumulated mass loss far enough so that the measured values are within 20% of the asymptotic value.

10.4.2 Substrate Quality

Several litter types decompose more quickly when the litter is newly shed, but the rate decreases in later stages as the litter "ages". This process has been discussed above (cf. Chaps. 2, 5, 6), and may be caused in part by changing concentrations of lignin, Mn, and N, factors that may have a causal relationship to the retardation.

In some cases, the retardation of decomposition can be traced back to the initial concentrations of these components. An example shows a clear effect of different nutrient levels on mass-loss rates as described by a single exponential. Six sets (Table 10.2) of Scots pine needle litter all have highly significant fits to the single exponential model when all mass-loss data are used, consisting of 10–12 samplings and up to 70% mass loss. All six sets have similar *k* values, ranging from 0.26 to 0.32 year^{-1}. This indicates similar overall rates for decomposition, with no trend in the *k* values, even though there is a clear trend in litter chemical composition. For example, N increases from 4.0 to 15.1 mg g^{-1}, and P from 0.21 to 1.31 mg g^{-1}. Furthermore, there is no relationship between nutrient levels and *k* values. The approximation that is made when using all data results in a consistently higher intercept as the linear regression adapts to the datasets (Table 10.2, part B). The increasing curvature with increasing nutrient levels is seen in Fig. 10.1.

Comparing these results to those obtained when the datasets are subdivided into an early phase with mass loss <40%, and a later phase with mass loss >40%, but <70%, reveals greater variability among the six sets. The separation into phases made it possible to distinguish trends in the data, and showed that *k* values for high-nutrient litter with mass loss <40% are almost double those of low-nutrient litter. For brown litter, the initial rate (*k*, Eq. 10.2) is related to the initial concentration of nutrients such as P ($R^2 = 0.950$, $n = 5$). When calculating the rate for later stages only (mass loss >40%), the rates are much lower than in the early phase (Table 10.2), and no trend is seen. Thus, splitting the single exponential into two phases may help us to resolve the process, and we may uncover large differences in rate between early and late phases of decomposition (Table 10.2). This example also indicates the limitations of the single exponential model.

Figure 10.1 shows an example with three sets of Scots pine needle litter with different levels of nutrients, and we have compared the pattern of the first-order kinetics graphs to the N levels. Figure 10.1A shows a needle litter with low initial concentration of N (4 mg g^{-1}), one line shows the observed values for $\ln(M_t/M_0)$ for this litter, and the other the constant fractional rate extrapolated. The two lines clearly parallel each other, and there is no trend toward a retardation of the decomposition rate. Figure 10.1B shows a litter with an initial N concentration twice as high. We can see that the calculated function, and the measured values start deviating after ca. 700 days of incubation (at ca. 58% mass loss). For a set of needle litter with almost four times as high an initial N concentration (Fig. 10.1C), the deviation begins even earlier, namely, after ca. 400 days of incubation (ca. 38% litter mass loss). For the two litters more highly enriched in N, there is a clear deviation from the single exponential model.

There is thus a clear deviation from the constant-fractional-rate model with increasing nutrient levels. The reasons for this could be a higher initial rate in the early stages, namely, with increasing concentrations of N and P, which would be the effect of a limiting nutrient. There could also be a rate-retarding effect of raised N levels on decomposition in the later stages, an effect that is related to the degradation

Table 10.2 A comparison of *k* values estimated using the constant-fractional-rate model given in Eq. (10.2) (Olson 1963), for an early stage (m.l.<40%), for a late stage (40%<m.l.<70%), and for early and late stages of decomposition combined (m.l.<70%). R^2 values are within parenthesis (B. Berg, unpubl. data)[a]

Designation	**Litter, decomposition, and model characteristics**		
A. Litter type/initial composition, and treatment			
Designation	Litter/treatment	Initial conc. (mg g^{-1})	
		N	P
1	Brown/unfertilized	4.0	0.21
2	Brown/unfertilized	4.4	0.32
3	Brown/fertilized 40 kg N year^{-1} for 6 years	4.4	0.3
4	Brown/fertilized 80 kg N year^{-1} for 6 years	7.0	0.34
5	Brown/fertilized 120 kg N year^{-1} for 6 years	8.1	0.42
6	Green	15.1	1.31
B. Single exponential model – all data combined			
Designation	m.l.<70%, $n=10$–12		
	k values (year^{-1})	Intercept	
1	0.2949 (0.980)	0.0128	
2	0.3103 (0.936)	0.0829	
3	0.3019 (0.948)	0.0790	
4	0.3179 (0.959)	0.0806	
5	0.2964 (0.911)	0.1365	
6	0.2602 (0.960)	0.1382	
C. Single exponential model – two phases			
Designation	m.l.<40%, $n=4$–5	m.l.>40%, $n=5$–6	
	k values (year^{-1})		
1	0.2949 (0.976)	0.2303 (0.984)	
2	0.3989 (0.953)	0.2029 (0.936)	
3	0.3880 (0.966)	0.2059 (0.969)	
4	0.4073 (0.977)	0.2267 (0.989)	
5	0.4592 (0.980)	0.1723 (0.928)	
6	0.4709 (0.991)	0.2025 (0.980)	
D. Asymptotic model			
Designation	Initial rate (% day^{-1})	Limit value (%)	
1	0.0768	93.2	
2	0.1087	78.2	
3	0.1055	77.4	
4	0.1112	78.0	
5	0.1299	72.2	
6	0.1360	68.0	

[a] Using the asymptotic model and mass-loss values for both stages combined (Eq. 10.4), the initial rates and limit values were estimated (Table 10.1). All litter types compared are Scots pine needle litter with different nutrient levels. Note that the magnitudes of the *k* values (parts B and C), and the initial rate (part D) are not comparable

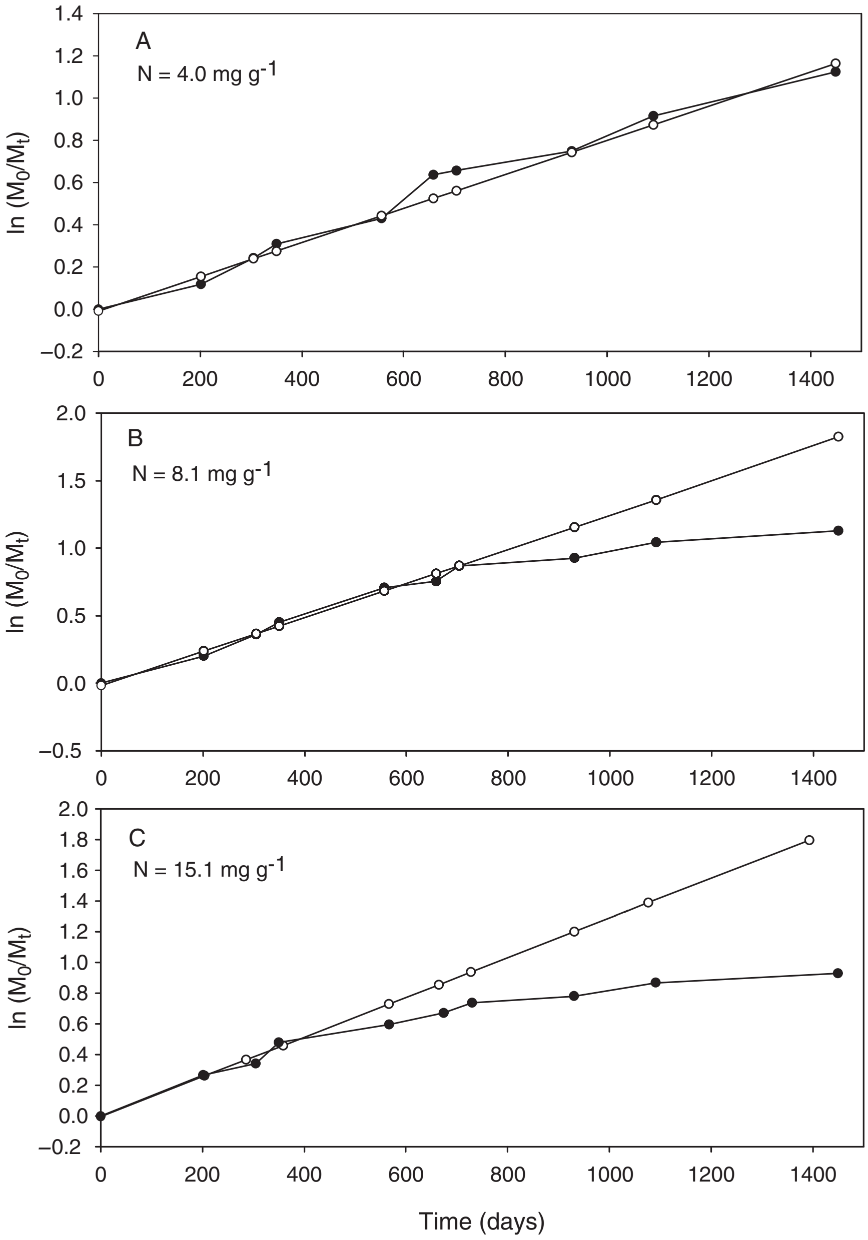

Fig. 10.1 Application of the single exponential model (constant-fractional-rate model) for Scots pine needle litter of three different N levels. On each plot, one line is estimated using all available data, specifically litter mass-loss values from 0 to ca. 66–70% for litter of different initial N concentrations (●), and the other is an extrapolation of the fractional rate as estimated for the early stages ((○) see Table 10.2). **A** For natural litter from a nutrient-poor plot, the rate was rather constant, as seen in the comparison of the two graphs. **B** At a higher nutrient level (N concentration of 8.1 mg g^{-1}), deviation from a constant rate starts at ca. 58% litter mass loss. **C** At an even higher nutrient level (N concentration of 15.1 mg g^{-1}), a deviation starts even earlier, at ca. 38% litter mass loss (B. Berg, unpubl. data)

of lignin. It is likely that both effects are active, resulting in higher initial rates, and lower ones in late stages. Thus, for a particular litter type, the higher the N level, the larger the deviation from a single exponential. The decomposition for all the litter discussed above may be described by an asymptotic function (Table 10.2D).

So, for what litter types would the constant-fractional-rate model be valid? The model fits well to the most nutrient-poor litter (Table 10.2, litter no. 1, and Fig. 10.1A). Although the fit is based on empirical findings; we may still speculate that the nutrient levels may play a role, as was suggested. As seen above, the mass-loss graphs for these litter types discussed above may be described by an asymptotic function that clearly indicates that the rate decreases to become close to zero. The fits with asymptotic models to the six sets of Scots pine needle litter (Table 10.2) are all highly significant, indicating that the model can describe the decreasing rate of litter decomposition, and incorporates the extremely slow decomposition in the very late stages of decomposition (Table 10.2, part D). The example above dealt with needle litter from Scots pine only. When making a similar comparison using different litter types (Table 10.3), a similar result emerged, namely, that the deviation from the simple model increased with increasing nutrient levels. We may also see that the rate constants mainly decrease the more rich in N and P the litter is. In comparison, the asymptotic function (Eq. 10.4) gives initial rates that mainly fit to the initial nutrient levels, and the limit value for decomposition (Berg and Ekbohm 1991).

This asymptotic model has been tested against approximately 150 datasets from foliar litter decomposition studies (Berg and Johansson 1998). It has given significant asymptotic limit values for practically all these datasets. For some decomposition studies using nutrient-poor litter species, the model has not given significant limit values, although sets of mass-loss values from identically designed experiments using more nutrient-rich litter, and run in parallel, have given significant fits. Thus, Berg et al. (2003) found that brown lodgepole pine needle litter, poor in N and relatively rich in Mn, did not give a significant limit

Table 10.3 A single exponential model was fitted to mass-loss values for seven litter types incubated under identical conditions, but having different initial concentrations of N. All litter types had 12 to 13 samplings, and the linear relationships were all highly significant (except for alder, $p<0.01$). The maximum incubation time was 1,393 or 1,448 days (in part from Berg and Ekbohm 1991)

Litter type[a]	Init. N	Init. P	Obs.	Single exp.	Asymptotic function	
	(mg g^{-1})	(mg g^{-1})	(%)	k (year^{-1})	k_{init} (% day^{-1})	Lim. val. (%)
Scots pine br	4.8	0.33	67.4	0.299	0.093	89.0
Lodgepole pine br	3.9	0.34	63.1	0.281	0.075	100.0
Silver birch br	7.7	1.05	59.9	0.164	0.187	56.9
Silver birch gr	17.4	1.80	63.0	0.182	0.206	54.3
Scots pine gr	15.1	1.31	65.9	0.259	0.136	68.0
Lodgepole pine gr	10.5	0.82	66.0	0.256	0.086	81.5
Grey alder gr	30.7	1.37	55.5	0.12	0.336	50.6

[a] *br* Brown, *gr* green, *Obs.* maximum observed mass loss, *Single exp.* single exponential, *Lim. val.* limit value

value. That study was carried out in two contrasting forest stands: one temperate with wet and warm climate, and rich in N and other nutrients, the other in a boreal system, with low temperatures, rather dry, and in combination with a nutrient-poor soil.

In earlier studies, Berg and Ekbohm (1991, 1993) found that the same litter type (lodgepole pine needle litter) gave a limit value at, or near 100% decomposition. There is a clear trend in this material indicating that the lower the litter N concentration, the higher the limit value (Berg 2000b; Berg et al. 2003), and we cannot exclude that one of the limitations of the model is related to the levels of N, and possibly Mn in the litter. Lodgepole pine needle litter from trees grown in Scandinavia is also rich in Mn (cf. Chap. 4), which we have hypothesized to promote the degradation of lignin and litter (cf. Chap. 6).

The models that so far best describe the long-term decomposition of the main foliar litter types are asymptotic ones (Table 10.2; also see Fig. 6.3). This does not imply that they have any generality, only that they fit very well to those foliar litter types investigated so far.

We mentioned above that N and Mn in litter, as part of the substrate quality, influenced the level of the limit value (cf. Chap. 6), and that they may influence the fit of the single exponential. It is possible that there are influences from the environment of the incubated litter. We take an example from a study in a fertilized forest with Scots pine (Table 10.4). Unified brown and green Scots pine needle litter was incubated in neighboring (paired) plots with control, and ones fertilized with N and P. After ca. 10 years of treatment, the ground vegetation had changed from moss,

Table 10.4 Limit values (Eq. 10.4) and single exponential rate constants (*k*, Eq. 10.1) calculated for Scots pine needle litter and Scots pine green needles incubated in a nutrient-poor Scots pine forest (Norrliden, Tamm 1991; B. Berg, unpubl. data)[a]

Concentration (mg g^{-1})						Single exponentia (*k*, year^{-1})		Asymptotic model (Eq. 10.4) Limit value (%, ±SE)	
Wsol	Lig.	N	P	Ca	Mn	Control	Fertilized	Control	Fertilized
Brown needle litter									
178.4	228.6	3.8	0.30	5.93	1.08	0.2831	0.2903	71.5 (7.7)	59.6 (2.4)
178.4	228.6	3.8	0.30	5.93	1.08	0.2825	0.3146	74.2 (11.7)	59.6 (6.1)
178.4	228.6	3.8	0.30	5.93	1.08	0.2891	n.d.	n.d.	n.d.
291.0	n.d.	3.9	n.d.	n.d.	n.d.	0.3364	n.d.	n.d.	53.1 (2.5)
231.4	n.d.	4.8	n.d.	n.d.	n.d.	0.3777	n.d.	n.d.	n.d.
231.4	n.d.	4.8	n.d.	n.d.	n.d.	0.2871	n.d.	n.d.	n.d.
Green needles									
199.7	211.9	14.0	1.62	2.40	0.84			62.0 (4.3)	59.6 (2.4)
199.7	211.9	14.0	1.62	2.40	0.84			57.3 (2.5)	60.8 (3.6)

[a] The incubated material in each comparison was identical between control and fertilized plots, and incubated for ca. 4 years. Two control and two fertilized plots were used. The plots were fertilized with N (80 kg ha^{-1} year^{-1}) and P (40 kg ha^{-1} every 4th year). Some substrate-quality data are given, and we may compare the outcome of Eqs. (10.1) and (10.4) within litter of the same chemical composition. *Wsol* Water solubles, *Lig.* lignin, *n.d.* not determined

bilberry, and heather to grass and low herbs. Brown, nutrient-poor needle litter had higher limit values in the control plots (70.5–74.2%) than in the fertilized ones (53.1–59.6%). Whereas this effect was observed for nutrient-poor needles, there was no measurable effect on green, and considerably more nutrient-rich needles (Table 10.4).

As mentioned above, a condition for using the single exponential model is that the litter is decomposing as a unified substrate. Thus, the decomposition of a litter for which the decomposition process is suppressed by, for example, slow lignin degradation, or accelerated by a large initial concentration of solubles (cf. Figs. 2.2 and 6.1) would not be well described by a single exponential approach. However, that may depend on how much of the decay process is being described. In the example of Scots pine needle litter, decomposition in the early phase was not suppressed by the increasing lignin concentration, and a single exponential describes this early phase well. Figure 7.6 showed that the decomposition of the same litter, incubated under different climatic conditions, is hampered to different extents. For a litter incubated close to the Arctic Circle at an annual average temperature of ca. 0–1 °C, approximately 600 mm annual precipitation, and an AET of 387 mm, raised lignin concentrations had very little effect (Berg et al. 1993b). In contrast, at a more southern site the effect of lignin was very pronounced. Although an analysis of such a climatic influence on decomposition kinetics has not yet been made, we predict that the single exponential model may be applied to a greater fraction of the decomposition process in colder climates.

Since lignin and N in combination have proven to be suppressing agents, we speculate that for a foliar litter poor in N, it would be possible to apply a single exponential to a higher mass loss than for a litter more enriched in N.

10.5 Models Based on Two or Three Substrate-quality Fractions

10.5.1 The Double Exponential

The double exponential model is a development of the single exponential, and is based on the assumption that the litter substrate has two main substrate-quality components with different decomposition rates. Its construction is simply an addition of two factors each defining a part of the litter substrate.

$$M_t = A\mathrm{e}^{-k_1 t} + B\mathrm{e}^{-k_2 t} \tag{10.5}$$

in which t is time, and k_1 and k_2 are rate constants for quickly and slowly decomposing fractions of the litter, respectively. The amount of each fraction is given by A and B, respectively. The model appeared for the first time in a paper by Lousier and Parkinson (1976) describing the decomposition of aspen leaf litter, and in the literature from the International Biological Program (IBP) Tundra Biome (Bunell et al. 1977).

10.5.2 The Triple Exponential

The triple exponential model is a development of the double exponential, and is based on the assumption that the litter substrate has three main components with different decomposition rates, rather than two. Its construction is simply an addition of three exponential factors for decay.

$$M_t = A\mathrm{e}^{-k_1 t} + B\mathrm{e}^{-k_2 t} + C\mathrm{e}^{-k_3 t} \tag{10.6}$$

in which t is time, and k_1, k_2, and k_3 are rate constants for quickly, slowly, and extremely slowly decomposing fractions of the litter, respectively. A, B, and C give the amount of each fraction, respectively.

Couteaux et al. (1998) used this model to describe the decomposition of Scots pine needle litter, and estimated the rates of the three different fractions. They subdivided the substrate into “labile”, “metastable”, and “recalcitrant” fractions, and obtained k values in the range from 10^{-1} to 10^{-4}% day^{-1}. They also applied this model to respiration of humus samples. A drawback of this model is that it assumes invariable k values, an assumption that is questionable when applied to the later stages of decay.

Chapter 11
Decomposition and Ecosystem Function

11.1 Introductory Comments

The microbial decomposition of plant litter is a basic process in the functioning of ecosystems, not only for the general release of nutrients to plants, but also for the buildup of a stable humus, and the accompanying storage of nutrients.

Nutrients are released from decomposing plant litter either through leaching from newly shed litter, or because of decomposition processes. Leaching, and the pattern of release due to decomposition, is dependent on litter type, its surroundings, and the kind of nutrient. Thus, nutrient release is closely tied to ecosystem structure and function. We can distinguish two main pathways for nutrients: one is release, and the other is storage in a stable form in the humus.

Humus accumulates as the stand grows and ages, as demonstrated by Ovington (1959), Forrest and Ovington (1970), Bormann and DeBell (1981), and Schiffman and Johnson (1989). In these studies, the accumulation followed a nearly linear increase with stand age. A model formulated to describe the linear accumulation of humus with time may be general, but lacks causality.

Humus accumulation rates may be estimated by a summation of the recalcitrant or resistant part of the decomposing litter. Evaluation of the resistant fraction is based on the concept of a limit value (cf. Chap. 6), which corresponds to the fraction of litter that decomposes extremely slowly. The level of the limit value is determined by causal factors such as the concentrations of lignin, N, and Mn in litter.

There is very good support for the observation that a long-term net accumulation of humus takes place, even over millennia (Jenny 1980; Wardle et al. 1997). Such an accumulation can be predicted using the limit-value approach to humus accumulation in undisturbed systems (Berg et al. 2001).

Neither C nor N was in the original mineral soil that existed before plants evolved, but entered the ecosystem from the atmosphere. Both C and N are macronutrients, and fulfill very different functions. Carbon makes up the skeleton of macromolecules that create a storage matrix for N and other nutrients. Nitrogen is a major nutrient that must be stored in the ecosystem, to supply plants with an steady flow of mineral N. Loss of N from the ecosystem would cause the vegetation on a given plot to move to an earlier successional stage due to N limitation, and the ecosystem may need N_2-fixing organisms to restore N to its prior level.

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The mechanism by which the ecosystem stores N depends on the structure of the litter produced by a given plant, the degree to which that litter decomposes, and the transformations it undergoes during decomposition. It would be reasonable to expect that each plant species would produce litter and litter remains that would store nutrients in concentrations high enough to enable the species to survive. A collection of plants making up an ecosystem may, for the purpose of survival, need a feedback mechanism based on nutrient availability.

Nutrient elements can be added to an ecosystem through abiotic weathering, aerosol input from outside the system, or fertilization. Ecosystems have the capacity to store at least some of these added nutrients. This chapter aims to evaluate what a storage mechanism for humus means in terms of the ecosystem. It also aims to describe N dynamics, in terms of the relative amounts of N being released vs. those being stored. The possible effects of climate change on such a storage mechanism are also discussed. Of course, this latter section is an extrapolation of existing, partially empirical data, and must be regarded as a prediction that needs to be validated.

11.2 Humus is Accumulating in Undisturbed Forest Ecosystems

11.2.1 Accumulation of Humus in Single and Paired Stands

A number of studies deal with the increase in ash-free forest floor material in growing stands. Normally, these have been monocultures. The authors of these papers did not always have the intention to follow the increase in humus per se, and in some cases data have been recalculated.

Already in the 1950s, Ovington (1959) followed the increase of dead, ash-free soil organic matter in a chronosequence of plantations of Scots pine, and found an increase that is linear with time. The stands in his chronosequence had a range in age from 7 to 55 years. In that period, the increase in organic substance in both the H-horizon and for total SOM showed excellent straight-line relationships, with $R^2 = 0.842$ and 0.859, respectively, up to a maximum SOM amount of about 45 t ha^{-1} (t, ton).

We may see (Table 11.1) that for six of the seven species for which we have found information, there is a significant linear increase with time, these species being Scots pine, Monterey pine, loblolly pine, Norway spruce, red alder, and common beech. These stands have been followed either in a time series with repeated samplings in each stand, or in a chronosequence. In all cases the age encompasses one stand age or less, the maximum age being 148 years, and the maximum accumulated amount 120 t SOM per hectare (Table 11.1). The annual increment in SOM varied considerably, indicating influences on accumulation rate. We did not have access even to litter-fall data in all cases, and therefore present only the increase rates calculated from the linear relationships. These ranged from 2,212 kg ha^{-1} year^{-1}

Table 11.1 Comparison of accumulation rates of SOM in forest floors in which accumulation has been followed over time. The estimated increase rate in the measurement period is given as the slope of the linear function

Tree species	R^2	*n*	*p*<	Max. age (years)	Max. measured amount (t ha^{-2})	Estimated annual increase rate in period: SOM (kg ha^{-2} $year^{-1}$)	Estimated annual increase rate in period: Carbon	Comments	Lit. ref.[a]
Scots pine	0.842	9	0.001		40	721	360	H-horizon	(1)
Scots pine	0.859	9	0.001	55	45	747	374	Forest floor	(1)
Scots pine[a]				ca. 90	ca. 70	ca. 1,350	ca. 675	Forest floor	(5)
Monterey pine	0.903	5	0.05	12	17	2,065	1,032	Forest floor	(2)
Red alder	0.787	7	0.01	41	39.3	865	432	Forest floor	(3)
Loblolly pine	0.935	14	0.001	47	18.8	475	237	Forest floor	(4)
Norway spruce	0.816	9	0.001	111	120	2,212	1,106	Forest floor	(6)
Norway spruce	0.887	7	0.01	29	9.0	750	375	Forest floor	(7)
Common beech	0.609	7	0.05	148	70	844	422	Forest floor	(6)
Common oak	0.340	6	n.s.	28	2.0	116	58	Forest floor	(7)

[a] (1) Ovington (1959), (2) Forrest and Ovington (1970), (3) Bormann and DeBell (1981), (4) Schiffman and Johnson (1989), (5) Tietema (2004), (6) Meesenburg et al. (1999), Meiwes et al. (2002), Berg (2004), (7) Vesterdal et al. (2002)

for a Norway spruce stand in central Germany, to 475 kg ha^{-1} $year^{-1}$ for a stand of loblolly pine, and 116 kg ha^{-1} $year^{-1}$ for common oak.

For the purpose of comparison with data presented in Chapter 13, we have transformed these data into corresponding carbon values by multiplying with a factor of 0.5. The authors (Table 11.1) have focused their attention to trees, which often are the component that does produce most litter. Very often in the literature, the ground vegetation and the understory are not included. We will see (cf. Chap. 13) that there may be good reasons to consider also ground vegetation as an important component.

11.2.2 How Far can Humus Accumulate?

In the study by Ovington (1959), the increasing amounts of humus measured as the stand aged were relatively low, reaching about 40 t ha^{-1} after 55 years. As already mentioned, Jenny (1980) and Paul (1984) suggested that such an accumulation would continue for millennia in the absence of disturbance, which would result in the buildup of considerable amounts of humus.

That humus can accumulate over long periods, if disturbances such as fire and forest management are excluded, is now an established fact, and amounts as high as 109 kg m^{-2} in a temperate forest system have been found, albeit after a duration of accumulation not precisely known (south Italy, Berg et al. 1993a). Forest floor masses of 49 kg m^{-2} have been reported after 3,000 years of accumulation in a boreal forest, resulting in humus layers up to 1.5 m thick (Wardle et al. 1997; Table 11.2). Such values may give us some perspective on the age of humus layers that have accumulated over shorter periods. In boreal Scandinavia, layers deeper than 20 cm are common; more than 9% of about 15,000 sampled plots (Swedish Forest Inventory) had humus layers deeper than 40 cm (Table 11.3), and almost 8% had depths exceeding 50 cm, suggesting an accumulation for periods up to a millennium. The concept of "Tangelhumus", found in the Alps and other central European mountains, and defined partly in terms of a humus layer up to 1 m thick, further supports real long-term accretion (Rehfüss 1990; Anonymous 1996).

A clear relationship is seen between the frequency of forest fires and humus accumulation (Wardle et al. 1997). With humus layers of up to 1.5 m being formed when undisturbed, it is reasonable to speculate that fire is the normal, and potentially the dominant agent of humus layer reduction. Recent measurements of extremely low humus respiration rates (Couteaux et al. 1998) indicate that a balance between humus formation from litter input and decomposition is unlikely within millennia (cf. Chap. 6).

Humus accumulation rates were similar among four stands of different age ranging from a 120-year-old stand to one that is 2,984 years old, Table 11.2, which supports the idea that an undisturbed system is not likely to reach a steady state in less than several millennia. In addition, we have not found any strong support for the concept of a steady state in humus accumulation in the systems we

Table 11.2 Observed and estimated amounts of humus of known age in north Swedish forests at ca. 66°N (Wardle et al. 1997), and in a Scots pine forest at the SWECON site Jädraås at 60°49'N (Berg et al. 2001). Given also are measured amounts of N and P

	Site			
	Northern Sweden – islands			Jädraås
Site characteristic	<0.1 ha	0.1–1.0 ha	>1.0 ha	
Age (years)	2,984	2,081	1,106	120[a]
Forest floor mass (kg m^{-2})	49.08	34.62	14.33	1.54
Increment (kg m^{-2} $year^{-1}$)	0.0164	0.0166	0.0130	0.0128[a]
Est. litter fall (kg m^{-2})[b]	0.08–0.14	0.08–0.14	0.08–0.14	–
Modeled litter fall 112 years (kg m^{-2})[a]	–	–	–	151.55
Est. limit value (%)[c]	87.8	87.6	90.4	92.1
Avg. limit value (%)[d]	83.0	83.0	83.0	89.0[e]
Est. forest floor mass (kg m^{-2})[f]	41.2–72.1	28.7–47.2	15.2–26.7	1.67
Missing fraction (needle litter basis, %)[f]	16	17	6	–
Excess fraction (total litter basis, %)[f]	46	37.6	86.3	8.4
N storage (g m^{-2})[i]	761	460	163	15[h]
P storage (g m^{-2})[g]	39.1[g]	28.7[g]	9.2[g]	0.72[h]

[a] It was estimated that at this site it would take 8 years before the litter could be considered to be humus and part of the F/H layer (Berg et al. 1995b)

[b] Litter fall for the three Hornavan groups was estimated using available Scandinavian data for pine and spruce forests between 59°N (north of the line Oslo-Stockholm-Helsinki) and 67°N (Berg et al. 1999a, 2000). The lower value gives needle litter fall, and the higher total litter fall

[c] This limit value estimated as 1–increment/needle litter fall

[d] Estimated from existing limit values ($n = 18$) for Scots pine and Norway spruce litter at sites in northern Sweden (Berg and Johansson 1998)

[e] Limit value for needle litter decomposition at the Jädraås site (Berg et al. 1995b)

[f] Berg et al. (2001)

[g] D. Wardle (pers. comm.)

[h] Calculated from Berg et al. (2003)

[i] Wardle et al. (1997)

Table 11.3 In the Swedish Forest Inventory, 14,234 forest plots were investigated in the period from 1984 to 1987, with measurements that included humus depth. The frequencies below do not include mires or mountain plots (Swedish National Survey of Forest Soils and Vegetation, Dept. of Forest Soils, SLU)

Humus thickness (cm)	Frequency (number of plots)	(% of total)
0–10	8,838	61
10–20	3,008	21
20–30	750	5.2
30–40	305	2.1
40–50	214	1.5
50–60	202	1.4
>60	917	6.3

report. We propose that the cessation of growth of a humus layer, or its destruction, is more likely to be dependent on disturbances or catastrophic events such as fire. We do not intend to suggest that such a lack of steady state is a general phenomenon, but that this appears to be valid at least for boreal and temperate coniferous forests.

The accumulation of humus should be viewed within the context of the complete ecosystem, and we will discuss the effects on humus accumulation of different soil systems under growing trees. A forest stand that has been clear cut represents a rapidly changing ecosystem. Its soil system alters rapidly due to increasing levels of available nutrients, increasing moisture, and a probable change in the microbial community. The following discussion of humus accumulation will therefore focus on soils under continuously growing trees.

11.2.3 A Mechanism For Humus Accumulation Under Undisturbed Conditions

Litter Chemical Composition and Limit Values

When Howard and Howard (1974), and Berg and Ekbohm (1991) showed that litter decomposition appeared to eventually come to a halt, they estimated limit values that were significantly different between the litter species they investigated (cf. Chap. 6). Their work was based on the assumption that the sum of decomposition processes resulting in litter mass loss would continue to slow down, without dramatic breaks in that pattern. In Chapter 6, we discussed the limit-value concept for the decomposition of foliar litter, and the effects of litter N and Mn concentrations on the extent of decomposition, as well as on the amount of recalcitrant remains.

When limit values for foliar litter decomposing in natural systems were regressed against concentrations of nutrients and of lignin, it was seen that litter N concentrations gave a highly significant and negative relationship (cf. Fig. 6.12, Table 6.8). The fact that, in this large dataset, the relationship to N concentration was significant indicates a general effect of N for a considerable number of species in deciduous and coniferous ecosystems in boreal and temperate forests.

Although limit values for litter mass loss have been estimated for a variety of litters using asymptotic functions, such limit values may not necessarily indicate that the remaining organic matter is completely unavailable for degradation by biological agents (see below). The residual organic matter could very well consist of a stabilized fraction that decomposes very slowly, or a fraction that does not decompose in a given environment, but would undergo further decomposition after a change in that environment. The discovery of an apparent final mass-loss value should not be considered trivial, however, especially if the limit value can be related to litter properties such as lignin concentration and nutrient status, or to climatic factors. When Berg et al. (1996a) compared C storage in the humus layer in paired stands of Norway spruce and Scots pine, the measured humus buildup could be related to different limit values for the two species, which in turn were related to different N levels (see section below). In a review, Cole et al. (1995) compared the organic matter buildup under red alder (high litter N level) and Douglas-fir (low litter N level). When Berg et al. (2001) evaluated these data using the limit-value approach, they found a much higher store of organic matter under the former than could be explained by simply comparing litter fall. Thus, the existing data support the hypothesis of a mechanism based on the limit-value concept to estimate organic matter buildup. Still, a set of experiments is needed to confirm individual steps in the mechanism.

Forest humus systems have different levels of nutrients (Tables 11.4, 11.5, and 11.6). Large differences exist between systems (Table 11.4) – for example, a Scots

Table 11.4 Concentrations of nutrients in ash-free humus in a boreal nutrient-poor Scots pine stand (Jädraås, Sweden), and a richer, temperate silver fir stand (Monte Taburno, south Italy). The values are based on ash-free organic matter (Berg et al. 2003)

Concentration of nutrient (mg g^{-1})							(µg g^{-1})			
N	P	K	Ca	Mg	Mn	Fe	Zn	Cd	Cu	Pb
Silver fir, Monte Taburno										
38.2	2.84	17.7	20.0	4.76	0.7	6.5	0.1	0.8	62.	9.7
Scots pine, Jädraås										
11.8	0.47	10.9	3.23	0.98	0.2	9.40	0.0	0.6	9.2	8.9

Table 11.5 Amounts of litter fall and its N concentration, as well as accumulation of ash-free SOM in soil under 50-year-old red alder and Douglas-fir stands. The data, from Johnson and Lindberg (1992) and Cole et al. (1995), have been converted to g organic matter per m^2 (Berg et al. 2001)

Fraction	Red alder	Douglas-fir	Difference
Nitrogen in litter fall			
N conc. in foliar litter (mg g^{-1})	18.8	7.4	
Amount of litter fall (g m^{-2})			
Leaf litter	312	105	
Non-leaf litter	136	73	
Understory litter fall	126	46.6	
Estimated accumulated litter fall over 50 years	25,980	15,105	
Limit values and estimates			
Estimated limit values (%)[a]	56	74.8	
Estimated accumulation over 50 years (g m^{-2})	11,431	3,806	7,625
Measured amounts of SOM (g m^{-2})			
O-horizon	7,960	2,350	5,610
Wood	1,890	1,320	570
Mineral soil 0–7 cm	6,040	6,180	
Mineral soil 7–15 cm	3,640	4,040	
Mineral soil 15–30 cm	6,880	5,580	
Mineral soil 30–45 cm	6,400	6,040	
Total in mineral soil 0–45 cm	22,960	21,840	1,120

[a] Using the equation of Berg et al. (2001), limit value = $-1.6474N + 86.95$

Table 11.6 Average limit values for decomposition and N concentrations for eight foliar litters. The potential capacity to accumulate humus (pot. humus) is given by (100–limit value)/100. The potential capacity to store N is defined at the limit value: pot. N stor. = N concentration at limit value × fraction remaining (in part from Berg 1998b, and Berg and Dise 2004a)

Litter	Initial N (mg g^{-1})	Limit value (%)	Pot. humus[a] (fraction)	N limit (mg g^{-1})	Pot. N stor. (mg g^{-1})
Lodgepole pine	4.00	94.91	0.051	13.60	0.69
Scots pine (brown)	4.19	81.3	0.187	12.76	2.39
Silver birch	9.55	77.7	0.223	22.71	5.06
Norway spruce	5.44	74.07	0.269	14.46	3.75
Scots pine (green)	12.18	67.2	0.328	–	–
Pyrenean oak	12.2	60.3	0.397	–	–
European beech	11.9	59.12	0.409	24.05	9.84
Silver fir	12.85	51.5	0.488	21.93	10.64

[a] *Pot. humus* Potential fraction becoming humus (LH factor), *N limit* N concentration at the limit value, *Pot. N stor.* potential amount of N stored in humus at the limit value per gram of initial litter

pine system has a humus N level of 11.8 mg g^{-1}, while a silver fir system has a humus N level of 38.2 mg g^{-1}, and generally higher levels of other nutrients. The soil microorganism community will have adapted to these different nutrient levels (cf. Chap. 3). Compared to N-poor systems, in a very N-rich system it is likely that a higher percentage of lignin-degrading organisms would not be sensitive to N, or less sensitive, which may mean that the limit values could be higher. In such a system, the concentration of N may have little, or no effect on the degradation of lignin and on the limit values, and we may speculate that other agents may have a greater impact; indeed, Berg et al. (2003) suggested levels of, e.g., heavy metals as a possible reason.

Nitrogen, Mn, and Heavy Metals may be System-Specific Indicators

The fact that significant linear relationships exist between limit values and initial litter concentrations of both N and Mn, and that there are causal explanations for these relationships, provides support for a strong regulating mechanism. The role of the initial concentrations of these nutrients is based on empirical relationships, and while these can be regarded as an index, they are not necessarily general. Although we have obtained a general relationship over several ecosystems, such relationships need to be proven and confirmed for other types of ecosystems.

Additional Stabilizing Factors

Litter at the limit value appears to be biologically stable in undisturbed systems. With decomposition rates as low as 0.0001 to 0.00001% per day, viz. values of the same magnitude as those measured for humus of the same stand (Table 11.7), we

Table 11.7 Fractions of different size and stability in far-decomposed Scots pine needle litter, and humus from the Scots pine stand of incubation (data from Couteaux et al. 1998). The *k* values given by Couteaux et al. (1998) have been recalculated to the corresponding mass loss in % year^{-1} for the purpose of comparison with values for litter decomposition

Fraction	Size (%)	*k* (% day^{-1})	Mass loss (% year^{-1})
Far-decomposed litter			
Labile	5	0.124	30
Meta-stable	15	0.087	3–6
Stable	80	10^{-4} to 10^{-5}	0.03–0.003
Humus			
Labile	5	0.124	30
Meta-stable	15	0.087	3–6
Stable	80	10^{-4} to 10^{-5}	0.03–0.003

can regard the litter as stable humus (e.g., mor humus). As such, it can build humus layers over millennia. There are, however, additional stabilizing mechanisms that could contribute to creating a humus layer. One such mechanism would be an increasing anaerobicity in the thickening humus layer. The thickness of the layer itself would hamper the diffusion of oxygen, and the ability of humus and litter to hold water would cause anaerobic pockets to develop. Lack of oxygen could prevent complete metabolism by aerobic microorganisms, and rather than releasing carbon dioxide and water as final products, organic acids would be produced. An increase in the anaerobic microflora would be associated with similar products, which could either inhibit or resist further degradation. Organic acids (e.g., acetic acid and benzoic acid) are well-known inhibitors of microbial activity, and combined with a lower pH, could reduce the rate of litter decomposition, thereby enhancing the rate of humus accumulation. Such mechanisms would require a certain precipitation and/or snow cover, and we discuss this further in Chapter 13.

Litter Components Change with Stand Development

Not all litter components behave the same as does foliar litter in terms of humus formation (cf. Chap. 9), and the types of plant material contributing to litter fall change with stand age (Fig. 11.1).

At our Scots pine case-study site (Appendix III), litter fall was observed for 7 years in three Scots pine stands, which were 18, 55, and 120 years of age at the start of the study (Flower-Ellis 1985). There was an increase in total litter fall in all three stands due to both increased foliar litter fall and the addition of more woody components with age (Berg et al. 1993d). Part of the increase in litter fall with stand age may be attributed to an increase in tree biomass, and increased foliar litter fall. However, as trees reach physiological maturity, cones develop, and part of the increase in litter fall is due to the addition of cones. Bark and twigs usually start falling later, in this case at an age of about 22–23 years, thereby increasing the proportion of woody components with stand age.

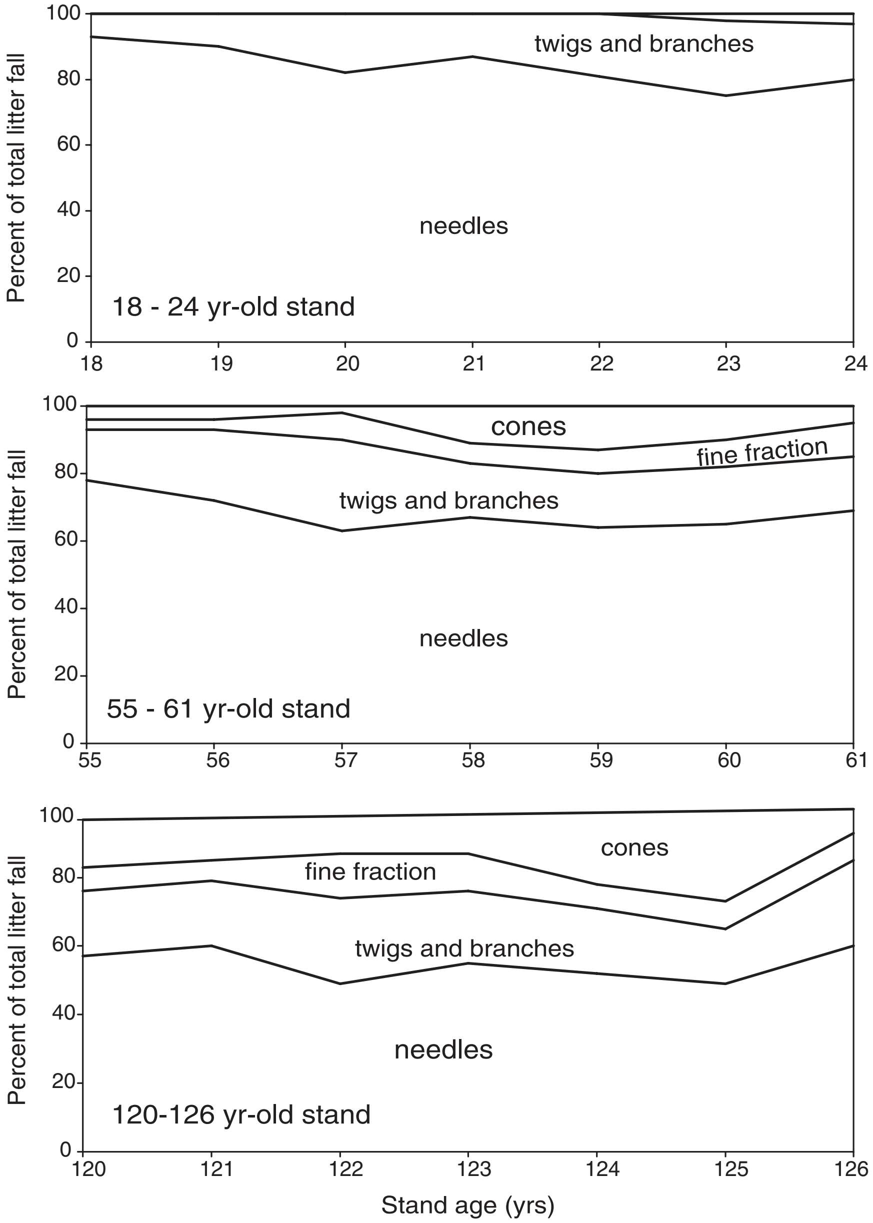

Fig. 11.1 Relative proportions of needles, fine litter, twig and branch litter, and cones during the period 1973/1974 to 1979/1980 in stands starting at *top* 18, *middle* 55, and *bottom* 120 years of age (Flower-Ellis 1985; Berg et al. 1993d)

What Litter Components can Form Humus?

The scientific literature has not yet thoroughly addressed the question of how the various litter components are transformed into humus. There appears to be an understanding that humus is formed simply from litter, as if plant litter were chemically and structurally homogeneous within a species. According to the existing definitions of humus (e.g., Bal 1973), all the components of litter are equally capable of forming humus.

The type of litter influences the type of humus that is formed. For example, mor, moder, or mull humus types in boreal systems have been partially investigated and explained empirically (e.g., Lundmark and Johansson 1986). Those discussions focused on the species from which different types of humus are formed, and not on the causes for humus formation based on long-term stable compounds. This observed difference between plant species in terms of formation of humus types may in part have its origin in differences in chemical composition, an aspect that directly influences the microbial communities and soil animals, and thus the decomposition process (cf. Chaps. 6 and 9).

This background may allow us to draw the conclusion that most foliar litter components form humus according to the schedule suggested in Chapter 6. In contrast, the information concerning the decomposition of the more nutrient-poor (especially N-poor) components is such that we judge their contribution to humus as being more uncertain. Relatively few studies have been published about the decomposition kinetics of such material, but Harmon et al. (1986) have conducted extensive work on wood decay. Their studies included branches, stumps, and stems, and the results (M. Harmon, pers. comm.) may be summarized as follows: the decomposition of N-poor woody material is highly dependent on which microorganisms, mainly fungi, colonize the wood. If white-rot fungi dominate as invaders, then decomposition is rapid and progresses to completion, leaving minimal remains. If, on the other hand, brown-rot fungi dominate in the attack, then the decomposition will not be complete, and a residue will persist. Brown-rot fungi, through their sheer dominance, can prevent ingrowth of the more efficient white-rot organisms. Following a brown-rot attack, a fragmented humus-like material is left that has a very low turnover rate, and can be found in the humus layer for a long time (Fig. 11.2).

Foliar litter types with different N concentrations have levels of stable remains proportional to their N levels (cf. Chap. 6). Compared to foliage, the extremely low N levels in different kinds of woody litter result in dramatically different decomposition processes. Woody material that is attacked by white-rot may be decomposed rather quickly, leaving little recalcitrant residue, while woody material attacked by brown-rot may turn into more stable organic matter (cf. Chap. 9).

An observation on the decomposition of woody material by Johnson and Todd (1998) illustrates the potential contribution of wood in a temperate mixed oak forest. They state that dead stems constitute a very common and visible component on the ground in older coniferous systems in the northwestern USA. Thus, it is often assumed that this woody debris has an important role in the functioning of the

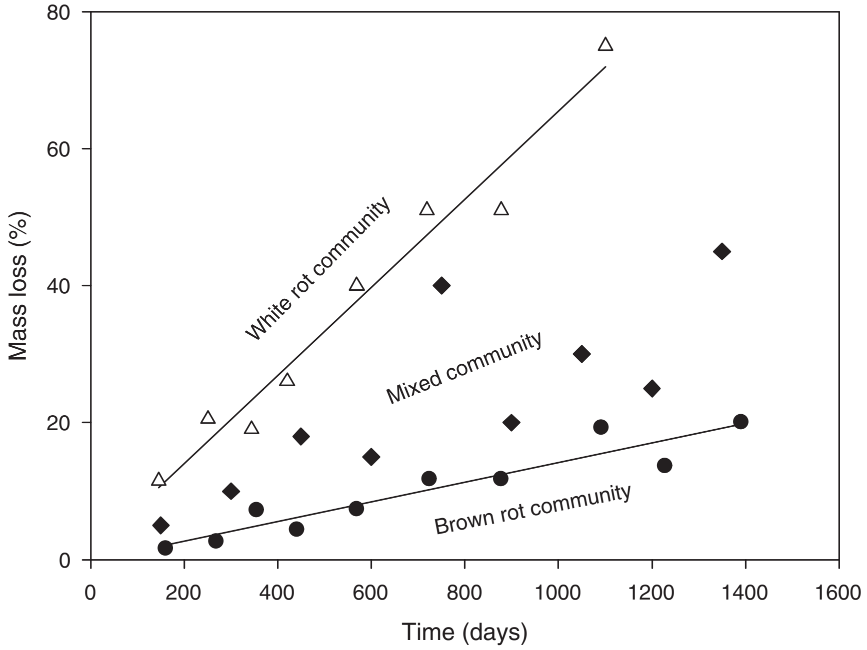

Fig. 11.2 A hypothetical decomposition pattern for woody litter material depending on whether it is being degraded by white-rots (△), brown-rots (●), or both (◆)

ecosystem, including that of habitat for animals, microorganisms, and new plants. However, they conclude that dead stems constitute a relatively unimportant component in the mixed oak forests in southeastern USA. Much of the larger-diameter woody residue that was left on the ground decomposed by more than 80% after only 15 years. They claimed that this residue had no effect on the C contents of the soil.

We can conclude that in the above study, the magnitude of the contribution of woody components to the formation of humus was possibly low, at least for the humus layer, since leaching was not investigated or discussed. We may further conclude that the quantitative contribution of wood to humus among boreal systems is unclear, and that the decomposition patterns that govern the importance of these contributions are unknown. Although oversimplified, we can speculate that systems dominated by white-rot fungi should result in a soil system in which a complete decomposition of woody materials dominates. Likewise, in systems in which brown-rot organisms dominate, a proportionally larger part of the humus would be based on woody materials. This reasoning could probably also be applied to woody root litter, although whether roots form significant amounts of humus is uncertain (cf. Chap. 9). However, the dominance of one group of fungi or the other in different systems is to date not well known.

Woody components are decomposed into humus in a pattern different from that of the more nutrient-rich foliar litter components. The attack on wood may be random, or controlled by environmental factors that give either the one, or the other kind of lignin-degrading organisms an advantage, based on, e.g., location, season, state of decay, or wood species. The general nutrient status of the stand can, of course, affect which organisms would dominate. When remains of partly decomposed woody material (often a brown powder) are seen in the humus layer, this should not be interpreted as reflecting the only kind of decomposition that occurs in wood, and does not imply that woody materials generally form humus. Furthermore, we do not know what proportion of the total inflow of woody material remains in the humus as partly decomposed material. For mature boreal stands, about 30% of the litter fall is not foliar, but consists largely of woody matter (Mälkönen 1974). Thus, in a system in which white-rot fungi dominate, we could expect that less would remain of such material, and its contribution to the humus layer to be smaller than would be the case in a system in which brown-rot fungi dominate. On the other hand, in boreal coniferous forests, brown-rots generally dominate (T. Nilsson, pers. comm.), which would mean that a higher fraction of woody material would persist longer as recalcitrant material. However, the longevity of this recalcitrant material of woody origin is unknown, and we cannot say if it forms humus in the same sense as does foliar litter.

In the case of fine (<1 mm diameter) roots, the picture is not very clear. We have, for example, not found any direct studies on the decomposition of fine roots. In addition, our own studies, as well as personal communications with other scientists, indicated that traditional decomposition experiments do not seem to give a true picture of mycorrhizal fine root decomposition. For example, dead fine roots of pine that were incubated in litterbags inside the humus layer have shown a strong resistance to decomposition. In contrast, there is evidence that the fungal component of the mycorrhizae of pine fine roots may be involved in the decomposition of humus. This indicates that the fungal component of mycorrhizae may have an important role as decomposer organism (cf. section below). In addition, large and rapid fluctuations in fine root biomass indicate that their decomposition may follow different patterns than that of foliar litter (cf. Chap. 9; McClaugherty et al. 1982).

The main contribution to humus from the fungal biomass surrounding the fine roots may be from dead and recalcitrant fungal mycelia. This would represent a very different mechanism for the addition of material to humus.

Foliar litter forms humus, and we can distinguish a connection between its chemical composition, and the potential for humus formation. The picture is less clear for the more nutrient-poor litter components, such as woody litter. We are unable to quantify their contributions to humus, at least partly because of a lack of knowledge about the ecology of lignin-decomposing organisms.

11.2.4 An Accumulation Mechanism can be Validated

The question of humus stability is intimately interlinked with the ecosystem, its organisms, and changes taking place in the system. In the discussion below, we focus on humus stability in undisturbed forest ecosystems, under continually growing forest. Using the growing forest as constraint on the ecosystem, we have used long-term accumulation of humus as a measure of its stability.

Three approaches have been used to test the validity of the limit-value concept as a tool for estimating humus accumulation (Berg et al. 2001): (1) a direct comparison between measurements of accumulated humus and storage estimated by the limit-value concept; (2) the effect of species, in this case foliar litter with different N concentrations, and mass of litter fall were compared to humus storage; and (3) the estimated N concentrations at the limit values were compared with the humus N concentrations in the same stands. All these studies have been conducted on a stand level, and thus in areas normally less than a hectare.

To verify the limit-value model for long-term C accumulation, conditions must be set on the test system. Such conditions are not always easy to fulfill. Both the correct quantitative information, and the site history should be available (Berg et al. 2001). The accumulation of humus may thus be estimated theoretically using knowledge of limit values, and the magnitude of litter fall. Because the N level of the litter largely determines the limit value, it may be used to estimate humus accumulation (Fig. 11.3; Berg et al. 1996b; Berg 2000b).

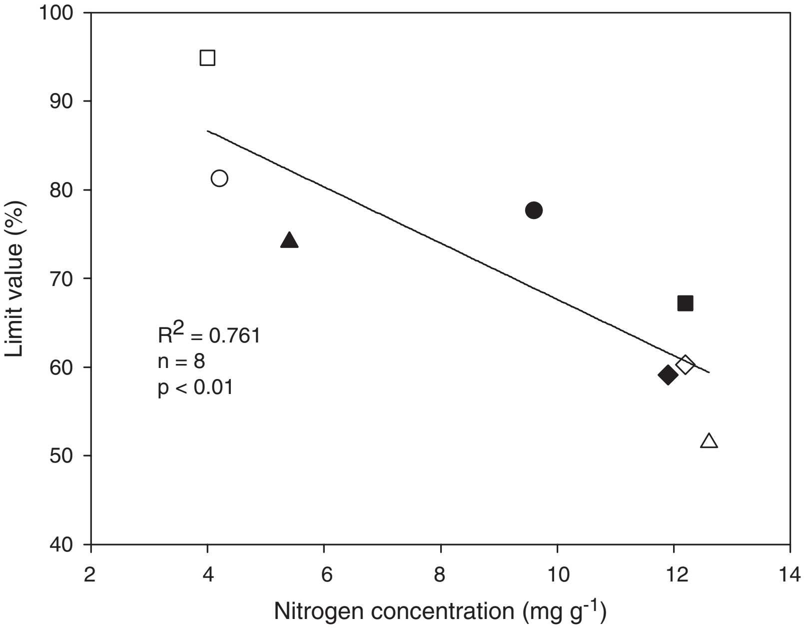

Fig. 11.3 The limit value for decomposition, and thus the magnitude of the recalcitrant (humus-forming) part of the litter is related to initial N concentration in litter. Average values for eight litter species: ○ Scots pine – brown needles, ■ Scots pine – green needles, □ lodgepole pine, ▲ Norway spruce, △ silver fir, ● silver birch, ◆ European beech, and ◇ oak spp. (Berg 2000b)

Direct Humus Measurements

Site data and history for a 120-year-old stand. A budget for humus was generated for a Scots pine forest, and validated with information from the same pine forest, for which there existed well-documented background and site history data (Berg et al. 1995b). For this forest site, there are extremely good data for litter fall, litter decomposition, and amounts of soil organic matter on the ground. An important fact is that a major fire event took place in the mid-1800s that destroyed the existing organic layer. The existing humus layer has been built up on the resulting ash layer from the litter fall of the existing stand.

A litter-fall model estimated litter fall for 120 years. Litter fall was measured for 7 and 10 years in each of two pine stands, which were 18 and 120 years old at the start of the study. The stands were growing on the same soil, and had the same climate and hydrology (Flower-Ellis 1985). The combined litter-fall measurements covered a period of 17 years. This extended sample period made it possible to adapt two litter-fall models (cf. below) for a mature stand. Root litter was not considered, as the pine roots had been observed mainly in the mineral soil in this stand (H. Persson, pers. comm.), and only lingonberry rhizomes and heather roots, which form a small fraction of the total root biomass, were found in the humus layer.

Litter fall usually increases with stand age until a maximum biomass is reached. Data from a chronological study (cf. above) can lead to a mathematical description of litter fall in terms of stand age. We consider two alternative models for litter fall (Fig. 11.4) as a function of stand age, using the above data. The first, and simplest, model assumes a linear increase in litter fall until canopy closure, after which it remains constant. For example, annual litter fall would increase in uniform steps of 16.2 kg ha^{-1} each year from year 1, reaching a constant input of 1,620 kg ha^{-1} year^{-1} in year 100. This was the measured 10-year average amount of litter fall in the stand (Berg et al. 1995b).

The second model assumes a logistic increase in litter production. The logistic model can be stated as

$$\frac{\mathrm{d}F}{\mathrm{d}t} = gL\left(\frac{F_{\max} - F}{F_{\max}}\right) \tag{11.1}$$

It can be solved to give

$$F_t = \frac{F_{\max} F_0}{F_0 + (F_{\max} - F_0)\mathrm{e}^{-gt}} \tag{11.2}$$

where F_0 is annual litter fall at time $t = 0$, F_t annual litter fall at time t, $F_{\max}$ maximum ("steady-state") annual litter fall, and g a constant intrinsic for the rate of increase in litter fall with stand age. The unit for litter fall was kg ha^{-1}.

Using serial approximations to achieve the best fit to data from both the 18- and 120-year-old stands, the following parameters were derived: $F_{\max} = 1{,}620$, and $g = 0.37$.

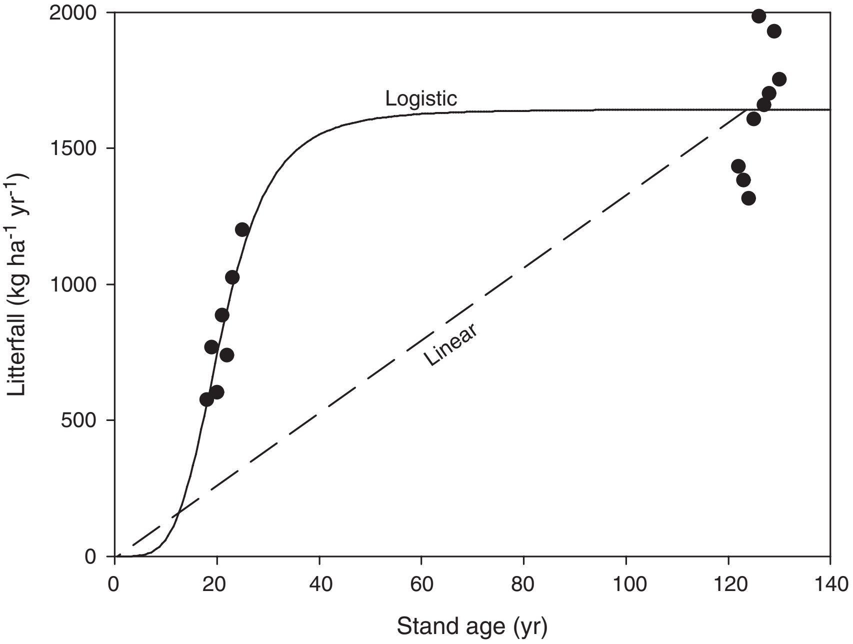

Fig. 11.4 Two simplified models for litter-fall variation with stand age, developed using data from a chronosequence of Scots pine stands. One model assumes a linear increase in litter fall with age, up to 100 years, followed by a constant litter fall. The other is a logistic, nonlinear model fitted to the data for the 18–25 and the 120–130 year old stands in a chronosequence (SWECON site, Jädraås, Appendix III; Berg et al. 1995b)

A budget was set up. Staaf and Berg (1977) determined that the amount of SOM was 1.54 kg m^{-2} in the combined A_{01}–A_{02} horizon. This value, based on ash-free matter, did not include distinguishable litter remains. The needle litter fall from Scots pine completely dominated the litter inflow. Based on eight measurements of the limit value, this needle litter left an estimated residual of about 11% (cf. Chap. 2; Berg et al. 1995b). Using that as a basis, the litter inflow for each of 112 years was estimated (cf. the litter formed in the last 8 years had not yet formed a stable humus). Addition over 112 years gave an estimate of accumulated organic substance of 1.67 kg m^{-2}. This theoretical result differed by only 8% from the observed level of 1.54 kg m^{-2} (Staaf and Berg 1977; Table 11.2). Because the chemical composition of litter can be important in determining the limit value, it is important to note that the foliar litter formed from the pines was chemically similar over different years (cf. Table 4.4; Berg et al. 1993b). Furthermore, the main part of the litter from the shrubs at the site had a chemical composition (lignin and N) that was close to that of the pines (Berg and Staaf 1981).

Three budgets covering millennia. Berg et al. (2001) set up further budgets by using data from Wardle et al. (1997). The average age of three groups of humus layers from three separate forest stands had been determined to be 2,984, 2,081, and

1,106 years, using ^{14}C analysis of ash from the latest forest fire. Wardle et al. (1997) determined the amount of ash-free humus to be 49.0, 34.6, and 14.3 kg m^{-2}, respectively (Table 11.2).

A simple regression model for needle litter fall from the completely dominant species (Scots pine and Norway spruce), based on measurements in boreal stands (northern Scandanavia, between 52 and 67°N), was used to estimate litter fall for all three groups of stands. With the use of the average limit value for needle litter of Scots pine and Norway spruce in northern Sweden ($n=18$), the fraction remaining was calculated, and the magnitude of annual accumulation was estimated. The annual accumulation was summed over the different periods. The accumulation thus estimated for foliar litter was 41.2, 28.7, and 15.2 kg m^{-2}. The former two values were 16 and 17% lower than the observed values, whereas for the 1,106-year-old humus, the estimate was 6% too high. When using total litter fall, the estimates were generally too high, the values being 46, 37.6, and 86.3% for the 2,984-, 2,081-, and 1,106-year-old stands, respectively (Table 11.2). It is possible that the method used to estimate litter fall is susceptible to error, and this may in part explain the magnitude of the deviation. Only data for litter fall were used, while the root litter component was not considered.

Different Species – Different N Levels – Predicted Differences in Paired Stands of Scots Pine/Norway Spruce, and Douglas-Fir/Red Alder

Eight paired stands of Scots pine and Norway spruce were analyzed in one experiment. The paired stands were of the same age, and they were growing on the same soil, and under the same climates. In each stand, litter fall was measured, the chemical composition of litter determined, and the amount of C in the humus layer on top of the mineral soil measured (Berg et al. 1996a).

Berg et al. (1996a) found that the needle litter of Norway spruce had, on average, higher N levels than that of Scots pine, i.e., 5.16 mg g^{-1} for Norway spruce litter, and 4.08 mg g^{-1} for Scots pine. This difference was statistically significant over all stands located at eight climatically different sites.

Limit values for spruce needle litter were lower than for pine. The average limit values for Norway spruce and Scots pine in these stands were 77 and 81.2%, respectively. This would correspond to a potential storage of 23 and 18.8% of foliar litter fall for spruce and pine, respectively.

The quantity of litter fall is one factor that influences humus buildup. An evaluation of the litter-fall data suggests that the pine plots have a significantly higher needle litter fall. However, there was a larger accumulation of humus in the spruce than in the pine stands. When determining the amount of C that had actually accumulated in the humus of the stands investigated, Berg et al. (1996a) found that compared to pine stands, on average 13.4% more humus was stored in spruce. The spruce forests thus had a higher accumulation of C, despite the higher foliar litter fall in the pine forests. A theoretical estimate, based on a uniform litter fall, suggested that humus accumulation should be 26% higher in the spruce stands, compared to the accumulation in pine. It is reasonable to suggest that the higher litter fall in the pine forests had reduced the difference between the theoretical and observed values.

Humus accumulation is lower in a stand poor in N (Douglas-fir) than in an N-rich stand (red alder) on the same soil. A recalculation of a study (Cole et al. 1995) of two stands of equal age and on the same soil, one of which was Douglas-fir (N level of 5.4 mg g^{-1} in the foliar litter), and the other red alder (N level of 23 mg g^{-1} in the foliar litter), showed that the latter had a clearly higher amount of soil C. Berg et al. (2001) estimated the limit value for decomposition by using the N concentrations of the foliar litter, and constructed a model for the buildup of the soil organic matter layer. From the model estimate, it was evident that the higher accumulation of humus/soil C in the alder stand could not be explained only by higher litter fall. In Table 11.5, the difference in estimated amounts of SOM (using the limit-value concept) was 7,625 g m^{-2}, and the difference in the measured amount 7,300 g m^{-2}, the latter value being the sum of SOM in the O-horizon, wood, and SOM in the mineral soil. This may be explained largely by the different limit values that were estimated from the different N levels (Table 11.5).

Comparison Between Estimated N Concentration at the Limit Value for Decomposition, and that Measured for Humus in the Same Stand

Litter N concentration increases linearly over the course of litter decomposition, and is highly correlated to accumulated litter mass loss (cf. Chap. 5; Fig. 11.5). By estimating and using limit values, and the linear relationship between N concentration in litter and its accumulated mass loss, the N concentration at a limit value can be estimated (Fig. 11.5, Berg et al. 1999b). The estimated N concentration at the limit value can therefore be compared to that measured in the ash-free mor humus in the same stand. Nitrogen can thus be used as an internal marker to confirm the limit value.

The limit value for decomposition was calculated for a larger number of litter studies (local needle litter). By extrapolation of the linear relationship between accumulated mass loss and the increasing litter N concentration, Berg et al. (1999b) estimated the N concentrations at the different limit values (Fig. 11.5). These estimated N concentrations were compared to those of the humus of the A_{01} and A_{02} layers in the same stands. Forty-eight stands with eight tree species were used.

In a comparison between the estimated and measured N levels for humus, they found that the estimated values for the N concentration in humus were 6.8% lower than those observed (Fig. 11.5B). For example, if the estimated humus N concentration were 1.00%, then the measured concentration would be 1.07%. This difference is of the same magnitude as that of the methodological error for N analysis. Berg et al. (1999b) concluded that the litter remains at the limit value had a relatively long-term stability, and indicated that there was a possibility of estimating humus N buildup (cf. below).

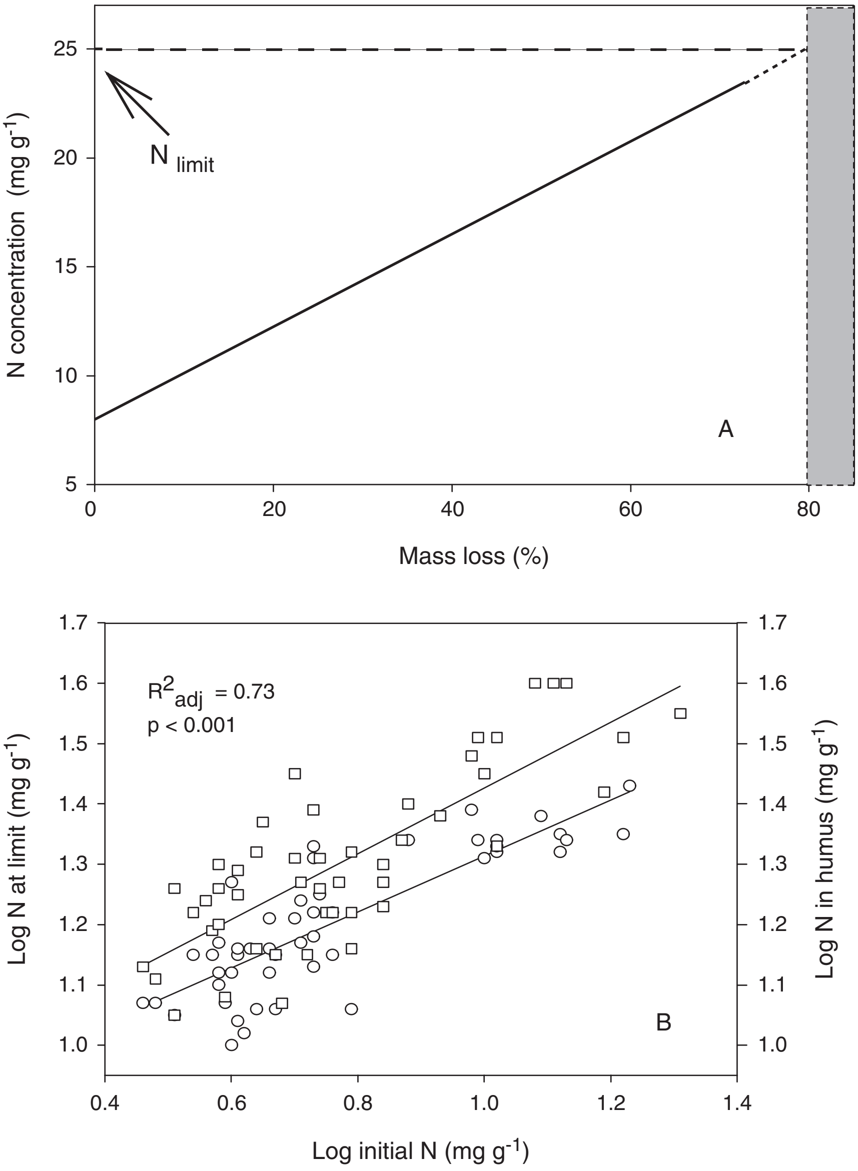

Fig. 11.5 **A** The N concentration in decomposing litter increases linearly as a function of accumulated mass loss. The N concentration at the limit value (N_{limit}) is estimated by means of linear extrapolation. **B** Comparison of the estimated N concentration at the limit value (○), and the N concentration actually measured in the ash-free humus layers (□) in the corresponding forest stands. Data from 48 decomposition studies with local foliar litter were used (Berg et al. 1999b)

11.3 How Stable is Humus?

11.3.1 Do Limit Values Indicate a Complete Stop in Litter Decomposition?

Although it is possible to estimate significant limit values for litter decomposition, we cannot conclude that such limit values necessarily indicate completely recalcitrant remains in the humus-near litter. Couteaux et al. (1998) applied both a three-factorial model (cf. Chap. 10), and a limit-value function to direct measurements of decomposing Scots pine needle litter, as well as to the humus formed in the same stand. They reported *k* values for decomposition of a stable fraction, close to the limit value, of 0.0001 to 0.00001% per day, which corresponds to a rate of about 1% per 30 to 300 years. That study included an analysis of stable, meta-stable, and labile components (Table 11.7). Of those three fractions, the stable fraction comprised about 80% of the total organic material, and could be considered as rate-limiting. The estimated *k* values may thus indicate a fraction that is well stabilized, and therefore decomposing at a very low rate (cf. below). We may emphasize that the *k* values for the resistant fraction in humus, and for far-decomposed litter were the same as was the size of the resistant fraction. The fact that allophanic (see Glossary) humus exists shows that an "eternal" storage is possible. Although allophanic organic material may be regarded as an extreme case, the level of stabilizing components (e.g., aluminum and iron) necessary to terminate the decomposition process is not known (Paul 1984).

11.3.2 Four Classes of Humus Turnover

We can distinguish four main classes of turnover, and major influences on the decomposition of humus. For a start, there is the class of humus decomposition that occurs in completely undisturbed humus. Then, there are two classes associated with elevated microbial activity: one is associated with strongly activated mycorrhizae, the other with mechanical disturbances caused by soil manipulation and drainage, leading to substantially higher decomposition rates. Analogous disturbances that occur when sampling humus probably explain the high rates of CO_2 efflux sometimes reported (e.g., Persson et al. 2000a). Finally, high turnover rates have been observed in humus subjected to very high N inflows.

Humus Decomposition – Undisturbed Systems

Respiration (litter CO_2 release) is commonly used to measure humus decomposition, and normally includes a disturbance of the sample, which can lead to increased respiratory activity. A major problem with describing soil respiration is the difficulty of separating root respiration, faunal respiration, and microbial respiration in intact systems (Hanson et al. 2000; Högberg et al. 2001).

There are few direct gravimetric measurements on humus decomposition, and we have not found any study that has given long-term data for humus decomposition in situ and in undisturbed samples. Two requirements for correct measurement are that this include ash-free humus, rather than whole humus layers, and that the system should not have been disturbed. An additional problem is that only part of the material classified as humus in the humus layer is stabilized (Townsend et al. 1995, 1997; Olsson et al. 1996; Couteaux et al. 1998), while a substantial part of the matter classified as humus is considerably more easily degradable than the stabilized fraction. For example, Staaf and Berg (1977) found that, of the substance that they classified as humus in Scots pine stands, about 15% was water-soluble. In the humus of a different Scots pine stand, Couteaux et al. (1998) found a labile pool of about 5%, a meta-stable pool of ca. 13–15%, and a recalcitrant pool of ca. 80–85% (Table 11.7).

Following a clear cut of a Scots pine forest, Berg and Staaf (1983) measured the disappearance of ash-free humus layers. A reinterpretation of their data, moving from a linear relationship to a more curvilinear one, indicates that nearly all of the 27% organic material that disappeared during the 4-year study period was probably lost already in the first 2 years. This could mean that once remaining dead root material and soluble matter had decomposed the first 2 years, no measurable decomposition took place the last 2 years.

Olsson et al. (1996) found mass losses ranging from 0 to 7% for pine forest humus, and 17 to 22% for spruce forest humus over a period of 15–16 years. If labile and meta-stable fractions were decomposed first, and were the main component of the mass loss recorded, this should mean that the Scots pine humus was stabilized to a similar degree as that found by Couteaux et al. (1998).

Decomposition rates measured in the laboratory (disturbed samples). There have been numerous respiration measurements (O_2 and CO_2) carried out on humus. However, almost any type of sampling involves some level of disturbance of the humus system and its microorganisms. When the humus is sorted, and roots or other inclusions are removed, the disturbance will be even larger. A disturbance of this kind normally results in greatly increased activity lasting for some days to a week. Because of this, samples are pre-incubated for up to 2 weeks to ensure they are "stabilized", before the measurements are carried out. This does not mean that they are so stable that they can be used to quantify humus decomposition, and give results that can be used to accurately model events occurring under undisturbed soil conditions.

In an investigation of respiration studies, the authors used 20 randomly selected reports, and recalculated the CO_2 release rates as percentage annual mass losses, to allow comparison among a large set of independent measurements. The resulting respiration values gave rates of between 5 and 30% C loss per year (e.g., Persson et al. 2000a). The lower values are of the same magnitude as for measured values of the decomposition of pine and spruce needles in late decomposition stages, and the higher value of the same magnitude as for the first year. Given that this sampled humus had been collected after an accumulation of tens, or even hundreds of years, such high rates cannot accurately represent the respiration rate of humus in undisturbed systems.

In their approach using respiration, Couteaux et al. (1998) investigated both humus and partially decomposed litter. During their study, about 20% mass was respired, at rates that differed strongly between the labile and the stable pools. The ratio between rates for the labile and recalcitrant pools was ca. 10,000:1, and the relative sizes of the pools were 5 and 80% of the total mass. These results suggest that many studies overestimate humus respiration as it would occur in an undisturbed system. In addition, in many of these experiments, it is likely that the properties of only a smaller, labile fraction of the humus sample will dominate CO_2 release.

Comparing the orders of magnitude of the above estimates, all for Scots pine forests, with those of Couteaux et al. (1998), we see that the higher rates (ca. 27% loss per year, Berg and Staaf 1983) coincide with those calculated by them for the labile fraction (ca. 30% loss per year). The lower rates correspond with the rates of the meta-stable fraction (ca. 3–6% per year). For the stable fraction (Couteaux et al. 1998), a rate of ca. 0.0001 to 0.00001% per year, or ca. 1% in 30–300 years, was found (Table 11.7). These calculations by Couteaux et al. (1998) deserve attention, because they represent a new approach for experiments based on respiration measurements.

Disturbances of Decomposition Rates – some Specific Cases – Mycorrhizae in Natural Systems

In undisturbed humus systems, there appear to be mechanisms that can change the composition of the microflora in ways that enhance its ability to degrade the otherwise stable humus. Hintikka and Näykki (1967) gave a good description of the mycorrhizal basidiomycete *Hednellum ferrugineum*, and its effects on the humus layer. The development of strong outbursts of soil respiratory activity, followed by a strong decrease in amounts of humus in the A_{01}–A_{02} layer, was described. The effect was observed patch-wise on boreal dry, sandy, nutrient-poor sediment, and till soils with a development of thick mycelial mats, and could be related to plant growth (see below). This is likely to be a powerful mechanism for humus decomposition that can transform potentially stable humus into a gray mycelial powder in a short time.

Thus, the same kind of humus in Scots pine forests that Couteaux et al. (1998) found to have an extremely low decomposition rate could disappear almost completely in a very short time, leaving only a gray powder. In their pioneering study, Hintikka and Näykki (1967) supported their investigation with field measurements of humus that was almost completely degraded, and compared respiration rates. An investigation into the frequency of this phenomenon of local increases in decomposition showed 13–14 such patches of about 0.5 to 2.0 m^2 in 1 ha of very nutrient-poor Scots pine forest (B. Berg, unpubl. data).

In another system, Griffiths et al. (1990) studied the effects of the ectomycorrhizal fungus *Hysterangium setchelli* on respiration in humus under Douglas-fir, and identified patches with very high respiratory activity. There appears to be a consensus among authors that the decomposition of humus material by ectomycorrhizal fungi provides an important source of nutrients for trees. This effect has also been observed for other mycorrhizal fungi (Unestam 1991). The current explanation is that when trees are subject to nutrient stress, their mycorrhizae are "activated", and switch their function from mutualists to decomposers. This means that nutrients are released in response to the trees' nutrient stress. The contrast between this activation and the more normal, low turnover leading to fast accumulation is dramatic. However, the phenomenon appears to be infrequent, and did not severely affect the kind of estimates of humus accumulation made by Berg et al. (1995b).

Disturbances of Decomposition Rates: Fire, Soil Manipulation, and Drainage

Fire is well recognized as a renewal agent for ecosystems, a general fact that does not need any further presentation, and so we will focus on the effect of fire on humus layers. After mapping the wild-fire frequency over large parts of northernmost Sweden for more than 1,000 years, Zachrisson (1977) found that, for example, in Scots pine stands there had been a fire every 50 to 60 years. Each fire removes at least part of the humus layer, which results in the generally thin humus layers observed in pine forests in northern Fennoscandia. Normally, only parts of the humus layer would disappear in each fire, but in each case, there occurs a mineralization of nutrients. This release of nutrients from the ashes may have a stimulating influence on the decomposition of the underlying remaining humus layer. Irrespective of nutrient effects, repeated fires have an influence on the accumulation and storage of humus. Thus, stand history is a dominant factor for determining humus accumulation rate (Wardle et al. 1997).

Disturbances of the soil system that increase decomposition activity have been noted within different contexts – for example, in different kinds of site preparation, or simply the mixing of a soil sample. Johansson (1987) observed faster decomposition of Scots pine needle litter incubated under plowed-up humus and mineral soil in scarified plots, compared to control litter. In an investigation of limit values, Berg and Johansson (1998) found that decomposition also advanced further after scarification of a plot's humus, and that significantly higher limit values were obtained for pine needles, increasing from 64% on non-scarified plots, to 97% for litter on scarified plots. Salonius (1983) made a careful investigation of material from L, F, and H layers, and found an increased respiration rate when these materials were mixed with mineral soil from the B-horizon. Unfortunately, the mechanisms underlying the increased decomposition rate following disturbance are not known in detail.

Of the more large-scale observations, Delcourt and Harris (1980) compared the effects of the intensive American cultivation of the 18th and the 19th centuries with current practices, revealing what happens when agricultural use of the soil is reduced. They concluded that in the past, cultivation caused disturbance of the soil, and resulted in large-scale release of C. Today, that situation is reversed, as the reduction in area under cultivation has converted the ground into a C sink.

Soil drainage increases the turnover rate of soil organic matter, as a result of both the direct effect of local disturbance, and the effect of a lowered water table. To explain this, we may return to the conceptual model that illustrates the strong influence of lignin and lignin-like transformation products on the decomposition of organic matter. These compounds cannot be degraded completely under anaerobic (oxygen-free) conditions, because the dominant decomposer organisms are fungi and oxygen-demanding bacteria. Ditching causes a lowering of the water table, allowing oxygen to penetrate to deeper soil layers. This causes an increase in the degradation of the larger polymer aromatic compounds, and thus of the whole organic matter pool.

Within this context, in Chapter 8 we have already described an effect observed by Vesterdal et al. (2002). Although a disturbance may cause an activation of the disturbed material, or of the disturbed soil layer, there may also be new formation of stable material on top of the material that has been disturbed (e.g., Sect. 8.2.1, Fig. 8.3).

Disturbances of Decomposition Rates: Systems with High N Loads

There are some observations indicating a decomposition mechanism for humus that appears to be initiated by high acid or high N loads in soil (Guggenberger 1994). Such an effect was also mentioned by Nömmik and Vahtras (1982) in their review on ammonium fixation to organic matter in laboratory experiments. They referred to the formation of soluble substances as an effect of this fixation.

Very high N loads appear to promote a disintegration of humus, partly because of increased microbial activity (Fog 1988). Fog (1988) proposed the hypothesis that a higher concentration of N in litter resulted in an increased production of soluble organic matter (DOM, dissolved organic matter, or DOC, dissolved organic carbon). His arguments were based on the observation that lignin-degrading soft-rot fungi (cf. Chap. 3) need, or at least tolerate, high ambient N levels. Therefore, in an environment rich in N, soft-rot fungi can to a certain extent replace white-rot organisms. Their degradation of lignin produces incompletely degraded lignin that can react with organic N compounds, which leads to water-soluble products that would then precipitate in the mineral soil. Fog's (1988) conclusion was that high N concentrations increase the formation of water-soluble, decomposition-resistant compounds, but decrease the amount of humus that is formed. Ulrich (1981) described a similar process, and called it a "disintegration of humus". Other scientists, including David et al. (1989), have reported higher concentrations of soluble organic matter with increasing acidity. Guggenberger (1994) concluded that the mobilization of DOC is not ruled exclusively by a low pH. On the contrary, he concludes that high inflows of total N suppress the complete lignin degradation carried out by white-rot organisms, but increase general microbial activity. He supports the conclusion proposed by Fog (1988) that the more N-tolerant soft-rot fungi produce partial degradation products, such as N-containing compounds, which are more water-soluble. Guggenberger also proposes that a generally higher microbial activity increases the production of microbial metabolites. In more recent studies of litter with moderate N levels, $^{13}CO_2$ release from litter was compared to leaching of ^{13}C from the same litter. The litter with higher N gave a higher leaching of C to the mineral soil (Flessa et al. 2000). It is possible that these studies indicate a general mechanism related to litter N level.

To the above observations, we may connect a comparison of amounts of humus in mineral soil under Douglas-fir and red alder. In the paper by Cole et al. (1995) described earlier, it was shown that a higher amount of C compounds had been leached into the mineral soil from the humus layer in the N-rich alder stand. This single study cannot on its own support a general conclusion that an N supply in a naturally richer environment is part of a mechanism for formation of DOC that later precipitates in the mineral soil. Nevertheless, this observation is consistent with Fog's (1988) hypothesis, and the results of the ^{13}C laboratory study described above.

We may combine some of these observations to extend the hypothesis. Both Nömmik and Vahtras (1982), and Flessa et al. (2000) describe chemical transformations in humus that may produce water-soluble substances. The theory proposed by Fog (1988), concerning microbial components, may hold more generally – if modified. We may speculate that in humus exposed to high N loads over a long period, a change takes place in the mycoflora (cf. Eriksson et al. 1990; Hatakka 2001). Lignin-degrading fungi that are not sensitive to, and may even be stimulated by, elevated N levels dominate the resulting fungal community. This would cause an acceleration of degradation processes, and would be dependent on the level of N deposition. This would also fit the observation by Guggenberger (1994).

11.3.3 Possible Effects of Increased Temperature on Humus Decomposition – an Artifact?

A general rule in ecology is Liebig's law of the minimum: a factor limits a physiological process only as long as no other factor overrules it (von Liebig 1847). Over the course of the transformation of litter to humus, there is at least one shift in such limiting factors.

The negative linear relationships between lignin levels, and the decomposition rates of litter change with climate, as indexed in terms of AET (Berg et al. 1993e; Johansson et al. 1995). When decomposing litter approaches humus, the effect of climate decreases, and the effect of lignin levels increase to such an extent that the effect of climate was not measurable in experimental systems using litterbags to model decomposition of an undisturbed organic substrate (cf. Fig. 2.8B). The comparison was based on data from a 2,500-km-long climatic transect ranging from the Arctic Circle to northern Germany, with a variation in annual average temperature from 0.5 to 8 °C, and in AET from 357 to 559 mm.

Strömgren (2001) arrived at similar conclusions by using an experimental system designed to measure the effect of soil temperature on soil respiration. After an initial period of 4 years during which soil temperature was kept 5 °C higher than in the control during the growth season, the soil microbial system adapted to the artificial climate change, and no change in CO_2 release from the ground was noted.

Rustad and Fernandez (1998) studied the decomposition of red maple and red spruce foliar litter in heated (+5 °C) and control plots in a spruce-fir forest in Maine, USA. Red maple leaves lost mass more rapidly in the heated plot during the first 6 months, but no treatment effects on mass-loss rate could be measured after 30 months. Red spruce litter mass loss was unaffected by heating during the first 18 months, but was greater in the heated plots (62%) than in the control plots (52%) after 30 months. In a similar soil-warming study in a northern hardwood forest in New York, USA, McHale et al. (1998) concluded that warming would have a short-term effect on CO_2 release until labile C was consumed. This result supports the observations made (Berg et al. 1993e; Johansson et al. 1995) for litter in humus-near decomposition stages, which suggest that factors other than climate dominate the decomposition rate of humus.

Support for this is also given by Berg and Matzner (1997) who reinterpreted data from Bringmark and Bringmark (1991), indicating a significant negative relationship between the N level in humus samples from a climate transect across Sweden, and their respiration rates. In a study along a climatic transect with coniferous forest stands, ranging from ca. 64°N in Sweden to ca. 40°N in Spain, Dalias et al. (2001) found that a standard plant material that had been incubated at a higher temperature was more recalcitrant to C mineralization than the same material incubated at a lower temperature. Such an experiment indicates that some humus-stabilizing processes proceeded at a higher rate in the warmer climate, which lends support to the observations given above (cf. Sect. 7.4.2).

11.4 Can Different Tree Species Form and Accumulate Humus at Different Rates?

From the above it follows that humus accumulation is dependent on both the magnitude of litter fall and the chemical composition of foliar litter (cf. above, Chaps. 2 and 6). The magnitude of litter fall, and the distribution of litter components control the quantity, while the chemical composition determines the substrate quality, and thus the magnitude of the limit value and the stable fraction. The term “stable fraction” must be used with some reservation. It has been demonstrated that humus that is stable in its ecosystem, and with the predominant microbial community, can be suddenly decomposed, probably due to a change in the mycorrhizal system (cf. above, Sect. 11.3.2). The term “stable humus” should rather be considered as “potentially stable humus”.

Different Tree Species

The general relationship between limit values and initial N levels in foliar litter (cf. Fig. 6.12) may be elaborated. The linear regression observed is based on 21 species, but 80 of the values originate from only eight species (Table 11.6). Comparing the mean values for N concentrations and limit values of these eight litter types gives us clear borders for these litter types, and results in a highly significant correlation ($R^2 = 0.760$; Fig. 11.3) between average N concentrations and average limit values. Although the litter types were collected over rather large regions, type-specific differences in the concentration of components such as N remain consistent (cf. Chap. 4). Thus, we see that boreal lodgepole pine would, on average, leave a small fraction of about 5.1% of the shed needle litter, while temperate silver fir would leave 48.8%, giving a tenfold variation in remaining fractions (potential humus; Table 11.6). This indicates a clear importance of tree species in determining the amount of humus accumulation.

Berg et al. (2001) defined potential storage efficiency using the remaining fraction of the decomposing litter and the litter fall. They called this the litter-to-humus (LH) factor, and it is calculated as

$$\mathrm{LH} = (100 - \text{limit value})/100 \tag{11.3}$$

This would give

$$\text{Litter fall} \times \mathrm{LH} = \text{Potentially accumulated humus} \tag{11.4}$$

Assuming a similar magnitude for foliar litter fall, the LH factor would give the relative amounts of litter remains being stored, and there would be an extreme factor of 10 between lodgepole pine and silver fir in terms of potential capacity to store humus (Table 11.6). When comparing the two pine species, there is a factor of 3–4 between lodgepole pine and Scots pine, and one of 1.4 between Scots pine and Norway spruce.

Although the negative relationships between limit values and litter N concentration represented a first major finding in this domain, there have been more recent investigations that indicate further relationships. Thus, Berg (2000a) reported that although Norway spruce needle litter fits into the linear relationship in Fig. 11.3, there was a clear relationship between limit values and initial Ca level within the species. In another investigation, Davey et al. (2007) found that also leaf litter of common oak had a weak linear relationship between initial Ca concentration and limit value. Thus, such a relationship may have some generality, although there still are only few studies in support of this. We thus do not know if this is a phenomenon across several, or only a few species. We may conclude that an increased Ca concentration may decrease the accumulation of humus due to a higher limit value.

A further influence appears to be that of Mn. We have commented earlier upon the effect of Mn on the degradation of lignin, and the positive relationships between initial Mn concentration in litter and the limit value (e.g., Table 6.8).

We emphasize the relationship to N simply because we have more information in this case, and can draw more far-reaching conclusions. Still, although the relationships between Ca, Mn, and the limit value are less studied and less clear than that for N, they could be as important either generally, or within given species.

Foliar litter fall may vary among systems. Even within a species, there are general relationships both with the nutrient availability of a system, and climate. Nutrient-enriched systems, and those in warmer, wetter climates have higher litter fall (Berg and Meentemeyer 2001).

There may be differences in annual litter fall between species even if both the soil and climate do not vary. Berg et al. (1996a, 2001) compared needle fall between eight paired stands of Scots pine and Norway spruce, and found a 7–8% higher annual litter fall in the Scots pine stands. Since both the amount of litter fall and the LH factor are variables in Eq. (11.4), a high LH factor may have a stronger influence than does the amount of litter fall. Thus, despite the higher annual needle litter fall in Scots pine stands described above, the Norway spruce stands formed more humus than did the Scots pine stands (cf. Table 11.6). Still, we must keep in mind that foliar litter is one component only, albeit a dominant one, and that when considering the sum of influences on humus formation, also ground vegetation may be considered (cf. Sect. 13.8.6).

Differing Litter Chemical Composition

Two chemical components, N and lignin, have an overall role in the retardation of litter decomposition (Berg and Matzner 1997). When plotting available data for initial concentrations of N and lignin for foliar litter, Berg (2000b) found that the litter types formed distinct groups (Fig. 11.6), and this despite sampling over a large geographical region the size of Scandinavia. For Scots pine, the sampling included stands of very different nutrient status. Nevertheless, Scots pine needle litter formed a homogeneous group that did not overlap with the lodgepole pine or Norway spruce groups (Fig. 11.6).

In this comparison, Scots pine needle litter had low concentrations of both N and lignin, whereas lodgepole pine litter had low N and high lignin concentrations. Norway spruce needles formed a group that had higher N concentrations than those of the two pine species, and lignin concentrations that were in-between. Silver birch leaves had lignin concentrations similar to those of the Norway spruce needles, and generally higher N concentrations. The leaves of European beech, collected from the whole of Western Europe, formed an extreme. In a sub-study, needle litters from Norway spruce, lodgepole pine, and Scots pine were collected annually in adjacent stands on the same soil. The variation within each group was of the same magnitude as that within the larger regions (B. Berg, unpubl. data). The effects of such differences are reflected in limit values among species (Fig. 11.3, and above).

We can conclude that plant species contributing to the chemical composition of litter fall represent a major factor affecting humus formation, at least in natural, unpolluted systems. The limited within-species variation in concentrations of the

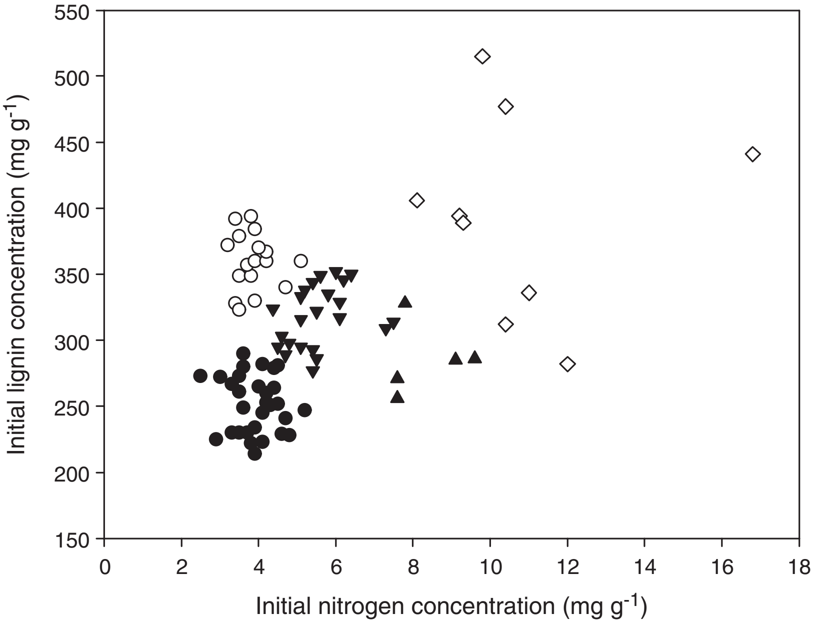

Fig. 11.6 Concentrations of lignin and N in newly shed foliar litter of Scots pine (●), lodgepole pine (○), Norway spruce (▼), silver birch (▲), and European beech (◇). All available data (redrawn from Berg 1998b)

two main components, lignin and N, over a large region supports this. Still, the variation in Mn and Ca concentrations may influence the level of the limit value, and the accumulation of humus. We have been discussing a limited litter material using mainly the effects of N on lignin degradation, and on the limit value. How an interaction involving, e.g., a variation in Mn concentration would influence this process we cannot say today. Nevertheless, we may speculate that a change in litter Mn concentration would influence the limit value – a decrease may give less decomposition, a lower limit value, and a higher sequestration – at least, it would be reasonable to speculate about that within a given species.

11.5 Storage of Nutrients in Humus

11.5.1 What Amounts of Nutrients can be Stored in Accumulating Humus?

Different litter types have different concentrations of nutrients and heavy metals. Nutrients such as K are normally released at a high rate, only a small proportion of the initial supply remaining in the litter (Laskowski et al. 1995). Several heavy metals (e.g., Pb, Cu, Zn) are, in practice, not released at all, and we could expect that decomposition is increasingly suppressed as the concentrations of the heavy metals increase. There are, however, few studies in the literature concerning the effects of different nutrients and heavy metals at natural concentrations. We may have the best level of knowledge about N, and as a result, we will focus on the effect of N.

Nitrogen

Nitrogen dynamics shows clear patterns that are easy to study and possible to relate to environmental factors. For example, it is well known that the concentration of total N increases during the decomposition of litter to humus (cf. Chap. 5). The amount that is stored in a recalcitrant form can be estimated (Berg et al. 1999b).

When litter decomposes, its N concentration generally increases. Irrespective of the net dynamics, the concentration of N increases with litter mass loss, and this relationship is linear (cf. Chap. 5). In systems that have not been artificially enriched in N, through either deposition or fertilization, the slope is repeatable, and correlated to the initial N concentration (Berg et al. 1997). The N concentration will continue to increase as long as the litter is decomposing, and will only stop increasing when the limit value is reached (Berg et al. 1999b, Fig. 11.5). The linear relationship for the increase in N concentration relative to mass loss can be extrapolated to the mass-loss value corresponding to the limit value, and thus give the N concentration that the litter will have when it reaches its stable phase. Using these data, it is also possible to calculate the amount of N that has been released from the litter (in the period from the start of decomposition until the limit value), and the amount that will be stored in the stabilized litter (or humus). Using data from field studies, Berg et al. (1999b) calculated such values for a set of litter species. The potential capacity of different litter species to store N was defined by Berg and Dise (2004a) as the amount of N remaining in stabilized litter or humus that was derived from 1 g of fresh litter. The capacity of the six different litter types studied to store N was related to their initial N concentrations. The richer the litter was in N, the more was stored (Fig. 11.7; cf. Fig. 5.12).

A more general validity of the N-storing mechanism may be expected over the boreal zone, as judged from the data presented in Fig. 11.5. These data, gathered from the whole of Scandinavia, represent a wide spectrum of N levels. As expected, litter with an increased N level formed N-rich humus, and the concentrations of N at the limit value and in humus were always higher than those in fresh litter (Berg et al. 1999b).

With knowledge of litter fall in a given stand, and of the chemical composition of the litter, the total inflow of N to the forest floor can be estimated. The input of N that will later be stored in stable humus can be calculated by combining the limit value with the linear relationship between N concentration and accumulated mass loss. The N concentration at the limit value can be calculated from the initial

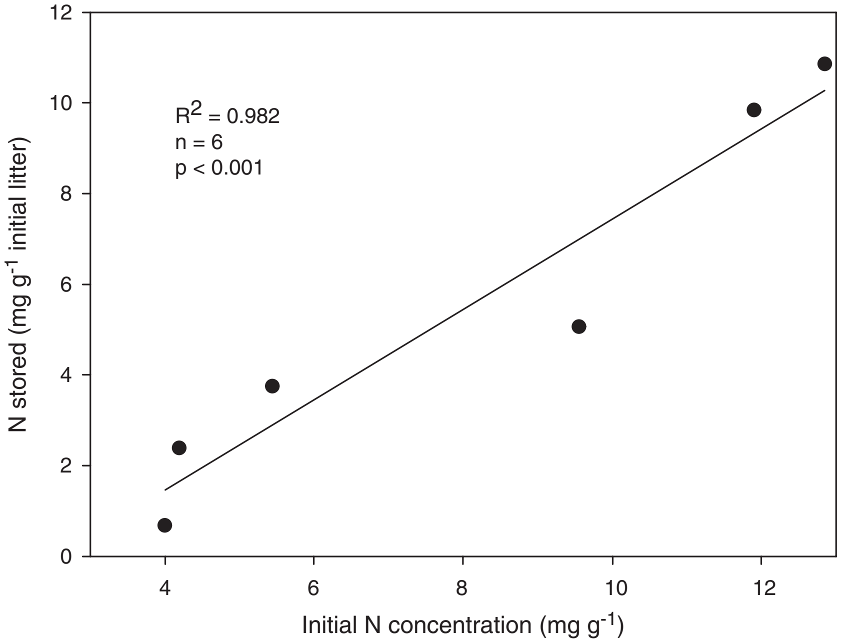

Fig. 11.7 Relationship between litter initial N concentrations, and the estimated fraction of N remaining in the litter, namely, the potential capacity to store N in humus (see potential N storage, Table 11.6; Berg and Dise 2004a)

concentration of N in litter, and the linear relationship between litter mass loss and litter N concentration (cf. Fig. 11.5). The resulting value is the concentration of N in the remaining stable humus-near litter. This means that we have a tool to calculate the annual accumulation of N in stable form. This tool also enables us to predict a future N concentration in humus after changes in the ecosystem – for example, a change in tree species.

This method has been validated using data from a set of plots with humus that had accumulated for between 2,984 and 120 years (Berg and Dise 2004b). For a first-generation Scots pine forest in a nutrient-poor system (Table 11.2), this way of calculating humus N gave a value of 18 g N m^{-2} stored after 120 years, compared to an observed value of 15 g m^{-2}. For three systems with humus accumulating for 1,106, 2,081, and 2,984 years, 163, 460, and 761 g m^{-2} have been recorded, respectively (Table 11.2). A calculation using the above approach (Berg and Dise 2004b) resulted in calculated amounts of 213, 453, and 677 g N m^{-2} for the three systems, respectively.

Fixation of ammonia. This may be important in the course of litter decomposition. Some N may be bound through chemical reactions involving decomposed lignin and ammonia (Nömmik and Vahtras 1982). This reaction is pH-dependent,

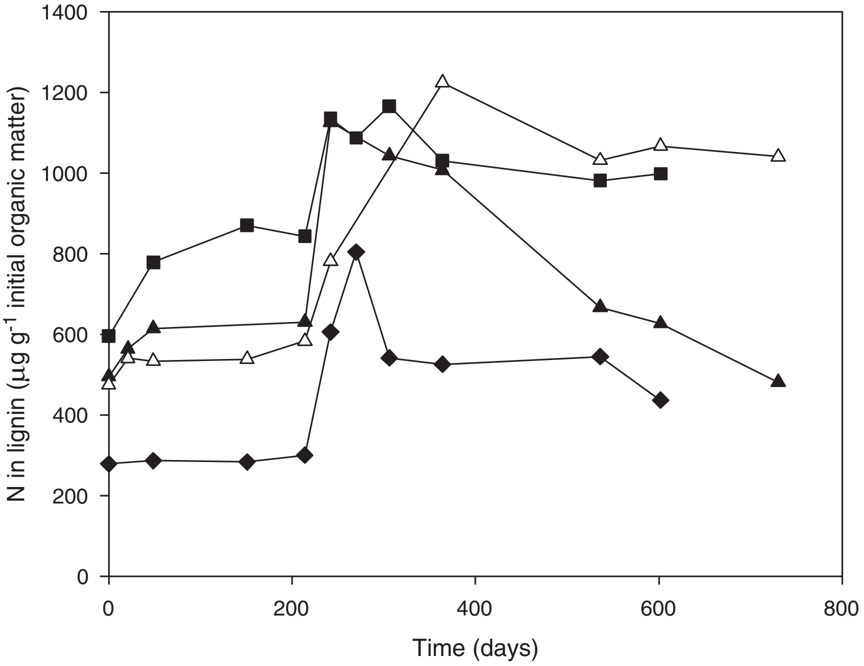

Fig. 11.8 Amount of N associated with the lignin fraction (micrograms per gram initial organic matter content) for four foliar litters incubated for 2 years in a sugar maple forest in Wisconsin, USA: ◆ sugar maple leaves, ■ red oak leaves, ▲ white pine needles, and △ Canadian hemlock needles (C. McClaugherty, unpubl. data)

and it has been shown that N concentration is limiting to the reaction rate, with more free N giving a faster reaction, but a higher total N concentration in the litter resulting in a lower reaction rate (Axelsson and Berg 1988). This suggests that in N-enriched litter, N is sequestered through the fixation process at a lower rate. The rate may be related to the number of available reactive sites in the litter material, but this is an unsupported hypothesis at present (Berg et al. 1999b; Berg and Dise 2004b).

Part of the N in newly shed litter is tied to lignin, and more N is bound during the course of decomposition. Flaig et al. (1959) investigated this process for different kinds of lignin. Berg and Theander (1984), and Berg (1988) found that for Scots pine needle litter, the concentration of N in the "lignin fraction" increased linearly with accumulated mass loss over the course of decomposition.

McClaugherty (unpubl. data; Fig. 11.8) followed the amount of N in the lignin fraction for four foliar litters over 2 years of decay. All litters showed an absolute increase in the amount of N bound to lignin during the first year of decay, nearly doubling on average. Sugar maple and red oak leaves retained their additional lignin-associated N during the second year, but two conifers, white pine and Canadian hemlock, lost some of their share, with the white pine value reverting to the initial amount. It is noteworthy that the accumulation of N in the lignin fraction occurred during the first summer of incubation.

Dinitrogen (N_2) fixation. This has been noted in decaying logs, and may be of importance in the N dynamics of wood decay. Using acetylene reduction to estimate the potential for N_2 fixation, Larsen et al. (1978) found that brown-rotted wood was more likely than white-rotted wood to support N_2 fixation. They also showed differences between species, with Douglas-fir having higher rates of N_2 fixation than subalpine fir or western hemlock. Jurgensen et al. (1984), and Griffiths et al. (1993) found that N_2-fixation potential increased as decay proceeded.

Chapter 12
Human Activities that Influence Decomposition

12.1 Introduction

Human activities impact the entire planet. Global climate change, and thinning of the stratospheric ozone layer are two anthropogenic factors with worldwide impact that may also influence the decomposition of plant litter. On a more continental scale, acid precipitation, including both wet and dry deposition of S and N, is diminishing, but remains important regionally. Ozone is often elevated in urban and industrial areas, with possible impacts on decomposition and other ecosystem processes. Also heavy metals that are released into the environment due to human activity may be detrimental to microorganisms. Some human activities are intended to increase productivity of agricultural and forest ecosystems, and the associated practices can have an impact on decomposition. There is an immense variety of activities that are undertaken in the pursuit of agriculture and forestry, ranging from pesticide application to prescribed burning, activities that to different extents may influence the decomposition of plant litter.

As has become clear throughout this book, decomposition is regulated primarily by factors that influence the ability of the microbial community to process organic matter. These effects may be exerted directly on the microbes, or indirectly, through modification of the substrates undergoing decomposition. Human activities that alter microbial processing will have an effect on the decomposition process. As environmental protection measures reduce many pollutants, decomposition processes are likely to be influenced even in places where pollution has been diminished.

Most human activities influence decomposition rates through a modification of climatic or other environmental factors. The climatic effects on decomposition have been discussed extensively in Chapter 7, so our discussion of global warming in this chapter will be limited. Similarly, we reviewed the role of N as a regulator of decomposition in Chapter 6, so here we discuss only the role of atmospheric N deposition in decomposition. Just as there are other natural factors that influence decomposition (cf. Chap. 8), there is a variety of anthropogenic factors that may be locally important, and we have chosen only a few as examples.

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12.2 Global Warming

Global warming is an active area of research today, and is the subject of both scientific and political debate. We have described in some detail the role of climate in regulating decomposition (cf. Chap. 7), and the following review of global warming experiments should be considered within the broader context of climatic effects.

Scenarios for global climate change often predict an average increase of 5 °C in the middle latitudes, with smaller changes near the equator and larger changes nearer the poles. Initially, one would predict that global warming would increase soil temperatures, which would promote microbial respiration, and result in the release of more CO_2 into the atmosphere, providing positive feedback for global warming (Bolin et al. 1986; Intergovernmental Panel on Climate Change 2001).

To study the effect of a potential increase in temperatures in the field, soil-warming experiments were set up in which buried heating cables were used in field plots (Van Cleve et al. 1990). These studies have the distinct advantage of having an undisturbed control, and can provide a longer-term record than most laboratory studies. Still, they have to date not been long enough to account for feedback mechanisms between climate change and the ecosystem. For example, a change in litter substrate, such as higher nutrient levels, might result from long-term warming (cf. Chap. 4).

Soil-warming experiments have indicated that the soil microflora will adapt to higher temperatures, viz. a higher temperature will not result in higher activity (Liski et al. 1999). Indeed, Giardina and Ryan's (2000) work summarizes data from over 80 plots on five continents to show the remarkable insensitivity to changes in temperature of decomposition rates for forest soils. Other studies, including laboratory experiments (Dalias et al. 2001), indicate that the substrate itself changes in composition when initially degraded at elevated temperatures. Both effects counteract an increase in soil temperature. An additional effect of a warmer and wetter climate would be an increased nutrient concentration (of N, for example) in the newly shed litter, both within (Berg et al. 1995a) and among species (Berg and Meentemeyer 2002). The raised N levels would probably stimulate decomposition initially, but from the later stages onward could inhibit decomposition. In conclusion, the mechanisms that we can distinguish today all indicate that an increase in temperature and precipitation would not be associated with an increased decomposition rate, but rather with an unchanged, or even lower rate, and would possibly result in an increased level of C storage (Berg et al. 1993a).

Predicting the effects of global warming on decomposition requires an understanding of both moisture and temperature dynamics. Timing and amount of precipitation can be as important as changes in temperature. If warming does increase initial rates of decay, but has little effect on the decay of more stable organic matter (e.g., litter in the late stage of decay), the important question becomes whether warming influences the amount of stable organic matter ultimately produced. For example, if accelerated initial decomposition increases N availability, then N-stabilized humus may actually increase. Clearly, this is an area in need of further investigation.

12.3 Regional Pollution

Industrial society inevitably creates by-products that can be considered as pollutants, in the sense that the substances are present in concentrations, and at locations, where they can damage biological processes. Some of these pollutants may be found in significant concentrations relatively near to their source, such as heavy metals from a smelter. Others may be derived from widespread processes, such as fossil fuel combustion, and be found over larger regions. For example, substances that give rise to acid precipitation come from a variety of anthropogenic sources, and may spread over areas of continental scale.

12.3.1 Atmospheric N and S Deposition

Atmospheric N and S deposition has been the focus of ecological research in North America and western Europe for several decades. The possible effects are numerous. To some extent, N and S inputs could actually serve as fertilizers. In some areas, the amount of N deposition has been large enough for N to no longer be a primary limiting factor for ecosystem productivity, a condition known as N saturation (Aber et al. 1998). Under N saturation, decomposition could be influenced by several different mechanisms (Jefferies and Maron 1997). A common form of input are N and S oxides, which are readily converted to acids. Acids can influence the pH of the soil system, and thereby alter the mobility, and thus the availability of nutrients. This in turn could influence both the composition and the functioning of the microbial community.

Sulfur dioxide. A significant set of studies on the effects of SO_2 deposition on decomposition have examined the impact of this pollutant on leaf litter decomposition rates (Newsham et al. 1992a), on the fungal community (Newsham et al. 1992b), and on the chemical content of the litter (Newsham et al. 1992c). In their study on fungal communities, Newsham et al. (1992b) used both an existing gradient of SO_2 and an experimental open-air field-fumigation system. They incubated six different species of leaf litter, and isolated and identified the invading fungi. In general, SO_2 did not influence the rate of fungal invasion into the litter, but it did change the species composition of the community. As SO_2 concentrations increased, sensitive fungal species disappeared and were replaced by more tolerant species. The next question is whether the change in composition was accompanied by a change in function.

The impact of SO_2 pollution on leaf litter mass-loss rates was generally small and not significant, though there was a trend toward lower mass loss with time under heavy SO_2 fumigation (Newsham et al. 1992b). In a parallel study, they inoculated four species of fungi onto sterile leaves, and assessed respiration under control and elevated SO_2. Only one of the four species showed a decline in respiration due to fumigation with SO_2.

An indirect effect of SO_2 on decomposition would occur if the litter chemistry were altered. In their third study, Newsham et al. (1992c) compared the chemical content of leaf litters formed under conditions of SO_2 pollution. Increased atmospheric SO_2 resulted in greater losses of Ca and Mg from the litter, and a lower litter pH. Although both Ca and Mg are important for fungal growth and metabolism, it is not clear whether the leaching was sufficient to retard the activity of the fungal community. In this group of studies, decomposition measured as respiration was suppressed under high SO_2, but mass loss was not. In a different study, using mixed deciduous litter and Scots pine needle litter (Wookey and Ineson 1991; Wookey et al. 1991), very similar results were achieved. Increased SO_2 decreased respiration, increased efflux of Ca and Mg from litter, and caused either a very small reduction of, or even had a positive effect on, litter mass loss.

Although SO_2 is an antimicrobial agent at very high concentrations, it does not seem to have a large or consistent effect on decomposition at levels of pollution normally encountered. Fritze et al. (1992) studied decomposition-related phenomena along a transect downwind from a coastal oil refinery. They found no effect of pollution on soil respiration, litter mass loss from Scots pine needles, or the C and N content of microbial biomass. The only notable effect was a decrease in length of fungal hyphae in more polluted areas of the transect.

Nitrogen deposition. Nitrogen is being added to ecosystems around the globe at unprecedented levels, but the long-term ecological implications of this N enrichment remain uncertain (Jefferies and Maron 1997). There are three principal ways that N deposition might influence decomposition. First, N enrichment could alter litter chemistry by changing concentrations and ratios of nutrients, and perhaps also by influencing the organic-chemical composition of litter. These changes could occur within existing species, or could be influenced by a change in community composition in response to enrichment. Second, N deposition could influence the microbial community. As described earlier, environmental N levels may have an effect on the lignin-degrading fungi (cf. Chap. 3), but the direction of this effect may depend on the level of enrichment, and the nature of the existing fungal community. Third, N enrichment may influence the kinetics of humus formation, and the nature of the compounds formed.

Several studies have utilized low-level chronic additions of N to study the impact of N deposition on ecosystem processes, including decomposition. The results are variable. The NITREX project, a series of large-scale N-saturation experiments conducted at seven sites in Western Europe (Wright et al. 1995), yielded several studies on the response of decomposition to increased N deposition. Emmett et al. (1995) found that adding N at two to four times the background level of 17 kg N ha^{-1} $year^{-1}$ over a period of 17 months had no effect on the mass loss of Sitka spruce needles incubated in litterbags on the forest floor, up to a mass loss of ca. 55%. The litter used in this study was not produced under N enrichment, and was thus uniform among treatments. Boxman et al. (1998) studied the decomposition of forest floor (L and F) material at three of the NITREX sites. They found large differences in decay rates among the three sites, but no differences related to the level of experimental N enrichment. The litters used were not grown under N enrichment. Simultaneous enrichment with N and S did cause a decline in mass-loss rates at an alpine NITREX site in Norway (Wright and Tietema 1995). Using reciprocal transplants of litter, this study distinguished between the direct effect of the treatment on the decomposition of heather leaf litter, and the indirect effect mediated by modification in litter quality. Combined N and S enrichments slowed decay through both direct and indirect mechanisms. The experiment did not separate the effects of N and S.

To test the importance of N enrichment on decomposition, Magill and Aber (1998) incubated four species of foliar litter in two different forest types, a red pine plantation, and a mixed northern hardwood stand dominated by black and red oak. Both stands were located at Harvard Forest (see Appendix III). There were three levels of N enrichment in each forest: control (0 g N m^{-2} $year^{-1}$), low (5 g N m^{-2} $year^{-1}$), and high (15 g N m^{-2} $year^{-1}$), applied in six uniform applications per year during the growing season, and continuing for 6 years. The lowest mass loss occurred in the high-N stands; the control stands had the greatest mass loss, though this was not much greater than that of the low-N treated stands. A general conclusion from this experiment is that increased exogenous N availability can reduce long-term decay rates, but may have little effect on early stages of decay.

Acid precipitation. Acid precipitation received considerable research attention during the 1970s and 1980s (Hutchinson and Havas 1980). Although the amount of acid precipitation has declined, it does continue today, and there may be a legacy from earlier, higher amounts of deposition. Kuperman (1999) studied leaf litter decomposition along a gradient of long-term bulk deposition across the Ohio Valley, increasing from Illinois through Indiana to Ohio (USA), as described by Armentano and Loucks (1990). After 19 months, spanning two growing seasons, mean mass loss (expressed as percent of initial dry matter) of white oak leaves was 36% in Illinois, 54% in Indiana, and 70% in Ohio. Dynamics of N, P, and S mirrored these mass-loss patterns, the greatest amount of all three nutrients having been released in Ohio, and the smallest in Illinois. The sites were described as having similar climates. It appears that N and S deposition may favor decomposition during the first 2 years of decay. How this might influence humus formation in these systems remains unclear, but higher N availability can increase the amount of humus stabilized (see Chap. 11).

12.3.2 Heavy Metals

Heavy metals, including Ni, Cu, Zn, Pb, Fe, and Cd, are often dispersed in the environment in association with industrial activities. Low concentrations of these elements occur naturally, and can be found in decomposing substrates (Laskowski and Berg 1993). These elements vary in their toxicity, mobility, and potential to alter decomposition patterns. Nevertheless, research has often found increased accumulation of litter in areas contaminated with heavy metals (Strojan 1978; Coughtrey et al. 1979; Freedman and Hutchinson 1980). Since these early studies, others have examined in more detail the role of heavy metals in decomposition. It is possible that the effect of heavy metals will vary with stage of decomposition and litter type. Thus, for Scots pine needle litter, Berg et al. (1991b) found only a weak suppression in the early stage, whereas in the late stage that requires degradation of lignin, a clear trend toward considerably slower degradation was seen. Berg et al. (1991b) suggested that lignin degradation was more sensitive to disturbances, although the exact reasons remain to be established.

During litter decomposition, most heavy metals are retained in the litter structure, and their concentrations increase, often exponentially. Laskowski and Berg (1993) described the decomposition of natural, unpolluted needle litter, and found that the concentration of heavy metals increased to levels that had been clearly inhibitory along a pollution transect.

12.3.3 Nuclear Radiation, Ozone, and Proximity to Urban Centers

Radiation. Gamma irradiation is not commonly encountered in nature, but studies in France and the USA have examined its impacts on numerous ecosystem properties. Woodwell and Marples (1968) examined the effects of chronic gamma irradiation on humus and litter decay rates in an oak-pine forest in New York State, USA. Irradiation had two effects on the system: a decline in leaf litter fall, and a slight increase in decay rates of litter. From an ecosystem perspective, the major effect was more via altering the amount and types of litter, rather than via modification of the decomposition process. As irradiation continued, leaf litter fall declined, but input of woody litter from dying vegetation increased.

Poinsot-Balaguer and Tabone (1995) studied decomposition in an irradiation study that had been ongoing for 16 years. In their study, decomposition was much lower closer to the radiation source. Lower decay rates were related to lower population densities of microarthropods. Both of these results could be attributed almost entirely to changing water budgets. Close to the source, larger woody vegetation had been killed and the remaining vegetation, comprised mostly of annuals, was sparse and of low stature, leading to strong reductions in soil moisture. Thus, in both these studies on gamma irradiation, it appears that radiation strong enough to kill vegetation had much less of an effect on decomposition than did moisture level and litter chemical quality.

Ozone. Ozone appears to have little direct or indirect impact on decomposition, despite the fact that it has a wide variety of effects on both the physiology and biochemistry of organisms. The coniferous forests of the San Bernadino Mountains, near Los Angeles, California (USA), were visibly damaged by air pollution during the 1970s. Studies indicated an ozone gradient decreasing from west to east. Fenn and Dunn (1989) studied litter from this gradient, and found that CO_2 efflux from needles in the L layer incubated under laboratory conditions was greatest from litter collected at the most polluted sites. In addition, fungal diversity and N content of the litter were greater at the more polluted sites. The possibility that ozone physically damaged the needles in a manner that favored their decomposition was rejected in a follow-up study by Fenn (1991), in which damaged and undamaged Ponderosa pine needles were incubated simultaneously, and exhibited no differences. The author ruled out climatic influences, and suggested that these results may be due to an increased N deposition paralleling ozone concentrations. Litter organic-chemical composition was not determined in this study.

In an eastern deciduous forest, Boerner and Rebbeck (1995) grew seedlings of three species of forest trees under three levels of ozone (zero, ambient, double-ambient), and then studied mass loss and N dynamics in a 1-year litterbag study. Mass loss was not influenced by the ozone concentration at which the foliage grew. Ozone increased the initial nitrogen release rate in sugar maple and yellow poplar, but not in black cherry, even though initial N concentrations in the litters were not affected by exposure to ozone.

Urban–rural gradient. Because so many pollutants vary concurrently along an urban–rural gradient, it is difficult to identify the impacts of individual components. However, the combined effects may be of significance to decomposition processes. Carreiro et al. (1999) collected red oak leaf litter along an urban-to-rural gradient beginning in New York City. They subjected the litter to a microbial bioassay to determine its decomposability. After 150 days of incubation in laboratory microcosms, there were significant differences in litter mass loss along the gradient, the values being 34.3% for rural, 31.1% for suburban, and 25.9% for urban sites. The lignin-to-N ratio and the concentration of hemicellulose were significantly lower at rural sites, but there were no other measured differences in litter composition. Indicators of fungal growth were greatest at rural sites, but bacterial indicators were similar across all sites. Although this study covered only the early stage of decay, it does demonstrate an influence of proximity to urban environments on initial litter quality, and thus on initial decay rates. Longer-term effects have yet to be described.

12.4 Effects of Selected Forest Management Practices

Many studies have been carried out on the effects of thinning, clear cutting, soil compaction, site preparation, and other management practices on decomposition and nutrient cycling in forests. The variables involved are often not easily controlled or measured, and the results differ from site to site, making it difficult to extract generalizations. Our purpose here is not to review the literature, but rather to describe a few sample studies.

Gadgil and Gadgil (1978) performed a particularly interesting study that demonstrates the complexity of studies on management practices and decomposition. They found that the presence of plants actually slowed the decomposition of Monterey pine needle litter by means of mycorrhizal suppression of decomposition. Clear cutting, by eliminating mycorrhizae in the soil, released the litter from the suppression, and enabled a more rapid rate of mass loss. Their experimental design controlled variations in both soil moisture and temperature. These data argue against the more common view that clear felling modifies decomposition primarily by altering the site's climate. Their finding, however, does not seem to have general implications. Indeed, Cortina and Vallejo (1994) studied Monterey pine needle litter decomposition in Spain, and found that clear felling resulted in a large decrease in mass loss relative to that of a control stand, with first-year mass losses of 25 and 37%, respectively.

Different litter types respond differently to clear cutting. In British Columbia, Canada, Prescott et al. (2000) studied the decomposition of lodgepole pine and trembling aspen foliar litters in forests and adjacent clear cuts. After 3 years of decomposition, the mass loss for aspen was essentially the same in forested and clear-cut areas. For lodgepole pine, mass loss was significantly ($p<0.05$) greater in the forest than in the clear cut after 1 year, and the differences remained significant throughout the 4 years of the study. The mass loss after 4 years, averaged over 16 stands, was 66% in the forest, and 60% in the clear cut.

Whole-tree harvesting removes large amounts of organic matter from the system, and can thus influence the environment for decomposition. Kranabetter and Chapman (1999) investigated the effects of three levels of harvesting (stem-only, whole-tree, and whole-tree plus removal or scalping of the forest floor), and two levels of soil compaction on the decomposition of leaf litter in trembling aspen stands in British Columbia. They found that the highest mass-loss rates occurred with whole-tree harvesting and soil compaction; the lowest rates occurred with the two most extreme practices: stem-only harvesting with no compaction, and whole-tree plus forest floor removal with compaction. They suggested that microclimatic differences might be able to explain the different decomposition rates.

Prescribed burning is sometimes used in forest management to control fuel buildup, and to stimulate nutrient cycling. Monleon and Cromack (1996) investigated the effect of prior burning on Ponderosa pine needle litter decomposition. Using a series of sites that had been burned 3 months, 5 years, and 12 years before the study, they found that in all cases, decomposition, measured over an 18-month period, was reduced on previously burned sites. They suggested that the differences were due more to changing the near-ground environment than to altering nutrient dynamics.

Although many more examples could be described, there is no simple summary to be derived. There are simply so many site-specific factors that can influence decomposition that simple generalizations about the effects of given management practices are not possible. Only if the effect of a management practice can be predicted at the microbial and chemical levels can the effect on decomposition be understood.

12.5 Long-term Perspective

Most of the studies presented here have been relatively short-term, although results from some of these could be extrapolated to obtain mechanisms for humus accumulation and storage. However, we must still assume that long-term storage of humus may be regulated in different ways among forest ecosystems. Wild fires have generally been the main agent depleting the C sinks of forest soils, with lesser amounts of C lost due to harvesting of forests, and conversion of land from forest to agricultural, or other uses. The current strategy of wildfire prevention, along with the present need to quantify C sinks and to determine their long-term stability, clearly illustrate the requirement for real long-term research efforts. We expect that such efforts will reveal surprises in terms of storage mechanisms.

Most studies on litter decomposition have been short-term, often covering only a fraction of the entire litter-to-humus process. As a consequence, many empirical conclusions and model-based predictions have, of necessity, attempted to extrapolate from information about the early stages, to encompass the whole process, with the result that much of the scientific literature in this field is based on rather incomplete assumptions. There is an urgent requirement for more reliable information about C and N sinks, given the current need for an improved understanding of the global balance of atmospheric CO_2 levels. More long-term approaches, and new techniques are required to generate information to increase our knowledge of the interaction between climate change and decomposition processes. Long-term studies that cover the full decomposition process for different litter species and types, which can reveal new facts about sequestration mechanisms, are very much needed. Further, we must regard ecosystems that are composed of different litter species as units with potentially very different properties relating to long-term decomposition and C sequestration. Long-term humus development may also be affected by site history, and techniques that can analyze long-term C sequestration would be invaluable tools.

Chapter 13
Estimating Carbon Sequestration Rates on a Regional Scale

13.1 Introductory Comments

In earlier chapters, especially Chapter 11, we discussed the accumulation and stability of humus on single plots and in single stands. We discussed the transition from the fraction of litter that we considered stable, to a developed humus layer. In our examples, we used the limit value for one main litter type, viz. foliar litter, to calculate amounts of humus. It is evident that the stable humus layers are built up from several litter components in addition to foliar litter from trees, although the foliar component normally is the dominant one. Ideally, we should have used limit values from a whole set of litter components, at least the major ones, and added stable fractions for litter components such as leaf litter from ground vegetation, from moss, and from other tree litter components such as cones and woody material, e.g., twigs. We can make the list even longer and for a proper quantification, this is evident. Unfortunately, the available information to do this is lacking. The only litter component for which there exists reasonable information is the foliar one, both as regards litter production and the decomposition process. We have discussed the possible formation of stable humus from other litter components, and we cannot exclude that, e.g., woody litter may produce only a small fraction. Litter production from, e.g., moss is not really quantified, and decomposition experiments are lacking. Direct litter production from roots is also unknown, and decomposition experiments have so far not given unequivocal results in undisturbed systems.

The fact that we could reconstruct quantitative accumulation of mor humus for a period of close to 3,000 years (cf. Chap. 11) using limit values and remaining fractions for foliar litter only suggests that, at least in boreal coniferous systems, foliar litter is one major, or dominant component of humus formation.

Most decomposition studies are made on a short-term basis, and give information with a short-term perspective, namely, years (cf. Sect. 12.5). Sequestration of carbon is a process that is a measurable result of the decomposition process, but it is observed and ideally studied over time periods spanning centuries, millennia, or at least decades. In this chapter, we have taken a step from litter to stable humus, and compare the buildup of humus initially for a set of single stands, and eventually over a region. The stands we compare and discuss are located over Northern Europe, whereas the specific region we use for the case study is the forested area of Sweden.

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When organic matter accumulates in boreal and temperate forest soils, two main fractions can be distinguished, functionally and spatially distinct. One fraction forms a more or less distinct organic layer, and the other is found in the mineral soil. These main fractions are best separated in mor humus, and considerably less in mull. Focusing on our regional case study that encompasses Sweden, the organic layer on top of the mineral soil (O-horizon) is mainly a mor humus layer, which has facilitated, or made possible, the quantification of amounts over time.

The organic-layer fraction may be built up rather quickly, but is vulnerable to forest fires. With a natural fire frequency as high as one major event per 50 to 60 years, organic layers at drier sites rarely have reached a mass of non-negligible magnitude. However, today's efficient prevention of fires has resulted in a significant general increase in the mass of the O-horizon, and on smaller, isolated plots that have not been reached by fire, an accumulation over millennia may be found (cf. Wardle et al. 1997).

An often expressed, a priori assumption in ecosystems studies is that the system is either in, or approaching a "steady state", a notion that has been effectively challenged by Botkin (1990). This is particularly important for budgets of carbon or other material found in the system, and this assumption deserves to be questioned. While it is so that following disturbances the amount of carbon stored in the soil of an ecosystem decreases, the idea that carbon accumulation eventually ceases in the absence of disturbance is not necessarily true. We offer several lines of evidence to suggest that a concept such as "steady state", at least in terms of carbon storage, is not universal. In fact, although we cannot exclude its existence, to our knowledge such a long-term steady state for undisturbed forest humus has never been shown.

In this chapter we will compare three methods to measure regional C sequestration, and Table 13.1 provides an overview of the main outputs of three methods used to estimate regional carbon sequestration in forest soils. The values for carbon sequestration rates will be presented using units such as kg C per hectare and year. To convert the measured values based on a given design into this kind of unit, an interpolation procedure called kriging is often used.

Some Comments to So-Called Kriging, or Kriging Interpolation

Moving from point-based sampling to estimates that extend over hundreds of square kilometers requires the use of geospatial statistics. A simple way to esti-

Table 13.1 Overview of the main outputs of three methods discussed to estimate carbon sequestration in forest soils

Method	Book section	Calculated component in ecosystem
Limit-value method	13.6	SOM or C in organic layer, O-horizon
N-balance method	13.7	SOM or C in organic layer plus mineral soil
Direct measurements	13.8	SOM or C in organic layer or O-horizon

mate the value of a variable between points has been to use inverse distance weighting (IDW) to calculate the values at any point. In the last decades, IDW has often been replaced with another interpolation technique known as kriging. Originally designed for mineral exploration, it has been found to be more suitable for such tasks as estimating forest biomass in the Amazon (Sales et al. 2007), and modeling climatic variables (Ertekin and Evrendilek 2007). Simply stated, kriging is an interpolation tool that allows the estimation of a value at an unmeasured point in the neighborhood of measured points. Kriging works by first determining the nature of spatial dependence of point values. The underlying assumption is that the closer samples are to one another, the more similar they will be, a phenomenon known as spatial autocorrelation. As one considers points farther away from one another, the autocorrelation diminishes and eventually becomes zero, or some small constant. Kriging then goes one step further by modeling the autocorrelation using a relationship called a semivariogram. This work is now handled by many GIS programs.

13.2 Long-Term Accumulation of Carbon in Organic Layers (O-Horizon) – General Comments

13.2.1 Direct Observations of Long-Term Humus Accumulation and Accumulation Rates

Strong accumulation of organic matter has been found in forest soils over different parts of Europe, even if we exclude mires and peat bogs. In the present chapter, we focus on undisturbed soils under growing forest. Soils such as peat are excluded.

We are not aware of any global inventory or study about forest locations where thick layers of real humus have formed, and therefore restrict our discussion to a number of single observations made over Europe. We discussed in Section 11.2.3 how litter remains with a high level of stability may accumulate and develop into thicker humus layers. The areas in Europe where such heavy humus accumulation has been observed today are widely spread.

We have thus found continuous humus layers to a depth of at least 1 m in pine forests in Spanish Galicia (northwestern Spain), under a silver fir forest on a mountain (Monte Taburno) east of Naples, Italy, as well as reports of humus layers up to 1.4 m deep in Swedish Lapland (Wardle et al. 1997). In addition, a humus form found in the Alps and other Central European mountains (Tangelhumus in German; Rehfüss 1990; Anonymous 1996) is characterized by its occurrence in layers up to 1 m deep. Furthermore, in an investigation of data from the Swedish National Forest Inventory, we found that more than 8% of all sampled plots (of >800,000 measurements) over the country had humus layers deeper than 40 cm (humus type mor), with a range up to 1 m.

Table 13.2 Litter fall (kg ha^{-1} $year^{-1}$) as a function of AET for different tree species. Standard error is given within parentheses (modified from Akselsson et al. 2005)

	Litter-fall function				
Tree species	Intercept	Slope	R^2	*n*	Source[a]
Norway spruce[b]	−3646.4 (642.1)	+12.09 (12.1)	0.47	13	(1)
Scots pine	−3593.7 (508.6)	+11.03 (2.0)	0.48	35	(1)
Downy and silver birch	−785.5 (51.3)	+5.81 (1.8)	0.79	-	(2)
Other deciduous	−785.5 (51.3)	+5.81 (1.8)	0.79	-	(2)

[a] (1) Berg and Meentemeyer (2001), (2) Meentemeyer et al. (1982)

[b] As modified by Akselsson et al. (2005)

Table 13.3 Comparison of measured sequestration rates for carbon as measured for specific stands in a.o. chronosequences, or in other separate detailed and long-term investigations on podzolic soils

Location	Sequestration rate (kg C ha^{-1} $year^{-1}$)	Tree species	Source[b]
Central Swedish Lapland	153	Mixed stands	(1), (4)
Central Sweden[a]	128	Scots pine	(1), (5)
Southwest Sweden	650	Norway spruce	(6)
Denmark	170–530	Various species	(2)
West Denmark (Jutland)	350	Norway spruce	(2)
East Denmark (Sealand)	80	Common oak	(2)
Central Germany	1,100	Norway spruce	(3)
Central Germany	320	Common beech	(3)

[a] Extremely nutrient-poor stand

[b] (1) Berg et al. (2001), (2) Vesterdahl and Raulund-Rasmussen (1998), (3) Berg (2004) as recalculated from Meesenburg et al. (1999) and Meiwes et al. (2002), (4) Wardle et al. (1997), (5) Staaf and Berg (1977), (6) Vesterdal et al. (2007)

One evident common factor among these sites is that they are found in areas where the humus may be more or less constantly wet for shorter or longer periods of the year (cf. Table 13.3). In Scandinavia and Central Europe, this means waterlogged even under a snow cover, if the humus is not frozen. Those study areas experiencing a Mediterranean climate, e.g., Monte Taburno, also had snow in winter, or at least humus that was not really dry. Spanish Galicia has a high annual rainfall (1,000–1,500 mm $year^{-1}$), implying that the humus would be thoroughly wet for a large part of the year in this area, although the summers would be dry. We can connect to the discussion in Section 11.2.3 about temporarily anaerobic humus, or a humus layer that has developed a certain thickness causing anaerobic pockets, or at least parts with a clear lack of oxygen. This may be a potential factor for humus buildup for the litter-degrading microbial community. That no heavy accumulation has so far been found at very dry sites is intuitively expected, and may be due to insufficient production of organic matter. Still, this needs to be investigated.

So far, measurements of rates of humus growth or carbon accumulation have mainly spanned relatively short-term periods until stand maturity, or chronosequences reaching the same age (Table 13.3; also see Table 13.4). One exceptional site has enabled us to calculate accumulation rates over a period of almost 3,000

Table 13.4 Comparison of measured carbon sequestration rates extracted from other studies, with those for the three approaches in case studies 1–3 for the forested land of Sweden (data from Berg et al. 2007)

Location	Measured, other studies (kg C ha^{-1} $year^{-1}$)	Limit-value method	N-balance method	Direct humus determination
General comparison				
Central Swedish Lapland	153	100–150	<100	280–330
Central Sweden	12	150–200	<100	141–280
Southwestern Sweden	650	250–420	200–300	280–420
East Denmark	170–530	250–420	200–300	280–420
Average values				
Whole country (Sweden)	n.d.	180	96	197
Scots pine ecosystems	n.d.	150	n.d.	285
Norway spruce ecosystems	n.d.	200	n.d.	187

years – still, rates that may be related more to the climate of that area than to humus age as such. Fast C sequestration in a Norway spruce forest in central Germany (1,000 kg C ha^{-1} $year^{-1}$) has taken place on a very rich soil and under a favorable climate. Other high sequestration rates are reported for a Norway spruce stand in southwest Sweden, with values over 600 kg C ha^{-1} $year^{-1}$. The low rates for coniferous stands (<160 kg C ha^{-1} $year^{-1}$) originate from northern locations, e.g., Swedish Lapland, or from nutrient-poor sites.

13.3 Factors that may Influence Carbon Sequestration Rates Over Larger Forested Areas

13.3.1 General Factors Both at Undisturbed Sites, and at Sites with Anthropogenic Influence

Some factors influencing regional C sequestration rates are immediately evident, such as climate, soil nutrients promoting tree growth, tree species, forest management, and N deposition, and we will examine these briefly below.

We discussed the concept of stable remains earlier (e.g., Sects. 6.2.3, 11.2.3), and how substrate quality influences the size of the stable fraction as defined by the limit value, or the stable remains according to Gundersen et al. (2006). When applied to single stands on relatively nutrient-poor soil, it has been possible to relate foliar litter fall and limit values (stable remains) to humus accumulation rates, with acceptable precision (cf. Sect. 11.2.4). However, over a region the number of factors that may influence the sequestration rate increases, climate being a prominent one, with warmer and wetter climates giving a higher production of litter. Subsequently, climate also has an effect on litter chemical composition (see Chap. 4). Also tree species may vary with climate and with soil type, resulting in litter inputs of different magnitude and of different chemical composition.

Even in undisturbed forest stands, a basic factor such as "stable remains" will have different meanings, as the amount of carbon sequestered can be related negatively to mineral soil concentrations of Ca and P (Vesterdal and Raulund-Rasmussen 1998). We have discussed this aspect in Section 8.2.2, and although currently an empirical finding, the negative relationships between accumulated amounts of carbon and selected soil properties appear clear. We may note that although Vesterdal and Raulund-Rasmussen (1998) investigated all main nutrients, they did not make a complete inventory of nutrients that may have an effect on decomposition and on carbon sequestration, and we cannot exclude that P and Ca, which were related to the amount of sequestered carbon (cf. Fig. 8.4), may function as general indices, either of general soil nutrient richness, or of potentially critical nutrients, e.g., Mn, in the mineral soil. This remains to be investigated.

There also appears to be an interaction between litter species and mineral soil type. To our knowledge, this kind of interaction was first reported by Vesterdal and Raulund-Rasmussen (1998), and we may anticipate new relationships as further studies are made. Thus, in their study, the accumulation of SOM under lodgepole pine was not dependent on soil nutrient status. However, SOM accumulation was related to soil nutrient status under Norway and Sitka spruce, and even stronger relationships were observed under common beech and common oak.

Climate. Over a region, this influences tree growth rate and litter fall (Berg and Meentemeyer 2002; Liu et al. 2004), and foliar litter chemical composition both within species (Berg et al. 1995a) and beyond (Liu et al. 2006), normally resulting in higher concentrations of at least N with increasing temperature.

Soil nutrients and tree growth. A soil enriched in nutrients can promote tree growth rate, resulting in higher litter fall. Natural soil properties may vary strongly even within small areas, and can create very different litter fall, e.g., among stands.

Soil nutrients as influencing factors for substrate quality and humus formation. Over a region, the availability of nutrients may vary, for both N and weathered nutrients. It appears that the bedrock may form a patchwork of mineral soil properties, which influences the availability of different nutrients based on concentrations and pH. We have discussed the effects of mainly N and Mn on the substrate quality in general, and on the level of the limit value.

Tree species. Different species produce litter at different rates, and have different substrate qualities, which could affect the sequestered amounts of C, as we have discussed earlier. This has also been emphasized by the study of Vesterdal and Raulund-Rasmussen (1998), and could be expected as a significant factor over larger areas.

Anthropogenic factors. As regards forest management practices, these may differ over a larger region. Ditching, site preparation, fertilization, clear cutting, and other harvest policies can influence SOM accumulation. As far as we can judge, most forest management will clearly disturb the sequestration of carbon, and this at least for the evident reason of soil disturbance.

Site preparation may be done in different ways; in some cases, the whole soil including the mineral soil is actually plowed immediately before planting the trees, and in other cases only small patches of organic matter are removed. The purpose is to activate the soil microorganisms, and support decomposition of organic matter. Such an activation may have a long-lasting effect. An example is an inventory of amounts of soil carbon in three layers made in a chronosequence up to 29 years after preparation. In the layer 0–5 cm, the amount of carbon increased, whereas in the layers 5–15 and 15–25 cm the amounts decreased during the whole time period. The top layer received a new inflow of carbon in decomposing litter, whereas the deeper layers did not (Sect. 8.2.1; Fig. 8.3; Vesterdal et al. 2002).

Clear felling means not only an interruption of litter input, but an additional disturbance of the upper soil layers. Furthermore, concentrations of available soil nutrients increase, as does the level of soil water due to the lack of root uptake. The absence of a growing forest, and its influence on the soil – e.g., in the form of root exudates, which now are absent – may change the properties of the remaining humus, and influence its stability.

Nitrogen pollution may have a large-scale fertilization effect, possibly resulting in increased tree growth and litter production, and with an ensuing effect on SOM accumulation. We have limited possibilities to fully discuss and quantify the effects of these factors here, and will focus on effects in natural undisturbed forests.

Afforestation and reforestation may mean an introduction of forest on land that has been agricultural, and thus on soil that may have been plowed and fertilized, and had crops over so long a time that the soil microflora may have been completely exchanged. It is possible that the soil simply has developed entirely new microbial properties that may either enhance, or prevent decomposition at least temporarily.

13.4 Spatially Explicit Database for Regional Modeling

For the upscaling of data to a specific region, we need forest information that is related to specific and identifiable geographical points, and the information mentioned in Section 13.3.1 could be part of such a database. The information should be organized into grid cells of a useful size, such as those normally found in, e.g., a national grid net. The grid cells could have different sizes depending on circumstances, e.g., a square kilometer, or 100 square kilometers. The total information associated with each cell can vary, but examples of information useful to our purpose would pertain to tree species, stand age, some measure of stand density, and the fraction of each cell covered by forest. It may be necessary to add information on, e.g., estimated litter fall, or climate factors.

Two of our case studies rely on spatially explicit models to calculate humus buildup and carbon sequestration. Because much of the data utilized for each model are unique, the database development will be discussed separately for each case study.

13.5 Three Case Studies: an Overview

Starting with decomposing plant litter, we present three case studies that demonstrate carbon sequestration. In case studies 1 and 2, we use the concept of stable remains in decomposing litter, and discuss an approach that can explain a potential buildup (Sects. 13.6 and 13.7). In case study 3, we use data on actual increases in humus depth as measured over 40 years (cf. overview in Table 13.1).

The two methods that are based on stable to very stable remains are the limit-value method (see Chaps. 2 and 11) and the N-balance method, an approach based on specific proportions between N and C in growing plants and in decomposing litter, and especially in soil organic matter (Gundersen et al. 2006). The limit-value method is a theoretical approach in the sense that it includes quantitative litter fall and litter quality as factors that influence the buildup of the O-horizon. Effects of wild fires, forest management, or other disturbances, and possible effects of mineral soil properties (cf. Chaps. 8, 12) are not included. The calculations are based on foliar litter fall in mature stands, and do not include the clear-cut phase.

To present our results, we will use the concept of “potential accumulation” for case study 1. We call the accumulation that we will estimate “potential”, because the calculations at this level do not include effects of forest management and other disturbances, and thus tend to rather represent potential accumulation. Furthermore, our estimates for case study 1 are based only on foliar litters, thus tending to underestimate accumulation. In all cases, estimated accumulation should be considered as an order-of-magnitude value, serving to illustrate a method and the potential for carbon sequestration in a particular forest, rather than actual accumulation. However, we will offer some validation data to support the reasonableness of the estimates.

As a third case study, we present a method to evaluate direct measurements of humus depth, an approach that includes the effects of forest management and disturbance. The average measured accumulation rate is thus a net rate including the site-specific effects of wild fires, climate change, and forest management, e.g., site preparation.

13.6 Case Study 1 – Limit-Value Approach

13.6.1 Geographical Database

In the database, all forested land is subdivided into (1) grids the size of 5 × 5 km, and (2) forest classes, namely, coniferous, deciduous, and mixed forests, as well as clear-felled areas. An example of the information is given in Fig. 13.1, showing

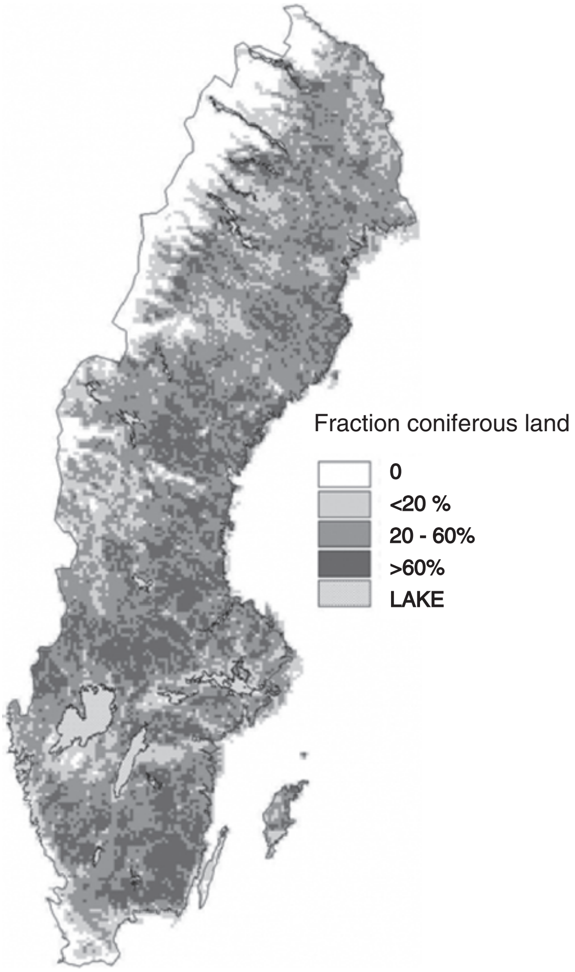


Fig. 13.1 Output from the geographical database giving the fraction of coniferous forest land in Sweden (resolution of 5×5 km; from Akselsson et al. 2005). The database originates from the Dept. of Forest Soils, Swedish University of Agricultural Science, Uppsala

the fraction of coniferous forest in each 5×5 km grid. The basis for this geographical database is an IRS WIFS satellite image interpretation of the forested land (Mahlander et al. 2004). The satellite data have a resolution of 180×180 m, and the resolution of the database is 5×5 km. Thus, for each 5×5 km grid, the fraction of different land-use classes is given as extracted from the satellite image.

Also information about tree species is found on the grid level. In the present case, the principal coniferous species were Scots pine and Norway spruce, and two birches as the dominant deciduous species. The fractions of Norway spruce and Scots pine in coniferous forests are known for each grid, as well as the fractions of birch and other deciduous trees in deciduous forests. The species that are grouped into the category "other deciduous" are mainly common oak and common beech. For mixed (coniferous–deciduous) forests, the fractions of coniferous and deciduous are included in the database. The information on species originates from the Swedish National Forest Inventory, and data from 15,318 specific sites were interpolated by kriging interpolation. In this way, data from specific sites were used to estimate values for all grid cells, giving each cell its fraction of coniferous and deciduous trees. Based on this, fractions of spruce, pine, birch, and "other deciduous" trees were calculated for each grid, and used for further calculations.

A climate variable was calculated and included, namely, actual evapotranspiration (AET; cf. below). Actual evapotranspiration is the sum of evaporation and transpiration in an ecosystem. Being a combined measure of heat and soil water, AET has been shown to be a good predictor of various plant processes (Meentemeyer et al. 1982), e.g., litter fall, which is used in this study. AET was calculated from monthly precipitation and temperature data from the Swedish Meteorological and Hydrological Institute (SMHI). The WATBUG model (Sharpe and Prowse 1983), based on the Thornthwaite and Mather (1957) water-balance procedures, was used. In addition to climatic data, the calculation required values for soil water capacity (field capacity). As field capacity data were not available for the sites, a general field capacity of 300 mm was assumed for the root zone in the whole country, with mainly till soils. This approximation was made in accordance with previous work (e.g., Meentemeyer 1978; Meentemeyer et al. 1982; Dyer et al. 1990), and makes it possible to use this climate variable on a regional basis. The first step for estimating AET for the grids was to calculate AET for 95 sites located all over Sweden that had detailed climatic data. Kriging to the 5×5 km grids was then performed based on 95 sites, and the resulting values for AET were included in the geographical database.

13.6.2 Expanding Data to a Regional Scale

To transfer data for stable fractions of litter to a regional scale in this case study, Akselsson et al. (2005) used linear relationships between foliar litter fall and actual evapotranspiration. Three linear relationships were used, namely, one for Scots pine, one for Norway spruce, and one common for all deciduous species (Table 13.2). This was the factor they used for scaling up. The relationship between litter fall and AET enabled the estimation of litter input rates of each species, or species group, into each cell. Beginning with litter fall and species composition, the limit-value approach described earlier (cf. Chaps. 2 and 6) can be applied to estimate potential carbon sequestration rates, as described below.

13.6.3 Calculation of the Buildup of Humus and Carbon

The annual foliar litter fall for each species group (Scots pine, Norway spruce, birch spp., and "other deciduous" trees) in a given 5 × 5 km grid cell was estimated separately using the equations based on AET (Table 13.2). The fraction of litter that would remain as stable matter was calculated as (100–limit value)/100 for each species/group of species, and multiplied by the estimated litter fall. This gives the annual SOM buildup (cf. Berg et al. 2001) for each group of tree species. The SOM from all groups was combined to give the average SOM buildup in each grid cell. In this initial approach, Akselsson et al. (2005) used the same limit value for the dominant tree species, viz. Norway spruce, Scots pine, and birch species. They took the general average value of 78.1% (stable fraction of 0.219), and 63.8% for "other deciduous" trees (stable fraction of 0.362).

The sequestration of carbon was calculated by multiplying the derived SOM buildup by the fraction of carbon in the foliar litter, and Akselsson et al. (2005) assumed a constant C fraction of 0.5. This simplification can be accepted, since the calculations were based on falling foliar litter, in their case with a minimum of ash (less than 2% initially). The result is the C sequestration rate (kg ha^{-1} $year^{-1}$) in the organic forest soil layers.

13.6.4 Potential Carbon Sequestration Rates

Estimates of potential carbon sequestration rates in the organic layers in forest soils in Sweden range from 40 to 410 kg ha^{-1} $year^{-1}$, with an average of 180 kg ha^{-1} $year^{-1}$ (Fig. 13.2B), as based on the limit-value concept. The general gradient gives decreasing C sequestration rates from the southwestern to the northern part of the country, mainly following the variation in AET (Fig. 13.2A). In the southernmost and the southwestern parts, the C sequestration rates range between 300 and 410 kg ha^{-1} $year^{-1}$, in mid-Sweden the levels are mainly between 150 and 200 kg ha^{-1} $year^{-1}$, and in the northern parts the sequestration is lower than 100 kg ha^{-1} $year^{-1}$, with a minimum of 40 kg ha^{-1} $year^{-1}$ at, and north of, the Arctic Circle. The annual C sequestration for the whole country is estimated at 4.8×10^6 metric tons (t).

The general patterns of AET distribution and C sequestration rates are similar in this approach (Fig. 13.2). AET ranges from 375 mm in the northern part of Sweden, to 540 mm in the southwestern part with higher temperature and more precipitation. Because litter fall was related to AET, and Akselsson et al. (2005) used a single average limit value for the three main tree species (Table 13.2), AET has a major effect on carbon sequestration rates, and this pattern would be expected. The approach of Akselsson et al. (2005) was based on foliar litter fall from mature stands, and on limit values for decomposition of the foliar litter fraction. Their rates are thus only potential rates for the foliar litter fraction, without consideration of the effects of wild fires, site preparation, or other forest management practices.

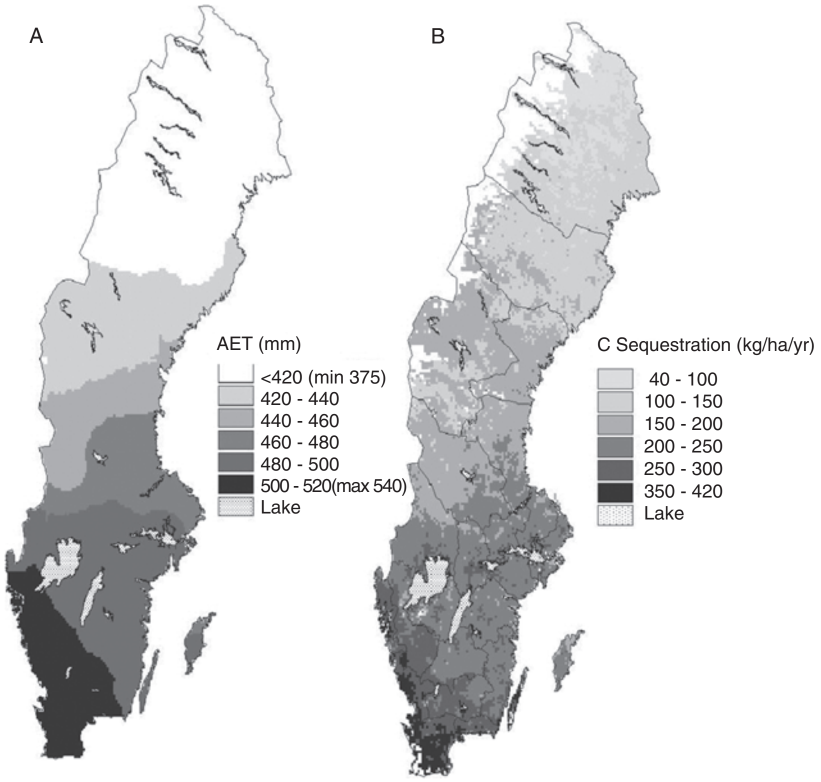


Fig. 13.2 **A** Actual evapotranspiration (AET) in Sweden, given as values for grid cells of 5 × 5 km size. AET was calculated using the Thornthwaithe and Mather (1957) water-balance procedures, and interpolated by means of kriging to cover 17,000 grid cells. **B** Carbon sequestration rates (kg C ha^{-1} $year^{-1}$) in the organic layers of forest soils in Sweden, based on the limit-value method (from Akselsson et al. 2005). Values were calculated for the same 5 × 5 km grid cells as those used for the AET climate index

Furthermore, the methods do not consider effects of non-foliar litters, or age of stand, but give the potential growth rate for sequestered carbon from foliar litter only. Such a potential is of value for the determination of the capacity of the forest system in terms of sequestration.

13.6.5 The Effect of Tree Species on Carbon Sequestration Rates

Foliar litter fall is higher in Norway spruce than in Scots pine forests, based on the litter-fall measurements (Table 13.2). Thus, in the present approach, this results in a higher annual mean C sequestration in Norway spruce than in Scots pine forests,

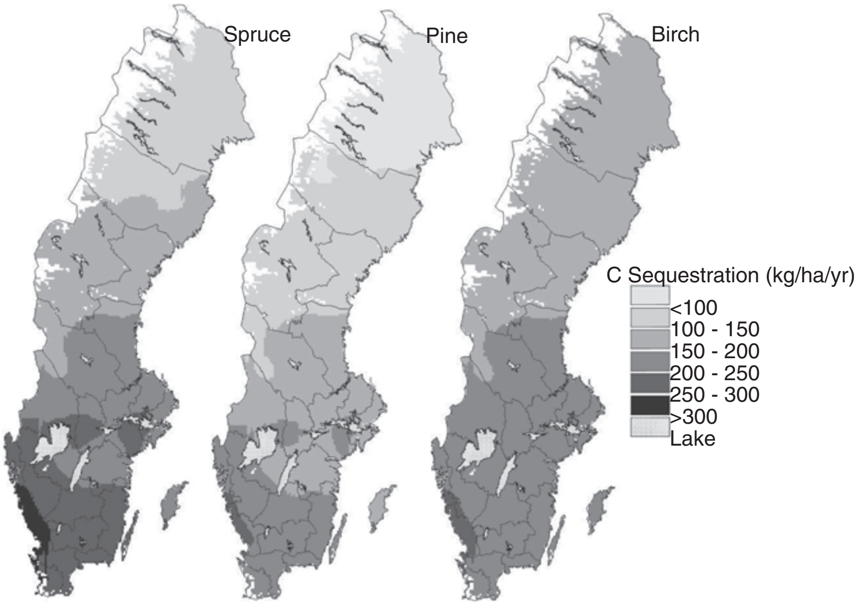


Fig. 13.3 Annual carbon sequestration rates in monocultural stands of Norway spruce, Scots pine, and birch spp. in different regions of Sweden (from Akselsson et al. 2005). The sequestration rates were calculated using the limit-value method

the values being 200 and 150 kg ha^{-1}, respectively. The mean C sequestration rate in birch forests is the same as for pine, but the gradient over Sweden is more emphasized in pine forests (Fig. 13.3), with a wider range (60 to 260 kg ha^{-1} year^{-1}) than for birch (150 to 260 kg ha^{-1} year^{-1}).

The litter class comprising "other deciduous" trees, viz. common beech and common oak, is limited to the southern part of Sweden. It has the highest fraction of stable matter, 0.36 (average limit value 64%; Table 13.2), which leads to a higher C sequestration rate (about 400 kg ha^{-1} year^{-1}), contrasting with Norway spruce, Scots pine, and birch litter, all with a stable fraction of 0.219. This effect can be seen in parts of southernmost Sweden (Fig. 13.2B) where forests of common beech and common oak make up a significant fraction of the forested area, comprising up to 22% of the stand biomass in the southernmost part.

13.6.6 Sources of Error in the Limit-Value Approach

So far, only foliar litter has been included in the calculations, and the potential rates of Akselsson et al. (2005) are thus potential rates for foliar litter only. Woody litter has different decomposition kinetics (cf. Sect. 9.2); at present, this makes it difficult to estimate its long-term contribution to C sequestration, which possibly is small. Furthermore, for the various root and rhizome litter types, we still lack sufficient long-term basic information from decomposition studies to apply the limit-value concept. This applies also to moss, the litter formation rate of which is unknown, as is any limit value for decomposition.

There are other evident error sources in this approach. Akselsson et al. (2005) used foliar litter fall as a reasonable first approach, and litter input is a primary error source, in terms of both origin and rate. Their data for calculating litter fall were those available from mature stands. Smaller inputs following clear cut, as well as the lower litter fall in younger stands were not considered. Foliar litter fall is, of course, only one of several fractions of total litter fall, and in mature boreal stands of Scots pine and Norway spruce, foliar litter may encompass ca. 70% of total litter fall, in contrast to ca. 100% in very young stands (Mälkönen 1974). On the other hand, as pointed out by Flower-Ellis (1985; see also Berg and Laskowski 2006), there are extremely few data on real total litter fall. The traditional litter trap for foliar litter is methodologically unsuitable to give correct recordings for "total" litter fall, i.e., foliar litter plus, e.g., branch, twig, bark, and cone or acorn litter. This means that available data in the literature for "total" litter fall in many cases simply may be incorrect, and probably underestimates. Furthermore, a general assumption on litter-fall data is that the forest is relatively homogeneous, i.e., either it has a naturally regulated high density, or when comparing forests, the management is similar. For example, litter-fall data are commonly expressed as kg per hectare, and often tree density is not given, but simply assumed to be similar among compared plots. A measure where litter fall is based on, e.g., basal area, which would reflect the biomass of trees, possibly could improve this.

Moreover, the input of root litter is very little known from a quantitative point of view, as are the inputs of moss, grass, and shrub litter. The more open Scots pine forests support a higher growth of mosses and shrubs, compared to the more closed and darker Norway spruce forests. A calculation based on only foliar litter fall from the trees thus underestimated the carbon sequestration in Scots pine forests, compared to Norway spruce (cf. Sect. 13.8.6).

Limit values reflect a stable fraction of foliar litter, but we simply know very little about the formation of stable material from woody litter and from fruits (e.g., cones and acorns), as well as of root litter. Available information suggests that, at least for some tree species, the decomposition of woody litter may have a different pattern than that of foliar litter. For litter from finer roots, different observations suggest that very small remains are left after decomposition under natural conditions. Decomposition patterns and kinetics based on litterbags may give erroneous results.

In addition, effects of mineral soil nutrients, e.g., Ca and P concentrations (cf. Sect. 8.2.2), on the long-term storage of humus in the O-horizon were not considered in the approach of Akselsson et al. (2005), but could have a clear impact on the actual carbon sequestration rate.

13.7 Case Study 2 – N-Balance Method

13.7.1 Background and Comments

The N-balance method makes use of the close relationship between C and N in both litter and SOM, and the fact that N accumulation can be estimated by means of mass-balance calculations (Gundersen et al. 2006). The method yields the accumulation of carbon in the organic and the mineral soil layers combined. To make the results comparable to those of the limit-value method, accumulation in the mineral soil has to be estimated separately, and subtracted. The method is based on the assumption that the C-to-N ratio in the accumulating SOM is the same as the current C-to-N ratio in the SOM layer, which means that C sequestration is proportional to N accumulation, and that an estimate of the net C sequestration rate can be made by multiplying the accumulation of N in the soil by the C-to-N ratio of the SOM layer (Gundersen et al. 2006). The basic calculation is given by Eq. (13.1):

$$\mathrm{C_{seq} = N_{acc} \bullet C / N_{SOM}} \tag{13.1}$$

where $\mathrm{C_{seq}}$ is the amount of C sequestered, and $\mathrm{N_{acc}}$ the amount of N accumulated in the soil. This is an upper estimate for the soil C sequestration rate, since especially at high N inputs, organic matter may accumulate at a lower C-to-N ratio than that of the current bulk forest floor mass. Furthermore, some of the C is incorporated into SOM in the mineral soil where the C-to-N ratio usually is lower than in the SOM of the forest floor. The estimated C sequestration rates encompass the sequestration in the whole soil profile, i.e., both the humus layer and the mineral soil. It also includes all forest stand ages, representing a whole forest generation.

Geographical Database for the Case Study

The basis for the calculations was an extensive geographical raster database for Sweden (Akselsson and Westling 2005), containing forest data, and data on deposition, land use, and hydrology. Modeled N deposition (nitrate and ammonium) in 5 × 5 km grid cells, from the Swedish dispersion model MATCH (Langner et al. 1996), sets the framework and resolution of the database. All calculations were performed on a GIS platform with this resolution, which means that they were performed for each of the ca. 17,000 5 × 5 km grid cells. The land-use information in the database, including the area of different forest types in each grid cell, is based on satellite image (IRS WIFS) interpretation. Four forest classes are included: coniferous forest, deciduous forest, mixed forest, and clear cuts (Mahlander et al. 2004). Data for forest properties originate from the Swedish National Forest Inventory sites, managed by the Swedish University of Agricultural Sciences (SLU). Data on tree species composition (e.g., fractions of spruce and pine in coniferous forest), and volume, growth, and dry weight of different tree parts for coniferous, deciduous, and mixed forests separately have been interpolated by kriging to the 5 × 5 km grids. The fractions of different tree species in the forest-type classes have been used to refine the land-use data. Based on this, fractions of spruce, pine, and deciduous trees have been calculated for each grid. Runoff values for the database originate from a map from the Swedish Meteorological and Hydrological Institute (SMHI), showing the annual mean runoff (1961–1990). A more detailed description of the database can be found in Akselsson and Westling (2005).

For the purpose of the present approach, data on the C/N ratio in the SOM layer were incorporated into the database. The ratios were derived from the Swedish National Forest Inventory (Fig. 13.4; Hägglund 1985). The regional C/N ratios for SOM are based on data from stands of different ages, and can thus be seen as averages for a forest rotation.

N accumulation (Fig. 13.5) has been estimated by means of N mass-balance calculations (Eq. 13.2) on a regional scale in Sweden (Akselsson and Westling 2005):

$$N_{acc} = N_{dep} + N_{fix} - N_{den} - N_{uptake} - N_{leach} \tag{13.2}$$

where N_{dep} is N deposition, N_{fix} biological N_2 fixation, N_{den} the N losses through denitrification, N_{uptake} the N losses through biomass harvest plus N accumulated in vegetation through net growth, and N_{leach} the N lost by leaching.

Nitrogen deposition values for different land-use classes for 1998 from the MATCH model (Langner et al. 1996) were used (Fig. 13.5A). N_2 fixation was set to a low constant value of 1.5 kg ha^{-1} $year^{-1}$. This was based on a study by DeLuca et al. (2002) where the N_2 fixation rate for northern Scandinavia and Finland was estimated at between 1.5 and 2 kg ha^{-1} $year^{-1}$. Denitrification was not accounted for, since denitrification fluxes are known to be small in well-drained soils (Persson et al. 2000b).

N losses (N_{uptake}) through harvest from the system and root uptake (Fig. 13.5C), here defined as the N removed from the system through harvest together with the N accumulating in the increasing standing biomass, were based on growth data. The internal circulation through uptake and litter fall was thus not included. Harvest intensity was quantified using province-based estimates of the fraction of net growth that was harvested during the 1990s (Anonymous 2000). Traditional forestry in Sweden is based on the harvesting of stems only, but during the last decade whole-tree harvesting, which includes the removal of branches, tops, and needles, has become more common, and this increases N removal by harvest. This additional removal has not been considered in the present calculations. N uptake thus corresponds to the amount of N in net growth minus the N in the branches and needles that were left on the forest floor after the final felling. The estimations were based on net growth for the three main tree species, and N concentrations in different tree parts.

Forest soils in Sweden have been considered normally to have a high N retention (Nilsson et al. 1998), and the N leaching from soils under growing forests is accordingly low. The calculations of N leaching in this study (Fig. 13.5C) were made for

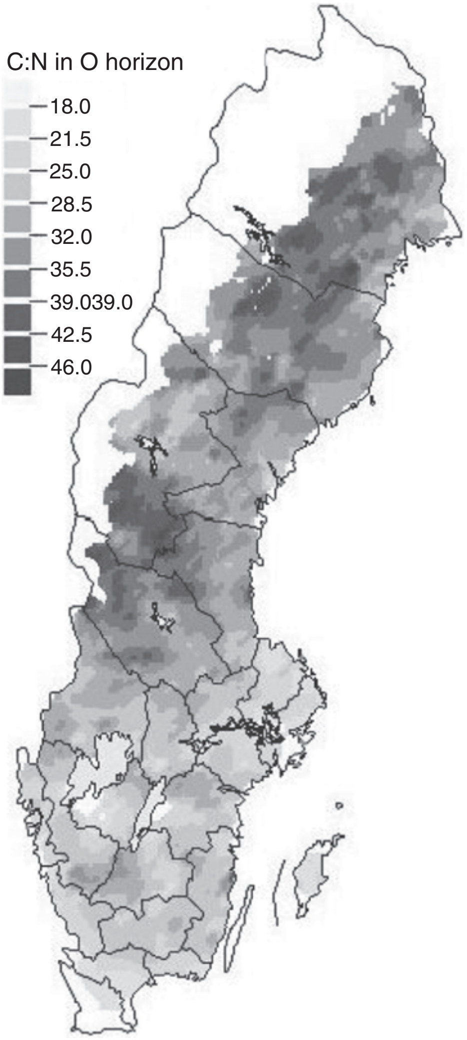


Fig. 13.4 C-to-N ratios in the organic layer in forest soils over Sweden. Interpolation was based on data from the Swedish National Forest Inventory (Swedish University of Agricultural Sciences, Department of Forest Soils 2003; Markinfo, http://www-markinfo.slu.se; Hägglund 1985)

southern Sweden and central–northern Sweden separately, using different methods. The calculation of N leaching in central and northern Sweden was based on a study that related leaching of nitrate and organic N to runoff (Bergstrand et al. 2002; Brandt and Ejhed 2003). Studies in southern Sweden where N deposition is higher than in the northern parts showed that concentrations of inorganic N in soil water in clear cuts were related to N deposition (Löfgren and Westling 2002; Akselsson et al. 2004). The positive linear regression function from those studies, slightly modified using an updated N-deposition database, was used for calculations of total N concentration in

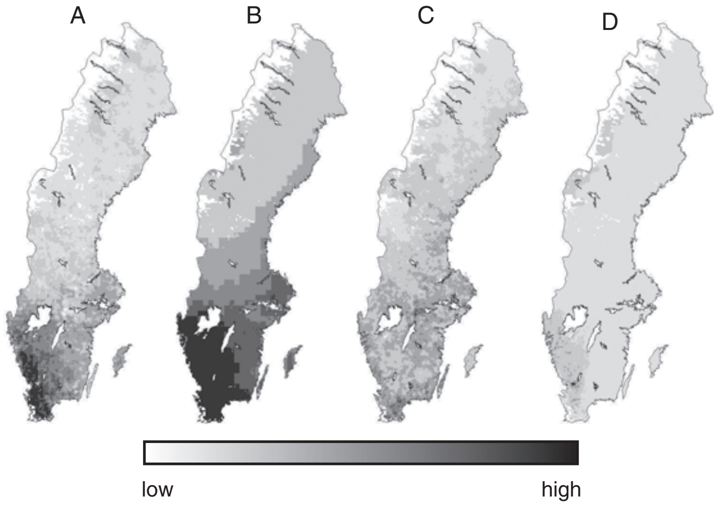


Fig. 13.5 Spatial patterns of some nitrogen processes necessary for calculating carbon sequestration using the N-balance method (cf. Eq. 13.2). **A** N deposition, **B** N losses through harvest+N accumulated in trees through net growth, **C** N leaching, and **D** N accumulation in soil from mass-balance calculations (from Berg et al. 2007)

soil water on clear cuts in southern Sweden (Akselsson and Westling 2005). Leaching was derived by multiplying N concentration by runoff. This was based on a special study for this area (Löfgren and Westling 2002), where concentrations of inorganic and organic N in runoff water from 20 catchments were compiled for the period 1984 to 1999. Concentrations were multiplied with runoff, on a seasonal basis, in order to estimate leaching for southern Sweden in each grid cell.

13.7.2 Carbon Sequestration on a Regional Level

The C sequestration rates estimated with the N-balance method ranged from −60 to +360 kg ha^{-1} year^{-1} (Fig. 13.6). The rates were highest in the southwestern part of the country. In the northern half, rates were generally lower than 100 kg ha^{-1} year^{-1}. The total annual C sequestration for the whole country was 2.2×10^6 t C per year, corresponding to a mean C sequestration rate of 96 kg ha^{-1} year^{-1}. The strong N-deposition gradient is decisive for the decreasing C sequestration from south to northeast. The estimates obtained with the N-balance method can be regarded as averages of soil C sequestration rates on the timescale of a rotation in managed forests, since all forest stages are included. The requirements for input data for the N-balance method are limited, making it possible to have an overview of data treatment, and results that are relatively easy to grasp. These properties are important for regionalization.

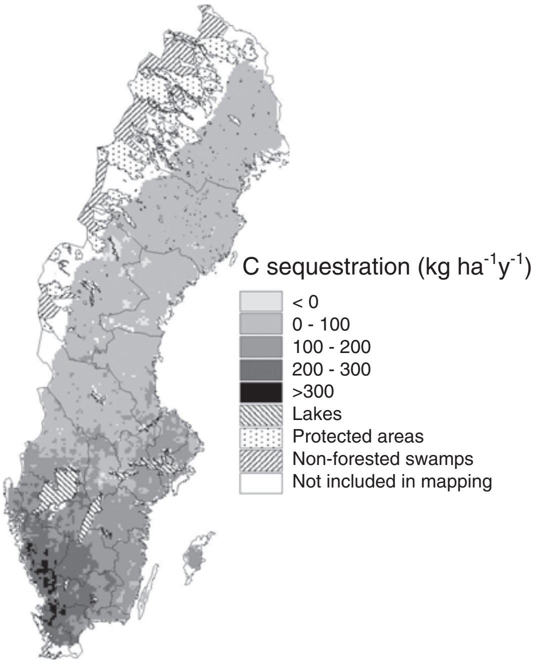


Fig. 13.6 Annual carbon sequestration rates in Sweden (kg C ha^{-1} year^{-1}) calculated with the N-balance method (from Berg et al. 2007)

The resolution of the input data does not support analyses within single grids, but rather should be considered as averages for the 5×5 km grid cells. Single-site approaches require site-specific input data. The regional approaches can, however, constitute a basis for single-site studies. The calculation with the N-balance method in this study was based on stem harvest, but different harvesting intensities, as well as other forest management strategies can have a considerable effect on the C sequestration rates in forest soils (Liski et al. 1998; Ericsson 2003; Ågren and Hyvönen 2003).

13.7.3 Assumptions and Uncertainties

The method has certain clear limitations, and the calculations are not valid for ditched organic forest soils, at present corresponding to 7% of the managed forest area (Hånell 1990). This means that the total annual C sequestration in Sweden may be somewhat overestimated with this method, since organic forest soils after ditching often convert from sinks into sources of atmospheric C (K. von Arnold, pers. comm.).

The overall uncertainty in the C sequestration calculations using the N-balance method is a result of the uncertainties in (1) the estimated N accumulation, and

(2) the assumption that the C-to-N ratio in the accumulating organic matter is the same as the C-to-N ratio in the existing organic layer in the soil. As an example: an uncertainty in the N accumulation rate of ± 1 kg ha^{-1} $year^{-1}$ is magnified and gives a range in calculated C sequestration rates of ± 20 kg ha^{-1} $year^{-1}$ in areas with low C-to-N ratios (e.g., 20), to ±40 kg ha^{-1} $year^{-1}$ in areas with high C-to-N ratios (e.g., 40).

The assumption of a same C-to-N ratio in the accumulating organic matter and in the SOM layer leads to uncertainties for two reasons. First, some of the C is accumulating in the mineral soil, which has a lower C-to-N ratio than does the SOM layer. The effect of this is, however, small, since most of the C is initially sequestered in the organic layer, and the difference between the C-to-N ratio in the SOM layer and that of the upper mineral soil is small. Second, it is likely that the SOM layer C-to-N ratio decreases as N deposition continues at a constant level, or decreases as the amounts of deposited N increase, as indicated by several N-fertilization studies (Beier and Eckersten 1998; Nohrstedt et al. 2000; Prietzel et al. 2004). The close relationship between C and N in organic matter implies, however, that large and rapid changes of C-to-N ratios are unlikely under prevailing N-input conditions. This has been investigated with N-fertilization experiments (Nohrstedt et al. 2000) with doses up to 2,400 kg ha^{-1} added in a 15-year period. The soil analyses performed 7 years after the last addition showed that the C-to-N ratio decreased significantly in the humus layer, and decreased with increasing N dose. Based on the regression analysis, the highest dose, representing as much as 86 kg ha^{-1} $year^{-1}$, led to a decreased C-to-N ratio, from 25 to 20. In another study, Prietzel et al. (2004) reported decreases in C-to-N ratios in the humus layer in six Douglas-fir stands in Western Washington (USA), fertilized repeatedly with urea, and ending with a total added amount of 900–1,100 kg ha^{-1} 8 years before the measurement. Compared to the controls, the C-to-N ratio had decreased at all experimental stands, by factors of > 1–8, the largest changes occurring at stands with the highest C-to-N ratios at the beginning of the experiment.

We may connect a simple sensitivity analysis to the above N-fertilization experiment. Thus, if the C-to-N ratio in the original SOM layer were 25, but that in the accumulating SOM only 20, then the former C-to-N ratio would have been overestimated by 20%, and the sequestration of C by 20%, too. This could be the case in our case study, where high N inputs in the southern part of the country may lead to lowered C-to-N ratios in the accumulating litter. Thus, although the assumption of a constant C-to-N ratio is approximate, and the N-accumulation calculations involve some uncertainties, the results can be considered to give a relatively reliable estimate, compared with the broad variation in results from other studies, as discussed below.

13.7.4 Comparisons with Other Studies

The levels of C sequestration rates based on calculations with the N-balance method should be considered relative to results from other approaches. The total annual C sequestration for the whole forested area of Sweden, 2.2×10^6 t C per year, is within the range of earlier estimations of C sequestration in the humus layer, based on observations of the increase in humus layer given in the Swedish National Forest Inventory, i.e., $1.9–4.9 \times 10^6$ t C per year.

It is evident that we must consider two pools in the soil (cf. Sect. 13.1). One pool is in the mineral soil, and is protected from fire and other disturbances. In this pool, leached C compounds are precipitated onto the mineral particles. The second pool is that in the organic layer, which is more vulnerable to, e.g., wild fires, and has a much faster dynamics. Based on data from the Swedish National Forest Inventory, the average C content in Swedish forest soils to a depth of 1 m (organic layer included), and developed since the last glaciation, is 80 t ha^{-1}, most of which is found in the mineral soil (Olsson 2000). This implies an average net accumulation in the mineral soil of less than 10 kg C ha^{-1} year^{-1} since the last glaciation, compared to 96 kg ha^{-1} year^{-1} for the organic layer.

Liski et al. (2002) estimated C sequestration rates in forest soils (organic layer+topmost 20 cm of mineral soil) in several European countries, using inventory data from 1950 to 1990, and a somewhat modified version of the dynamic soil C model, FORClim-D (Perruchoud 1996). They estimated that the average C sequestration rate in Sweden for 1990 was 90 kg ha^{-1} year^{-1}, i.e., nearly the same level as that recorded with the N-balance method (96 kg ha^{-1} year^{-1}).

13.8 Case Study 3 – Direct Measurements of Humus Depth

13.8.1 Introductory Comments

Measurements of the amount of humus in, e.g., a mor layer, or an O-horizon, may vary considerably also within a relatively small area, often making it difficult, or even impossible to determine this amount with any accuracy, or to follow any spatiotemporal changes. Well-defined profiles, as found in mor humus developed on sediment soil, may give a relatively good basis for such determinations, whereas humus developed on till soil, or perhaps on a slope, will create a more difficult situation, or even an impossible one.

With a sufficiently high number of measurements over a long time period, this kind of problem may be overcome, at least to some degree. In 1961, long-term measurements started in Swedish forested land: simple registrations of humus depth, combined with analyses on humus samples. By 2001, more than 800,000 single measurements had been made, rather evenly distributed over the 40-year period, and an evaluation was initiated. These values will serve as the foundation for the third case study.

13.8.2 General Design of the Humus Inventory

By far the most common type of humus layer is mor, and a distinct O-horizon was distinguished in all the cases used in the analyses. Below, we discuss the humus accumulation and carbon sequestration taking place in the humus layer on top of the mineral soil.

These measurements were used in a first evaluation of humus accumulation rates, and Berg et al. (2007) limited the analysis to podzols. Over the whole study period, a total of 131,494 average values for humus depth were calculated, each value being an average of at least five simple measurements. Of these, Berg et al. (2007) used 82,513 values for podzols simply because of a clear and distinct O-horizon.

The measurements of humus layers in this approach were carried out in four separate inventories in the periods 1961–1972, 1973–1975, 1983–1987, and 1993–2001, and covered the forested land of Sweden. Data on these investigations can be found on http://www-markinfo.slu.se. The initial sample plots were chosen randomly within a predetermined sampling pattern, and during each sampling year 10 to 20% of those plots were sampled. Humus depth was measured, and at the same spot, a sample of the O-horizon was taken and used for carbon analysis and bulk density determinations.

13.8.3 Scaling up from Field Measurements on Humus Depth in Plots, to C Sequestered on a Country Level

An overview. The 82,513 measurement values distributed over the country were transformed into corresponding values for grid cells in the national grid net using kriging. Thus, measured humus depths from a given sampling design were transformed into corresponding average values for amounts of sequestered carbon in grid cells with a dimension of 25 × 25 km.

The calculation and conversion of humus depth to amount of carbon can be described in three main steps. First, the increase in humus depth was determined. Second, the bulk density of humus, given as amount of carbon per mm and hectare, was calculated. Third, the increase rate in the amount of carbon, given as kg per hectare and year, was calculated.

13.8.4 Changes in Organic-Layer Thickness Over Time

Humus-layer thickness. In a first step, the measured humus depths were converted to average humus depth for 25 × 25 km grid cells. The country was thus subdivided into such grid cells corresponding to the national grid net. In this analysis, kriging was applied to all points within a circle with a radius of 55 km (cf. Sect. 13.1). The center of this circle was also the center of a 25 × 25 km quadratic grid cell. The resulting value of humus depth for the center of the circle was assigned as the average value for the corresponding quadratic cell.

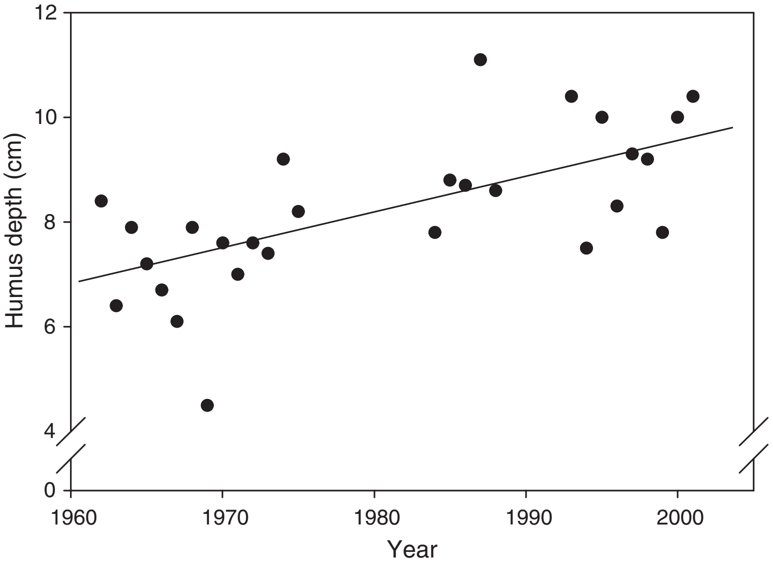


Fig. 13.7 To determine humus-layer growth rates, all measurement values for humus depth within a circle were used and interpolated using so-called kriging interpolation. This means that all values within the circle were calculated to be representative for a quadrate of 25 × 25 km. Such calculations were made for each annual sampling and humus depth related to time. The figure gives an example of a relationship for one of the in all 641 quadrates that were used. For the whole country of Sweden, such relationships were calculated (i) for the whole forested area in each 25 × 25 km quadrate representing the average value for humus depth change, (ii) for those areas in each quadrate where Scots pine or Norway spruce dominated, giving representative values for the humus depth increase for each of the species (from Berg et al. 2007)

The same procedure was used to estimate humus thickness for each grid cell for each year. Repeating the calculations enabled the estimation of changes and rates of change.

This calculation was made for each year, and after 40 years of measured humus accumulation, rates (given as mm per year) were calculated for each of the quadrates by using a linear relationship between time and the thickness of the humus layer (Fig. 13.7). The data available within each circle (55 km radius) allowed interpolation for different forest types, based on tree species. With two dominant coniferous species, viz. Scots pine and Norway spruce, there were enough measurement plots to allow kriging for plots of each species, namely, 552 for Norway spruce, and 602 for Scots pine (cf. below). The total number of forested quadrates was in all 641 with both coniferous species represented as well as deciduous ones. The linear relationships calculated for these quadrates thus represented the average values for all forest types, and were representative for the country. In all, Berg et al. (2007) calculated 1,795 linear relationships for spruce and pine forests as well as for all species. Of these, 1,731 were positive, and almost all were significant ($p < 0.05$). We may comment that, of all the calculated relationships, only 64 were negative and none of these relationships was significant (Table 13.5; cf. Figs. 13.8, 13.9), meaning that the thickness of the humus layer was increasing over time.

Significance of Increases in Humus Depth Over Time

There is a general tendency for the average thickness of the organic layer to increase with time. The areas with statistically significant increases in humus depth are distributed all over Sweden. All values from all four inventories are summarized in Fig. 13.9, and we may see that the average humus depth for the whole country was 7.47 cm (SD 8.52) in 1961. By 2001, the humus-layer thickness became 9.03 cm (SD 6.41). These two values are significantly different (they were based on 53,146 and 9,305 observations, respectively), and demonstrate a general tendency. Berg et al. (2007) thus calculated an average increase rate of 0.054 cm per year.

The humus growth rate is better distinguished when comparing data for the three main, climatically different regions "North", "Middle", and "South" (Fig. 13.9), and Berg et al. (2007) subdivided Sweden into these three arbitrary regions (Fig. 13.8).

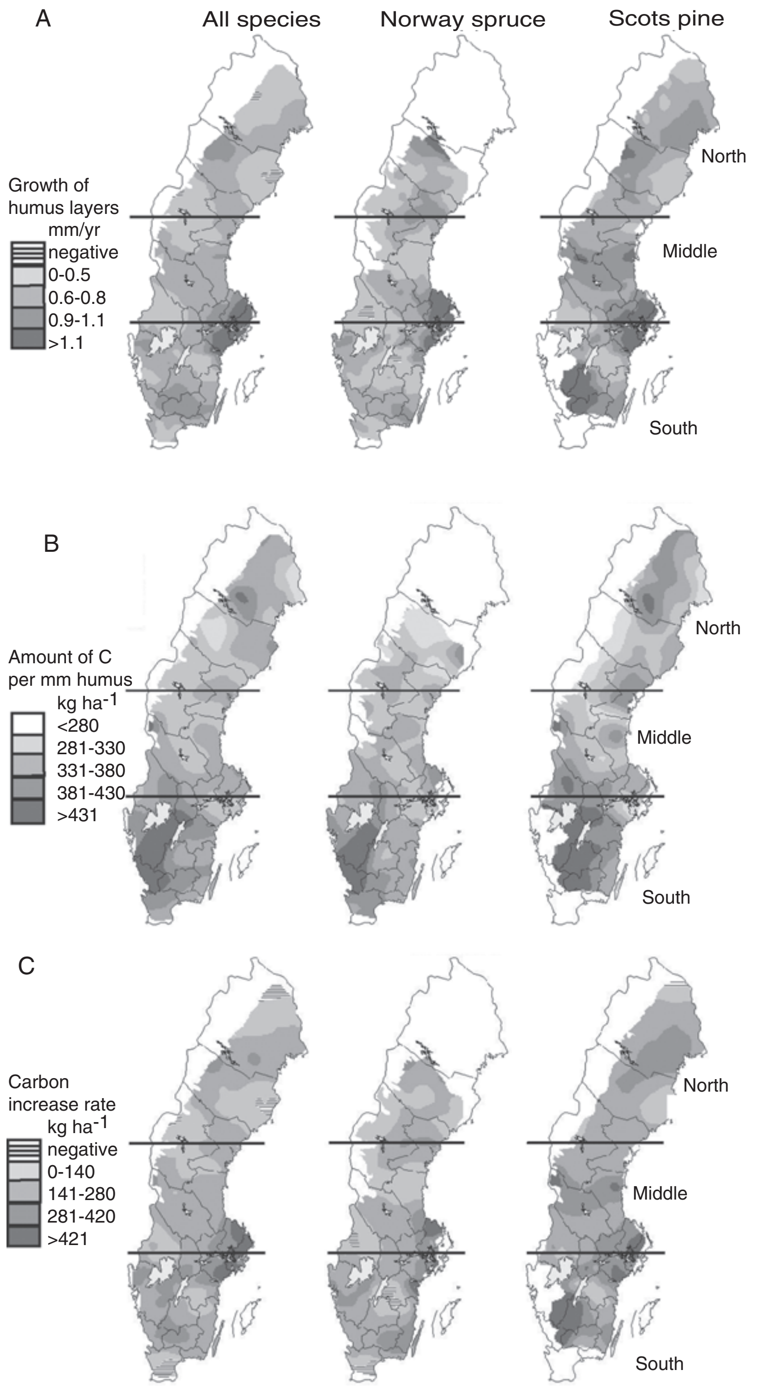
The three main areas with non-significant relationships were located in the region called South (Fig. 13.8) with long-term agricultural traditions, but since ca. the 1960s an extensive and ongoing afforestation is taking place, turning former arable land into forest. In the region North, relatively slow forest growth results in low litter fall, and a low humus accumulation rate that may explain the non-significant accumulation rates recorded there (Fig. 13.8A).

Table 13.5 Numbers and types of significant linear relationships between humus depth and time. Three types of forest are identified based on dominant species. Dominance was determined using percentage of the total basal area as a measure. The numbers of linear relationships, as well as of positive and negative ones are given

	Linear relationships			
Forest type	Fraction of the basal area	Total number	Positive	Negative
Spruce-dominated	>70%	552	531	21
Pine-dominated	>70%	602	594	8
All species[a]	-	641	606	35

[a] Includes Scots pine, Norway spruce, and deciduous trees, in all combinations and is representative of the total forested land

Fig. 13.8 **A** Annual growth of humus layers (mor humus) over Sweden. **B** Amount of carbon per mm humus layer (carbon bulk density) expressed as kg C mm^{-1} ha^{-1}. **C** Annual rate for carbon sequestration in the humus layer in Swedish forests. The data of all figures are for the period 1961–2001. For this study, Sweden was subdivided into three arbitrary regions: the region *North* encompasses Sweden north of 63°13'N, the region *Middle* Sweden between 63°13 N and 59°30 N, and the region *South* lies south of 59°30'N (from Berg et al. 2007)


A
All species
Norway spruce
Scots pine
Growth of humus layers mm/yr
negative
0-0.5
0.6-0.8
0.9-1.1
>1.1
North
Middle
South
B
Amount of C per mm humus kg ha-1
<280
281-330
331-380
381-430
>431
North
Middle
South
C
Carbon increase rate kg ha-1
negative
0-140
141-280
281-420
>421
North
Middle
South

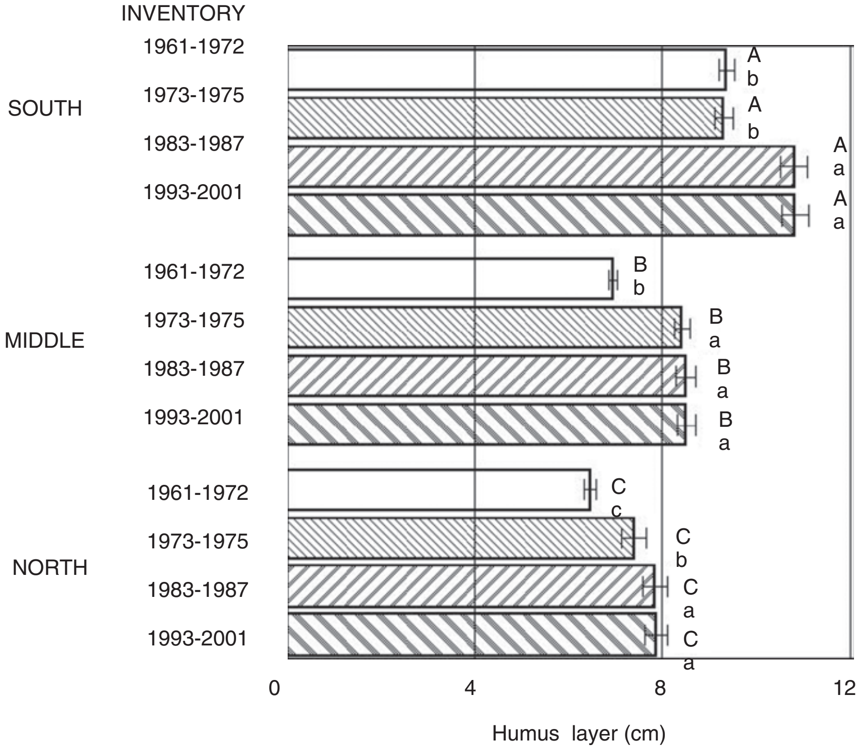


Fig. 13.9 Average humus-layer thickness in four different inventories for three main regions of Sweden (cf. Fig. 13.8). Different *capital letters* indicate significant differences ($p < 0.05$) between the three regions for a given inventory. Different *small letters* indicate differences between inventories within the same region. We may see that already the initial amount in the first inventory was higher in the southern region than in the northern (from Berg et al. 2007)

Using a simple diagram, Berg et al. (2007) illustrate that already before the measurements started, the humus layers were thicker in the southern third of the country (9.4 cm, region South), and medium in the middle part (6.9 cm, region Middle), in contrast to the north (6.45 cm, region North). This thickness in humus layers is significantly different among the three regions (Fig. 13.9).

There was a clear indication that this pattern is maintained over time. Thus, in the region South the humus layers had increased to an average value of 10.8 cm in the last inventory (over 40 years), which is significantly higher than the value recorded in the first inventory. In the region Middle, the increase was significant over the same 40-year period, with an increase from 6.9 to 8.5 cm. The increase in the region North was also significant, with an increase from 6.5 to 7.87 cm (Fig. 13.9). Based on these data, we can conclude that the measured humus-layer thickness has increased in general over large parts of Sweden in the last 40-year period.

When analyzing the results from individual grid cells, they found that the growth rates of the humus layer in the 40-year study period ranged from ca. 0.1 to >1.2 mm year^{-1} among the 25×25 km grid cells. The pattern is patchy, but there is a general tendency to higher growth rates in the south than in the north.

Areas with a decrease in humus-layer thickness were observed mainly in the region North (Fig. 13.8) in three small areas where the tree growth normally is lower than further to the south. Also in the southernmost part of the region South, the humus layer decreased. This latter area has long-term agricultural traditions, and is being reforested.

Humus-Layer Growth Rates, with Focus on Forests Dominated by Scots Pine or Norway Spruce

For forests dominated by Scots pine, Berg et al. (2007) obtained rates for the SOM-layer growth ranging from ca. 0.1 mm per year mainly in the northwestern parts of the country, to 1.6 mm per year in the southern parts (Fig. 13.8A). They also examined forests dominated by Norway spruce, and obtained values ranging from a minimum of ca. 0.1 mm per year, to a higher rate of > 1 .2 mm per year in smaller, local areas. Areas with the highest growth rates of humus layers are found in Scots pine forests; the humus layers of Norway spruce-dominated stands grow more slowly. We can compare this to the observation of Berg and Meentemeyer (2001) – as recalculated by Akselsson et al. (2005) – that at least foliar litter fall is higher in Norway spruce forests.

13.8.5 Calculations of Bulk Density of Carbon in the Humus Layer

The measured growth of the humus layer was given in units of millimeters, and this needed to be transformed into corresponding carbon units. For this purpose, Berg et al. (2007) used the carbon analysis made at each sampling point, and transformed the bulk density data determined for humus into corresponding carbon values. The humus density they used was in all cases based on local samples, and a clear variation was seen with species and over the country (Fig. 13.8B). Carbon bulk density was expressed as kg carbon per mm and hectare, and varies over the country with a factor of ca. 2 (Fig. 13.8B).

13.8.6 Calculated Carbon Sequestration Rates, and Some Patterns

General Comments to the Whole Case-Study Region

In the third step, humus growth rate (mm year^{-1}) was used to calculate the corresponding increase in carbon pool (kg C ha^{-1} year^{-1}) by multiplication with carbon bulk density (kg mm^{-1} ha^{-1}; Fig. 13.8). Thus, using humus depth (Fig. 13.8A) and humus carbon bulk density (Fig. 13.8B), Berg et al. (2007) calculated the annual increase in sequestered carbon from the rate of increase of the humus layer.

In areas that had a significant humus accumulation rate, the carbon sequestration rates ranged from <140 to >420 kg C ha^{-1} $year^{-1}$. The average rates, i.e., the rate for the "all combinations of forest type" forests, was 176 kg C ha^{-1} $year^{-1}$ (SD = 141). The maximum C sequestration rate for a single 25 × 25 km quadrate in this kind of "average" forest was 561 kg ha^{-1} $year^{-1}$.

The growth rate of the stored amount of carbon did not show any simple pattern over the country. Thus, in the northern parts (region North), Berg et al. (2007) found areas with both low (<140 kg C ha^{-1} $year^{-1}$), and relatively high (281–420 kg C ha^{-1} $year^{-1}$) increase rates for sequestered carbon (Fig. 13.8C). There was a general positive relationship to AET, but it appears that local conditions, possibly related to soil conditions, tree species (cf. below), and forest management, may have been dominant.

Carbon Sequestration Rates in Scots Pine vs. Norway Spruce Forests

Areas with high increase rates were clearly more frequent in pine-dominated than in spruce-dominated forests. Pine-dominated forests in the western parts of the region South showed a very high increase rate for stored carbon, >430 kg C ha^{-1} $year^{-1}$. Also in pine forests in the southeastern parts of the region Middle and the northeastern part of the region South, the increase rate was high, at 290–430 kg C ha^{-1} $year^{-1}$. The maximum C sequestration rates obtained were 717 and 714 kg ha^{-1} $year^{-1}$ for the forests dominated by spruce and pine, respectively.

For these two groups, either Norway spruce or Scots pine dominated, which means that the basal area covered more than 70%. The average rates were 176 kg C ha^{-1} $year^{-1}$ (SD = 123) for Norway spruce-dominated forests, and 263 kg C ha^{-1} $year^{-1}$ (SD = 141) for Scots pine-dominated forests. The difference between systems, 87 kg C ha^{-1} $year^{-1}$, was highly significant, and it appears that Scots pine forests on average can sequester more C than can Norway spruce forests.

This comparison was made using only areas within which both forest types were represented by a sufficient number of plots to enable comparison. Scots pine stands were located on soils typical for planting pine, and Norway spruce on soils in which spruce normally is planted. The values calculated by Berg et al. (2007) thus represent sequestration rates under actual conditions integrating climate and soil properties, but do not show the capacity of the pine or spruce ecosystem as such (cf. Table 13.5).

The different values for Scots pine and Norway spruce should not be considered as average values for the species over the country, but rather as representative for two types of ecosystems, and as such they may give some guidance to studies on the capacity of different systems to sequester carbon. The typical Scots pine system has a more open canopy, and the inflowing light promotes a rich ground vegetation that normally covers the ground completely. This may be, e.g., mosses, heather, cowberry, and bilberry, or herbs and grasses. In Norway spruce ecosystems, we normally find such dense canopies that the sparse light reaching the ground may support considerably less ground vegetation. In earlier chapters, we have discussed the possible humus contributions from woody litter components from trees, and from roots. We cannot exclude that the difference in ground vegetation may explain the contrast between these two systems, particularly as both have rather similar amounts of woody components, and Norway spruce additionally somewhat higher foliar litter fall. We may speculate that if the reasoning holds that woody components such as branches make very small inputs to the sequestered carbon, then this may be of similar effect for both spruce and pine forests. The 176 kg C per hectare and year sequestered in Norway spruce forests is rather similar to the average value of 180 kg C ha^{-1} $year^{-1}$ estimated by the limit-value approach. This may be further support for ground vegetation being a source of C in pine forests.

13.8.7 Possible Sources of Error in Estimates of C Sequestration Rates

The measurements were made in forests that were, and still are, subject to forest management, including clear felling, site preparation, and ditching. This method to determine sequestration rates, in contrast to the limit-value approach, includes both inputs and losses, and can thus be considered a net approach.

This means that this approach registered a net increase in humus and carbon. Management practices such as site preparation and ditching initiate and increase humus decomposition, and have been in use since the 1960s. Notwithstanding this, there is a general increase of the humus layers of ca. 0.054 cm per year (Fig. 13.9), documented over the whole country. Seeing that there appears to be an effect of forest management on humus-layer thickness, this value should be considered a net rate, and is probably an underestimate of the potential accumulation.

A technical error source in this method is also afforestation of old farmland. For the ongoing measurements, any plot that is farmland is not included in the census until it is planted with trees. Directly thereafter, it is classified as forested land, and the thickness of the newly forming humus layer is determined as soon as this becomes measurable. These low spot values will decrease the average thickness for, e.g., a 25 × 25 km cell, and with several such newly planted plots, this can amount to a significant larger-scale decrease – although all humus layers are indeed growing.

13.9 Carbon Sequestration Rates in the Three Case Studies, Compared to Quantitative Measurements in Single Stands and Chronosequences, as well as among these

The present measurements have been carried out in the organic layer only, and indicate a clear increase despite ongoing management practices. We have compared the rates calculated in the three case studies with more detailed, longer-term measurements for Sweden, and for Denmark for which this comparison can meaningfully be carried out (Table 13.4). The detailed measurements have been made at single sites, and we compare these with the calculated rates for the corresponding region.

We note that for mixed stands in Swedish Lapland, the rates are similar to those calculated (Table 13.4) by means of the different approaches used here, the N-balance approach giving a lower value. For central Sweden, the measured rate in a very nutrient-poor Scots pine forest is within the range obtained with the three methods, still a bit lower than the estimated average rate for that area based on the limit-value approach and the direct measurement method. For southernmost Sweden, we have compared to detailed measurements carried out in south Sweden, and in eastern Denmark at the same latitude and under a very similar climate, and found that the detailed measurements range from 170 to 650 kg C ha^{-1} year^{-1} among species (cf. Chap. 8); this largely coincides with those of the three case studies, which range between 200 and 420 kg C ha^{-1} year^{-1}. The large ranges here may be related to a stronger variation in species. We may note that in this area of higher N deposition, the N-balance approach gave results closer to those of the other two methods. The two methods for stable remains thus may have different accuracy, depending on the environment.

The approaches in the three case studies are mainly empirical, and to discuss mechanisms and detailed explanations is today premature. Still, we may point out some observations that may be of guidance. The limit-value approach supposedly gives the potential accumulation for one litter component, likely the main single component. This average value is 180 kg C ha^{-1} year^{-1}. The direct measurement approach gives an average of 197 kg C ha^{-1} year^{-1}, which is rather close (Table 13.4) – these two average values may support each other.

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Appendix I
Glossary

Short definitions of phrases and terms used in the book.

Accumulated mass loss The total amount of mass lost from a decomposing substrate, usually expressed as a percent of initial mass.

Aerobic Oxygen-demanding. The term as used here refers to microbial processes that require the presence of oxygen.

Allophane A soil dominated by amorphous (noncrystalline) clay-sized aluminosilicates. These are frequently found in highly weathered volcanic deposits.

Ammonium/ammonia fixation Fixed NH_3 is the NH_3 retained by the soil organic matter or decomposing plant litter after intensive extraction and leaching with either diluted mineral acid or neutral salt solutions [1]. Not to be confused with dinitrogen fixation.

Anaerobic Does not require oxygen. The term as used here refers to microbial processes that can proceed without the presence of oxygen.

Annual mass loss (see Period mass loss)

Biomass (1) Organic matter present as live microbial tissue. (2) The mass of organic material produced by living organisms, including both living and nonliving tissues.

Breakdown This term is used here to indicate "… a reduction in particle size of the organic resource" [2], or **comminution**. A similar effect is brought about by abiotic factors such as freezing and thawing, or wetting and drying cycles.

Constant fractional rate Refers to decay rate according to first-order kinetics (e.g., radioactive decay) in which the decomposition of material proceeds at a constant rate for all periods of the process, until the original material has been completely used up.

Continentality For our purpose, the effects of climate continentality concern temperature and precipitation. Thus, when comparing temperature and precipitation along a transect from the sea toward the inland, the annual average precipitation decreases, and also the mean annual temperature decreases. The temperature amplitudes increase both over the day, and over the year, e.g., between July and January.

Decomposition We have used the word “decomposition” or “mass loss” to denote the loss of mass from plant litter due to microbial decomposition or leaching of water-soluble substances. Decomposition can also be defined as litter CO_2 release plus leaching of compounds. Breakdown (see above) is not included in the concept.

Fulvic acid Colored material that remains in solution after removal [3, 4] of humic acid by acidification.

Humic acid The dark-colored organic material that can be extracted from [3, 4] soil by various reagents, and that is insoluble in dilute acid.

Humic substances A series of relatively high-molecular-weight, brown- to black-colored [3, 4] substances formed by secondary synthesis reactions. The term is used as a generic name to describe the colored material, or its fractions, obtained on the basis of solubility characteristics. These materials are a distinctive characteristic of the soil (or sediment) environment, in that they are dissimilar to the biopolymers of microorganisms and higher plants (including lignin).

Humin The alkali-insoluble fraction of soil organic matter or humus [3, 4].

Humus Sum total of the stable organic substances in the soil, not including undecayed animal and plant tissues, partially decomposed material, and the soil biomass [3, 4].

Leaching The loss of nutrients and incompletely decomposed organic compounds [5] from the intact remains of decomposing litter, due to the action of water.

LH factor Litter-to-humus factor. The remaining fraction of the litter when decomposition has reached the limit value, namely, (100–limit value)/100 [6].

Limit value Calculated value for the extent of decomposition of a given litter type at which the decomposition rate approaches zero.

Litter The same as litter remains (see Newly shed litter).

Litter CO_2 release The mineralization of carbon from litter. Gives mass loss from litter minus leaching of compounds (see Decomposition).

Litter remains Undecayed plant and animal tissues, and their partial decomposition products [3, 4].

Newly shed litter Plant litter that has been shed so recently that the decomposition processes have not yet started. This is complicated by the presence of newly shed litter, which starts decomposing when still attached to the plant.

Non-humic compounds Belonging to known classes of compounds, such as amino acids, carbohydrates, fats, waxes, resins, and organic acids. Humus probably contains most, if not all, of the biochemical compounds synthesized by living organisms [3, 4].

Period mass loss The mass loss of litter over a defined period, e.g., 1 year. Period mass loss is calculated using the actual remaining amount at the start of the period as amount of substrate.

Potential accumulation (or potential sequestration) of carbon. The accumulations that we estimate are called “potential”, because at this level, the calculations can not include all possible eventualities of forest management and disturbance, thus tending to overestimate accumulation. Furthermore, our estimates for case study one1 are based only on foliar litters, thus tending to underestimate accumulation. In all cases, the estimated accumulations should be considered as order-of-magnitude values, and serve to illustrate the potential for carbon sequestration in a particular forest, as contrasted with actual sequestration.

Sequestration We have used the term for long-term storage of mainly C and N, and occasionally other nutrients. This follows the definition given by Webster’s Dictionary [7], and refers to the fact that the compounds are bound and removed from the biological activities in their system, unless the system is subject to such changes that it may be considered altered. Our definition differs from that currently used by plant physiologists, namely, that a compound (e.g., C) bound into live plant tissue is sequestered. The binding of, e.g., CO_2 to plant tissue is one of several steps in the process of sequestration, and only part of the C taken up by plants is sequestered, the rest being released as CO_2 during decomposition.

Soil organic matter The same definition as for humus [3, 4].

Steady state Sometimes used also when dealing with the humus layers. We have not found any strict definition of the term dealing specifically with humus, but only a suggestion to an application for a specific boreal region of country size. Thus, Schulze et al. [8] suggested that today’s humus layers over a larger region, accumulated after the last glaciation, reflect a steady state, namely, the amount that has accumulated considering all possible influencing factors, including fire and anthropogenic influences. A problem with such a definition is that when, e.g., forest fires are suppressed, as is the case today, the basic conditions for the definition to be valid are changed. On a smaller geographical scale, e.g., a stand level, it would not be useful. In this book, we have avoided using the term “steady state” for humus. The reason is that we have not found any evidence for the validity of such a concept. We cannot exclude, however, that in ecosystems with developing humus layers, steady states do exist.

References

[1] Nömmik and Vahtras (1982)
[2] Swift et al. (1979)
[3] Stevenson (1982)
[4] Waksman (1936)
[5] This book
[6] Berg et al. (2001)
[7] Gove (1996)
[8] Schulze et al. (1989)

Appendix II
Scientific Names of Vascular Plants

We have listed here the vascular plant species mentioned in the text. Where the same species has different common names in American and European English, we have given both, indicated with (A) and (E), respectively, followed by the Latin/botanical name. Various dictionaries give different common names for the same species, and our purpose here has been to give the correct common names as they were used here, rather than to list the most widely accepted. Plants are divided into two groups: gymnosperms and angiosperms. Within each group, species and genera are arranged alphabetically by the American common name.

II.1 Gymnosperms

Firs

Douglas-fir (A, E) (*Pseudotsuga menziesii* Mirb. Franco.) (=*Pseudotsuga douglasii*)
European silver fir (A), common silver fir (E) (*Abies alba*) (=*Abies pechinata* D.C.)
Pacific silver fir (A, E) (*Abies amabilis* Douglas ex J. Forbes)
Subalpine fir (A) (*Abies lasiocarpa* (Hook.) Nutt.)

Hemlocks

Eastern hemlock (A), Canadian hemlock (E) (*Tsuga canadensis* (L.) Carr.)
Western hemlock (A, E) (*Tsuga heterophylla* (Raf.) Sarg.)

Pines

Aleppo pine (A, E) (*Pinus halepensis*) Miller
Austrian pine (A, E) (*Pinus nigra* Arnold)
Chinese pine (*Pinus tabulaeformis*)
Chir pine (*Pinus roxburghii*)
Corsican pine (A, E) (*Pinus nigra* var. *maritima*)
Eastern white pine, white pine (A), Weymoth pine (E) (*Pinus strobus* L.)
Jack pine (A, E) (*Pinus banksiana* Lamb.)
Korean pine (*Pinus koraensis*)
Limber pine (A, E) (*Pinus flexilis* James)
Loblolly pine (A, E) (*Pinus taeda* L.)
Lodgepole pine (A, E) (*Pinus contorta* var. *latifolia* Engelm.)
Lodgepole pine (A), shore pine (E) (*Pinus contorta* var. *contorta*)
Maritime pine (E) (*Pinus pinaster* Ait.)
Norway pine (A), red pine (A, E) (*Pinus resinosa* Ait.)
Ponderosa pine (A), western yellow pine (E) (*Pinus ponderosa* Laws.)
Scots or Scotch pine (A, E) (*Pinus sylvestris* L.)
Stone pine (E) (*Pinus pinea* L.)

Spruces

Norway spruce (A, E) (*Picea abies* (L.) Karst.) (=*Picea excelsa* Link.)
Red spruce (A, E) (*Picea rubens* Sarg.) (=*P. rubra* (DuRoi) Link)
Sitka spruce (A, E) (*Picea sitchensis* (Bong.) Carr)
White spruce (A, E) (*Picea glauca* (Moench.) Voss)

II.2 Angiosperms

Alders

Gray alder (A), grey alder (E) (*Alnus incana* (L.) Moench.)
Nepalese alder (A, E) (*Alnus nepalensis* D. Don)
Red alder (A), Oregon alder (E) (*Alnus rubra* Bong.) (=*A. oregona* Nutt.)

Aspen

Bigtooth aspen (A, E) (*Populus grandidenta* Michx.)
Quaking aspen, trembling aspen (A, E) (*Populus tremuloides* Michx.)

Beeches

American beech (A) (*Fagus grandifolia* Ehrh.)
European beech (A), common beech (E) (*Fagus silvatica* L.)
Japanese beech (A, E) (*Fagus crenata* Bl.)

Birches

Black birch, sweet birch (A) (*Betula lenta* L.)
European white birch (A); common birch, silver birch, weeping birch, white birch (E) (*Betula pendula* Roth.) (=*B. verrucosa* Ehrh.)
Hairy birch (A), downy birch (E) (*Betula pubescens* Ehrh.)
Yellow birch (A) (*Betula alleghaniensis* Britt.) (=*B. lutea*)

Grasses

Perennial ryegrass, English ryegrass (A), Italian ryegrass (E) (*Lolium multiflorum* Lam.) (=*L. perenne* var. *multiflorum* (Lam.) Parnell)
Small six-weeks grass (A) (*Vulpia microstachys* (Nutt.) Munro)
Soft chess (A), soft brome (A, E) (*Bromus hordaceus* L.) (=*B. mollis* L.)
Wild oats (A, E) (*Avena fatua* L.)

Maples

European maple (A), Norway maple (A, E) (*Acer platanoides* L.)
Red maple (A, E) (*Acer rubrum* L.)
Sugar maple (A, E) (*Acer saccharum* Marsh.)

Oaks

Black oak (A) (*Quercus velutina* Lam.)
Chestnut oak (A), basket oak (E) (*Quercus prinus* L.)
Common oak, pedunculate oak (E), English oak (A) (*Quercus robur* L.)
Durmast oak (E) (*Quercus petraea* (Mattuschka) Lieblein)
Eastern red oak, northern red oak (A), red oak (E) (*Quercus rubra* L.) (*Q. rubra* du Roi) (*Q. borealis* Michx. f.)
Pyrenean oak (E) (*Quercus pyrenaeica* Willd.) (=*Q. toza* D.C.)
White oak (A), American white oak (E) (*Quercus alba* L.)

Other Woody Plants

Black cherry (A, E) (*Prunus serotina* Ehrh.)
European ash (A), common ash (E) (*Fraxinus excelsior* L.)
European blueberry (A), bilberry (E) (*Vaccinium myrtillus* L.)
European mountain ash, mountain ash (A), Rowan (E) (*Sorbus aucuparia* L.)
Filbert (A), common hazel (E) (*Corylus avellana* L.)
Flowering dogwood (A), cornel (E) (*Cornus florida* L.)
Heather (A, E) (*Calluna vulgaris* (L.) Hull)
Lime (*Tilia cordata*)
Lingonberry (A), cowberry (E) (*Vaccinium vitis-idea* L.)
Sierra palm (A), mountain palm (E) (*Prestoea montana* (R. Graham) Nichols.)
Tabonuco, gommier, candle tree (A, E) (*Dacryodes excelsa* Vahl)
Yellow poplar, tulip poplar (A, E) (*Liriodendron tulipfera* L.)

Appendix III
Site descriptions

Stråsan, Sweden

An optimum-nutrition experiment was established at Stråsan, central Sweden (60°55′N, 16°01′E), on a till soil. The site is located on a steep, west-facing slope at a mean altitude of 350 m. The annual mean temperature is 3.4 °C, the annual precipitation 775 mm, and the average AET 422 mm. The area was planted with Norway spruce in 1958. For the fertilization experiment, started in 1967, the area was subdivided into 30 × 30 m plots. A detailed description of the experiment is given by Tamm et al. (1974). Fertilizer was added once annually, the dosages for the medium-dosage plots (N2P2) being given in Table III.1. Solid fertilizer was dispensed by hand (ammonium nitrate and superphosphate). During the course of the decomposition experiment, fertilizer was applied in early May in 1967 through 1982. In early May 1984, K, Mg, Mn, B, Zn, Cu, and Mo were added as well.

Jädraås, Sweden

Jädraås (site no. 6:51) in central Sweden, about 200 km NNW of Stockholm, has a Scots pine monoculture. The site is sometimes called Ih 5. It has a forest about 130 years old (in 1980) located at 60°49′N, 16°30′E, at an altitude of 185 m. The forest is situated on a very nutrient-poor sediment soil. The annual mean precipitation is 609 mm, and the long-term average temperature is 3.8 °C. The ground vegetation is composed mainly of European blueberry, cowberry, heather, mosses, and lichens. The humus form is mor, and the soil profile a podsol. The soil texture is fine sand. Additional information on this site is provided by Axelsson and Bråkenhielm (1980).

Black Hawk Island, Wisconsin, USA

Black Hawk Island is a 70-ha island located in the Wisconsin River, near Wisconsin Dells, at 43°40′N and 89°45′W, and 260–280 m elevation. Mean annual precipitation is 800 mm, and AET is 605 mm. The island is covered mostly with old-growth

Table III.1 Dosages of fertilizer applied to the fertilized (N2P2) plots in the optimum-nutrition experiment at Stråsan. No fertilizer was applied to control (N0) plots (data from Tamm et al. 1974, and from A. Aronsson, pers. comm.)

	Dosage applied (kg ha^{-1} $year^{-1}$)	
Year	N	P
1967	120	40
1968	120	
1969	120	40
1970	80	20
1971	80	
1972	80	
1973	80	
1974	80	40
1975	80	
1976	80	
1977	60	40
1978	60	
1979	60	
1980	60	40
1981	60	
1982	60	
1983	60	
1984	60	40
1985	60	
1986	60	

forest, and includes stands dominated by each of the following species: sugar maple, red oak, white oak, Canadian hemlock, white pine, red pine, and bigtooth aspen. Soils were highly variable across the site, and included entisols, spodosols, alfisols, inceptisols, and histosols. The vegetation and soils are described in greater detail by Pastor et al. (1982).

Harvard Forest, Massachusetts, USA

Harvard Forest is located in Petersham, Massachusetts, USA (42°30′N, 72°10′W), and is part of the Long Term Ecological Research (LTER) network. The two sites referred to in this book are both located in the Prospect Hill tract at altitudes between 340 and 360 m. The red pine stand was planted in 1925, and the second-growth mixed hardwood stand was last cut in about 1900. The mixed hardwood stand was dominated by red oak and red maple, with lesser amounts of black birch and American beech. Forest floors at both sites were mors. Soils were very stony inceptisols, of glacial origin. Average annual precipitation was 1,120 mm, and AET 580 mm. Mean annual temperature was 7 °C; mean monthly temperatures ranged from 19 °C in July to −12 °C in January. N deposition (wet+dry) was about 8 kg ha^{-1} $year^{-1}$.

Appendix IV

A Data Base for Litter Chemical Composition, and Limit Values for Decomposition – DELILA

A main part of the background material for this book has been compiled into a developing data base – DELILA. The acronym was created from the terms decomposition, litter initial composition, limit values. The data base has at present three sections, encompassing initial chemical composition of foliar litter and quantitative foliar litter fall, both related to geographical and climatic parameters. Furthermore, it includes limit values for decomposition as related to litter chemical composition, and all sections are continuously updated. Actual litter mass loss values are added, allowing new estimates to the limit value section. All data are downloadable. Although the data base contains data for all Europe, the focus is northern Europe.

The data base is maintained by the Danish Centre for Forest, Landscape and Planning, University of Copenhagen, and is available at the website http://en.sl.life.ku.dk (search for DELILA). The data base is also summarized in a report: "DELILA, a data base for plant litter dynamics and carbon sequestration." Editors B. Berg and P. Gundersen, Forest & Landscape Working Papers No. XX (2007), Danish Centre for Forest, Landscape and Planning, University of Copenhagen.

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