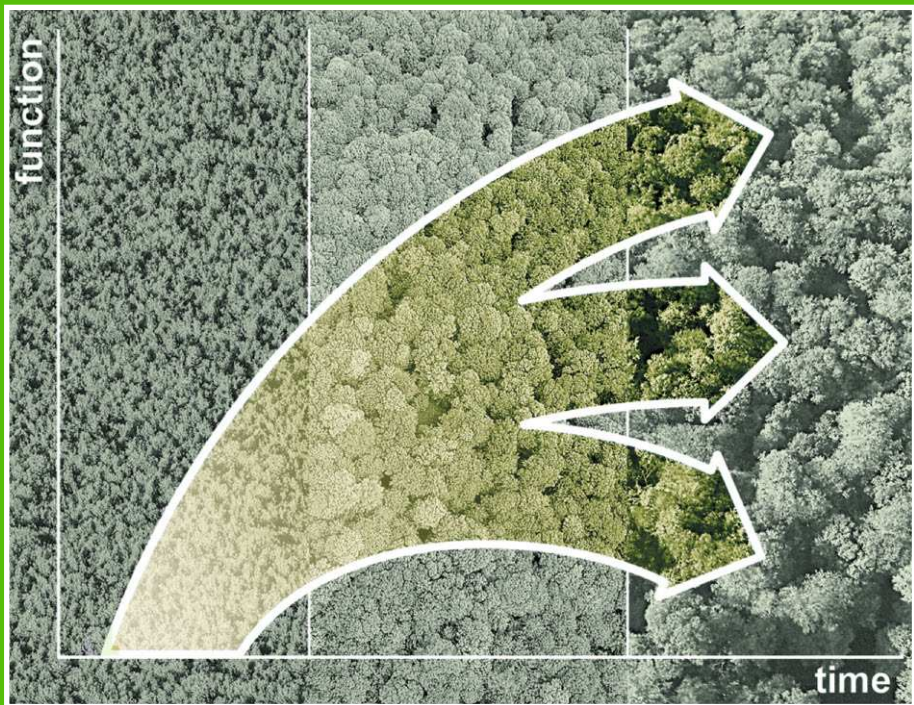Christian Wirth, Gerd Gleixner,
Martin Heimann

Editors

Old-Growth Forests

Function, Fate and Value

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Old-Growth Forests

Function, Fate and Value

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Cover illustration: This book explores how ecosystem functions change with progressive forest devel-opment from young over mature to old-growth forests. The photographs by Thomas Stephan illustrate the change in canopy structure with stand age in a mixed beech forest in the Hainich National Park, Thuringia, Germany.

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This book is dedicated to Ernst-Detlef Schulze

Homage to Ernst-Detlef Schulze

During the course of a very long career I have met legions of scientists but none comparable to Ernst-Detlef Schulze. I have had the pleasure of knowing him since the beginning of his extraordinary career and he is certainly one of the most distinctive and unforgettable scientists that I have encountered. I first met him when he came to the University of California at Los Angeles for a master's degree after studying forestry in Göttingen, Germany. Unfortunately, he set a very bad example for me as to what I should expect from master's students for the rest of my academic career, which was just starting. In less than a year while he was at UCLA, he completed a successful thesis performed at 3,000 m elevation, during the wintertime, on the gas exchange of needles of bristlecone pine – the oldest-known living tree – foreshadowing his lifelong interest in old forests and long-lived trees.

But that arduous thesis was only a part of his accomplishments during that brief period. He also participated in a tropical program in Costa Rica, where he completed a publishable study on soil respiration. Then, to cap off his stay at UCLA he traveled by vehicle to the Arctic on his way home. I am sure I am forgetting many other things he did in his spare time during his short stay with us. As far I can see he has never slacked off the torrid pace to this day since that awesome start. He went on to study for his PhD with the pioneering and leading plant physiological ecologist Otto Lange at the University of Würzburg. He subsequently went on to establish a vigorous plant ecology program at the University of Bayreuth. He then became a founding director of the Max Planck Institute for Biogeochemistry in Jena, Germany.

Since those early days, I have had the privilege of working with Detlef in many parts of the world – the redwoods of California, the tropical dry forests of Mexico, the temperate forests of Argentina, and the sand dunes of the Kalahari. In all of these studies he used his unique approach to science. He dives into the system with ferocious intensity, learning about the system as he goes by probing until he finds the critical measurements needed to test his hypotheses. His desire to learn, first-hand, about the functioning of the diversity of ecosystems of the world can be appreciated by those who visit his institute, where there are displays of wonderful

pictures of all of the ecosystems where he has worked. Clearly he has been inspired, as have all ecologists, by the pioneering studies of Alexander von Humboldt seeing, doing and learning.

His deep knowledge about science and science history is phenomenal. A field trip with him is incredibly interesting since he can tell you everything about an area that you would want to know: its history, the geomorphology, and its natural history. If he is driving during his exposition, the trip can be very exciting and certainly death defying.

Detlef has published extensively. It is lucky that electronic PDF files have been developed this past two decades since without them I would have run out of file cabinet space for his prodigious contributions. He has led the way in melding process level physiological ecology with ecosystem and landscape functioning. His strong contributions and interests in the carbon cycle in recent years are reflected in the final chapters of his monumental Plant Ecology textbook at one level and, at another, his work with the IPCC and the Framework Convention on Climate Change.

For a long time, Detlef has been interested in bringing attention to the old-growth forests of the world and the important role they play in so many environmental and social dimensions but in particular in carbon storage. This book is a fitting tribute to Detlef's deep interest in this topic as well as to his enormous accomplishments. He should be very gratified to see all of the new and exciting insights that have been brought together in this volume. Hopefully it will provide a stimulus for greater protection of those remaining islands of a once vast sea of old-growth forests with their extraordinary storehouses, of not only carbon, but also biotic diversity.

Harold A. Mooney
Stanford University, Stanford, California, USA

Preface

How do old-growth forests function in comparison to younger and managed stands? There exists a whole suite of negative attributes that are commonly used to characterise the old-growth stage (e.g. 'senescent', 'over-mature', 'break-up', 'decay') implying that these forests are less vigorous, less productive and less stable than earlier stages of forest development. Another line of thinking that goes back to Clement's climax concept [Clements FE (1936) Nature and structure of the climax. J Ecol 24:252–84] and Odum's ecosystem theory [Odum EP (1969) Strategy of ecosystem development. Science 164:262–270] emphasises the notion of a compositional and biogeochemical equilibrium: The same set of species replaces itself via gap-phase regeneration, and input of carbon and nutrients equals the output. It is the latter perception, which suggests the inability of old-growth forests to sequester carbon, that led to the exclusion of non-managed old-growth forests from the carbon accounting schemes of the Kyoto-Protocol of the United Nations Framework Convention on Climate Change (UNFCCC). In the last two decades, an increasing number of ecological studies employing novel methods, improved sampling designs, and large datasets have yielded results that challenge these views of decline or neutrality.

Synthesising the new findings and integrating them into a more comprehensive picture of old-growth forest functioning was the goal of a symposium entitled "Old-growth forest: function and value of a vanishing ecosystem", which was held at the Max-Planck-Institute for Biogeochemistry in Jena, Germany, on 12–13 September 2006. A second, equally important purpose of this symposium was to celebrate the 65th birthday of Ernst-Detlef Schulze – one of the founding directors of our institute – to whom this book is dedicated. His endless scientific curiosity in general and his long-standing fascination with old-growth forests in particular inspired a large portion of the research documented in this book.

During the production of this book it turned out that many authors were willing to go far beyond a mere review of existing studies. A large number of chapters in this book present new original data and comprehensive meta-analyses based on large datasets that have so far not been evaluated in the context of old-growth forest research. Many people have contributed to this book. In particular, we would like to

<div align="right">
Christian Wirth
Gerd Gleixner
Martin Heimann
</div>

Jena, February 2009

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Part I
Introduction

Chapter 1
Old-Growth Forests: Function, Fate and Value – an Overview

Christian Wirth, Gerd Gleixner, and Martin Heimann

1.1 Old-Growth Forest Perception

Most of us, scientists and laymen alike, are deeply fascinated by old-growth forest. We travel to places like the Tongass National Forest[1] in Alaska or the Biatowieža National Park[2] in Poland to enjoy the sight of forests left to their own devices, with their majestic trees, intriguing structure and rare wildlife. For us, the fascination arises from a mixture of interest, aesthetic pleasure and maybe a slight alienation. However, let us hear a different view on old-growth forests:

> "There, a desolate tract of land lies, a sad and sullen region, never used as a man's abode. Its mountains are covered with forests, dark and dense. Trees without bark and without tops, stand bent or half-broken, withered by age. Others, far more than those first ones, lie down full length, only to decay on those heaps of wood already rotten and to suffocate the seedlings that were about to come through. Nature seems to be worn out here; earth – heaped with the ruins of what she brought forth – carries piles of debris, instead of her flowery green, and holds trees loaded with parasitic plants, poisonous fungi and mosses, those impure fruits of rottenness . . ."

The man who wrote these lines in the eighteenth century was the famous French scientist Comte de Buffon, author of the multi-volume book *Histoire Naturelle* (Lepenies 1989). As a naturalist, Buffon was certainly susceptible to the beauties of organismic diversity, and yet he perceived old-growth forests as ugly and hostile. For it to become beautiful, nature had to be tamed and transformed. The French palace gardens with their strictly geometric arrangement of artfully pruned trees perfectly reflect the spirit of Buffon's time (Gaier 1989). Interestingly, by that time in the eighteenth century, the days where people in Europe had to fear the forests were long over. Wolves and bears had been exterminated, and the bands of robbers had nowhere to hide, since Central Europe was almost devoid of primary forests.

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[1] http://www.fs.fed.us/r10/tongass/

[2] http://www.bpn.com.pl/
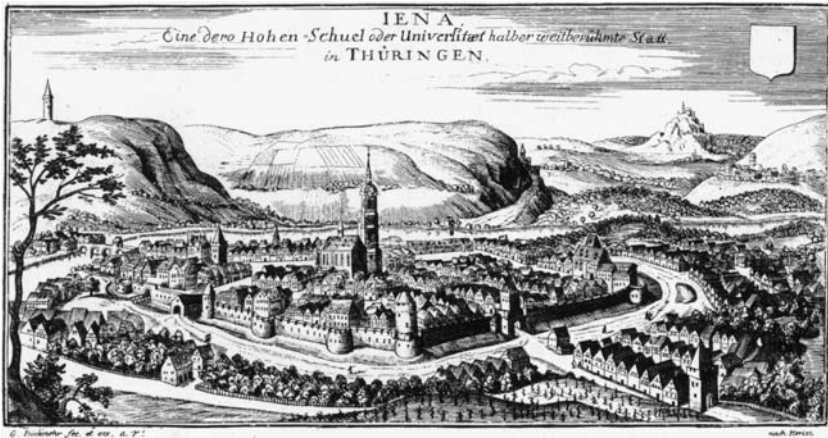
Fig. 1.1 Engraving by Caspar Merian d. J. (1627-1686) of the town of Jena and surroundings in the year 1650

The engraving in Fig. 1.1 shows the landscape around Jena, Germany, the home of our Max-Planck-Institute for Biogeochemistry, in 1650 (Lepper and Heinrichs 1999). The surrounding hills, which would naturally be covered by a species-rich temperate deciduous forest, had been turned into sheep-runs interspersed with croplands on more level ground. Soils were eroded and wood was a scarce resource. The few places in Europe where remnants of primary forests, and within them parcels of old-growth forests, could be found were either feudal hunting grounds (e.g. Białowieża), or inaccessible land on steep slopes or in swamps. The remaining common forest was over-used as pasture woodland, through collection of firewood and litter raking. European societies responded to this by developing the science of forestry with the primary goal of restoring the wood supply for the boom in industry. Heinrich Cotta (1817), one of the German pioneers of forest science, stated *"In former times we had no forest management but plenty of wood, today we have the science but no wood left."* Another important reaction towards the devastation of nature and the industrialisation of human life was the awakening of a positive, almost enthusiastic attitude towards nature in general and forests in particular. This is manifested in countless poems, songs and novels praising the beauty of nature. The European romanticism of the early nineteenth century was probably the first large ecological movement in the Western world (Trepl 1994), but also in the United States, where the deforestation of the Eastern forests was rapidly progressing, novelists like Henry David Thoreau were advocating a simple life in mother nature's arms. Beyond these extremes of disgust and praise lies the perspective of indigenous communities, who seem to embrace nature as a sacred, living entity and perceive the forests around them with an 'easy acceptance' as Steve Comer, a Mahican Indian of North America, nicely expresses it (Standing Woman and Comer 1996).

1.2 Old-Growth Forest Services

Today, a mere 23% of the world's forest area can be classified as intact[3] (Green-peace 2006). These intact forests, mostly primary forests located in the tropics and the boreal zone, are the regions where we can still expect to find a large fraction of old-growth forests, i.e. forests that show little signs of past stand-replacing disturbances and that have matured to reach a dynamic equilibrium driven by intrinsic tree population processes. Currently, the area of intact forest in the tropics – and with it the area of old-growth forests – is shrinking at a rate of 0.5% per year. Many developing and threshold countries cut down their forests, as Europeans and North Americans did in the past, to fuel their budding economies, and developed countries like Canada, the United States and Russia also continue to harvest old-growth forests. In the short-term, individual groups and societies might profit from forest destruction. However, with old-growth forest vanishing at an unprecedented pace, mankind as a whole loses the ecosystem services provided by these forests.

What are the ecosystem services provided by old-growth forests? As outlined above, these may be of a spiritual and/or aesthetic nature. However, there are also many profoundly materialistic services such as the provision of genetic resources, non-timber products, and habitat for wildlife (hunting and ecotourism), the sequestration of carbon, the prevention of floods and erosion, to name only a few. Finally, old-growth forests provide cultural services as the object of scientific studies. In Europe we are facing a situation where true lowland old-growth forests are virtually non-existent. Given this reality, we have lost an important reference point for research in forestry and forest ecology. The loss of natural ecosystems is always associated with a loss of information. In retrospective it becomes clear that, in Europe we do not even know what possibly unique services we are lacking today due to the disappearance of old-growth forests, simply because they had vanished long before we could accurately study them.

1.3 Aims and Scope

In the past decades a large number of studies have been conducted in old-growth forests worldwide addressing such diverse topics as carbon, nutrient and water cycling, population dynamics, disturbance regimes, and habitat diversity using a diverse set of approaches and techniques. These include long-term observations,

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[3]Intact forest areas were originally defined in the context of boreal ecosystems according to the following six criteria (see Achard et al., Chap. 18): situated within the forest zone; larger than 50,000 ha and with a smallest width of 10 km; containing a contiguous mosaic of natural ecosystems; not fragmented by infrastructure; without signs of significant human transformation; and excluding burnt lands and young tree sites adjacent to infrastructure objects (with 1 km-wide buffer zones)

chronosequences studies, the micro-meteorological eddy covariance technique, stable isotopes, remote-sensing, and modelling, amongst others. This book aims to synthesise current knowledge on the characteristic functioning of old-growth forests to evaluate the consequences of the world-wide loss of this type of ecosystem (Fig. 1.2).

The book is divided into six parts: part I serves as an introduction and lays the definitional foundation for the chapters following. Part II is devoted to aboveground processes, ranging from deadwood dynamics to canopy fluxes. Part III reviews belowground processes and covers the topics of root, nutrient and soil carbon dynamics. Part IV presents regional accounts of tropical and temperate forests in Europe, and North and South America, and the Canadian boreal forest. Part V deals with the human dimension, including the effect of land-use, and technical and political strategies for the protection of old-growth forests.

In the introductory chapters of the book (part I), Wirth et al. (Chap. 2) review definitions of old-growth and critically discuss their usefulness in the context of functional ecology. They also present a meta-analysis that estimates the fractional cover of old-growth forest in different forest biomes without human impact as a reference point. In addition, the plethora of related terms used in the broad context of old-growth forest (pristine, primeval, intact, etc.) is reviewed. Part of the definition of old-growth forest is the presence of old trees. Taking a dendroecological perspective, Schweingruber and Wirth (Chap. 3) explore to what extent trees differ from other life forms (shrubs, herbs) in their longevity. In this context, they also examine the mechanisms underlying the death of cells, tissues and whole plants.
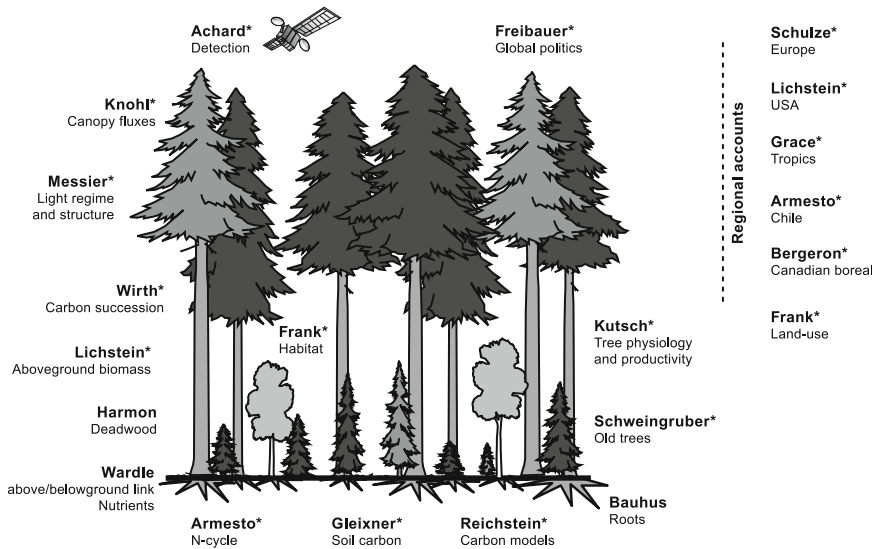
Fig. 1.2 Topics covered by the different chapters in this book. Only the first author is listed. *Asterisks* Contributions with co-authors

Part II on above-ground processes starts with a contribution by Kutsch et al. (Chap. 4), who follow up on Chap. 3 by asking whether and how tree age and size influence the physiology and productivity of individual trees and forests. This chapter adds new insights to the ongoing debate about 'age-related decline' (Ryan et al. 1997). Based on a re-analysis of the dataset of Luyssaert et al. (2007), the authors are able to show that changes in structure exert a stronger control on net primary productivity than age *per se*. To evaluate the role of changes in species composition on successional trends in productivity, they further analyse two extensive datasets of leaf physiology of temperate and boreal tree species, and are able to identify potential mechanisms that operate against an 'age-related decline'. Along the same lines, Wirth and Lichstein (Chap. 5) explore how successional species shifts during the old-growth stage control carbon stock changes in the aboveground biomass and in deadwood. They present a novel model that uses widely available tree traits (e.g. maximum height and longevity) to translate qualitative descriptions of successional pathways of 106 forest cover types of North America into quantitative predictions of aboveground carbon stock changes. They compare their results with observed biomass and deadwood trajectories from long-term chronosequences and inventories (see also companion Chap. 14 by Lichstein et al.). Old-growth forests are usually characterised by the presence of very large trees and a complex horizontal and vertical structure. These three elements create a unique understorey environment that differs from earlier successional forests. Based on an extensive review of the literature on old-growth forests in boreal, temperate and tropical biomes, Messier et al. (Chap. 6) review the distinct structural and compositional features that influence the understorey light environment and how such light conditions affect the structure and dynamics of the understorey vegetation. Knohl et al. (Chap. 7) explore the effects of aboveground structural complexity on the ability of old-growth forests to absorb carbon from the atmosphere, their interaction of carbon and water cycle and their sensitivity to climatic variability. To this end the authors review the micro-meteorological literature and the results from paired catchment studies. Woody detritus is an important component of forested ecosystems and particularly of old-growth forests. It can reduce erosion, stores nutrients and water, serves as a seedbed for plants and as a major habitat for decomposers and heterotrophs. Woody detritus also plays an important role in controlling carbon dynamics of forests during succession. Harmon (Chap. 8) reviews the successional dynamics of deadwood and uses a heuristic model to illustrate major controls on carbon trajectories in deadwood.

The opening chapter of Part III on belowground processes is presented by Wardle (Chap. 9) who focusses on the feedbacks between vegetation properties, nutrient leaching and processes driven by the decomposer communities. Based on a review of millennial chronosequences across the world, he depicts the inevitable fate of all old-growth forests under the absence of disturbance: a progressive ecosystem retrogression driven by phosphorous losses that induces a decline in species diversity and productivity over long time-scales. The function and distribution of roots and their association with mycorrhizal fungi plays a pivotal role in forest ecosystems for soil carbon storage and nutrient and water retention. Bauhus

(Chap. 10) explores the question of whether the above-ground structural complexity typical of old-growth forests is mirrored belowground, and what the likely functional consequences are. Gleixner et al. (Chap. 11) look at the processes and mechanisms responsible for formation and dynamics of soil organic matter. They explore how changes in litter input and quality, soil respiration and the export of dissolved organic carbon influence the changes of soil carbon stocks with stand age and succession. This is accompanied by an extensive review of soil carbon chronosequences. A case study in a German old-growth forest is added that illustrates the importance of deep soil layers for carbon sequestration in the soil. Reichstein et al. (Chap. 12) present a theoretical companion chapter that provides an overview of recent approaches to soil carbon modelling. They focus on the question of whether there is a theoretical limit to soil carbon storage, and to this end analyse the behaviour of state-of-the-art models. They find that there are several plausible formulations that predict that, under certain conditions, soil carbon pools never reach a steady state.

Part IV presents regional accounts, the first of which, by Bergeron and Harper (Chap. 13), is devoted to the old-growth forests of the Canadian boreal forest. Old-growth boreal forest is considered rare since disturbances occur too frequently to allow forest stands to reach old age. The authors present recent research on historical fire regimes in Canada that proves this assertion to be false. They further describe structural and functional features typical of old-growth stages of three important forest types and discuss silvicultural techniques suitable to preserve them. For the temperate forests of North America, Lichstein et al. (Chap. 14) compiled a comprehensive collection of biomass estimates for old-growth stands and analysed the complete forest inventory of the coterminous US (99,253 plots with 2,875,227 trees) to test existing hypotheses on biomass dynamics, especially the shifting mosaic hypothesis by Bormann and Likens (1979), which proposes a late-successional decline in stand biomass. In the first part of their chapter, Schulze et al. (Chap. 15) take a global perspective and examine the age-dynamics of biomass and stand density based on the Luyssaert (2007) dataset. In the second part, they highlight the specific situation in Europe, where old-growth forest dynamics cannot be understood without the consideration of direct and indirect human impacts. This is illustrated by several case studies. Armesto et al. (Chap. 16) give an account of the temperate old-growth forest of South America with a focus on Chile. Their chapter focuses on three aspects of old-growth forest functioning. First, they illustrate the importance of plant–animal interaction for the functioning and maintenance of old-growth forests. Second, they take a closer look at the peculiarities of nitrogen dynamics in old-growth forests under the low levels of nitrogen deposition typical of the southern hemisphere, and thus add to the results presented in Part III on belowground processes. Third, they discuss strategies for the protection of old-growth forests, and present an encouraging example. Finally, Grace and Meir (Chap. 17) close this part with a chapter on old-growth dynamics in global tropical forests. They highlight distinctive features such as low natural disturbance levels and high population turnover, and discuss the implications for their ability to act as carbon sinks and to respond to environmental changes.

Part V addresses the past, present and future of old-growth forest. Achard and colleagues (Chap. 18) give an account of the status of intact forests on our planet. They focus on the hotspots of forest cover loss in tropical and boreal countries, discuss the underlying socio-economic drivers, and demonstrate the pivotal role of remote-sensing-based inventories in the verification of international treaties. One important function of old-growth forests in the context of the conservation of biological diversity is the provision of habitat for plants and animals. Frank et al. (Chap. 19) explore why old-growth forests tend to harbour more species than any other type of forest, and also present a synthesis on past and present threats to old-growth forest worldwide. Finally, Freibauer (Chap. 20) looks into the future and discusses the prospect of old-growth forest protection in the context of international treaties such as the Kyoto-Process and the Convention on Biological Diversity.

The book closes with part VI, a synthesis by Wirth (Chap. 21), who focusses on three major questions: (1) How does the structural complexity of old-growth forest influence ecosystem and ecological function? (2) How can we understand old-growth forest function in the context of succession and ecosystem development? (3) What is the current status and likely future of the planet's old-growth forests? Despite the considerable scientific advance summarised in this book, the synthesis reveals that major gaps remain in our knowledge, and that concrete research needs must be formulated. As noted by Freibauer (Chap. 20) and Schulze et al. (2002), ecological theory, namely the assertion of equilibrium behaviour in old-growth forests according to Odum (1969), had a profound influence on the formulation of the Kyoto-Protocol, with negative consequences for old-growth forest protection. However lamentable this is, it proves that political decisions are influenced by scientific ideas. It is one of the aims of this book to provide a refined and more comprehensive picture of the functioning of old-growth forest that could serve as a basis for future political decisions. At the very least, we should know what is at stake.

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Chapter 2
Old-Growth Forest Definitions:
a Pragmatic View

**Christian Wirth, Christian Messier, Yves Bergeron, Dorothea Frank,
and Anja Fankhänel**

2.1 Introduction

Many of us possess an archetype of old-growth forest appearance. We expect
majestic trees, small pockets of regenerating trees thriving to reach the sun, heaps
of dead wood covered with mosses, snags spangled with cavities and bracket fungi,
and rare wildlife. However, thinking twice we may realise that this archetype (1) is
not a scientific definition but merely a picture, and (2) is not generic but rather
describes the late stage of succession in the temperate forest biome where the great
majority of ecologists live and work. In boreal forests, trees rarely reach majestic
dimensions and yet may attain great ages. In some pine forests trees become very
old, but gap phase regeneration is impeded by recurring surface fires. In tropical
forests trees grow tall, but dead wood does not pile up because of high decomposi-
tion rates. These examples illustrate that there are many ways for a forest to grow
old, and that it is probably a futile task to aim at providing a concise scientific
definition of old-growth forest that encompasses the full spectrum of successional
and structural options.

   This chapter consists of four sections. Section 2.2 reviews existing attempts to
define old-growth forest and discusses their merits and problems. Subsequent
sections are devoted to the more applied aspects of old-growth forest definitions
and their implications. Specifically, Sect. 2.3 presents a literature analysis con-
ducted to understand how the term 'old-growth' is actually used in the literature, as
well as how often and why it is replaced by competing terms. Section 2.4
explores how disturbance regimes and successional dynamics interact in determin-
ing the occurrence of old-growth across the globe, and the topic of old-growth
forest conservation is briefly covered in Sect. 2.5. The chapter concludes by
discussing the usefulness of definitions in the context of the functional focus of
this book.

2.2 Old-Growth Forest Definitions and their Limitations

Simple definitions based on a single criterion are rare in ecology, especially if the *definiendum* ('old-growth forest') is itself a complex dynamic system that is a result of gradual transitions involving several processes. Most definitions today employ multiple criteria (Spies et al. 1988; Hunter 1989; Wells et al. 1998; Messier and Kneeshaw 1999; Kimmins 2003) and these criteria broadly fall into three groups: The first group emphasises structural and compositional features; the second highlights the successional processes that have led to, and currently maintain, the old-growth stage; while the third group summarises criteria related to biogeochemical processes. Figure 2.1 lists a number of criteria and shows how often they have been used in 39 different publications devoted to defining the term 'old-growth' (adapted from Kneeshaw and Burton 1998). It is immediately apparent that existing definitions are based largely on structural criteria, with successional and biogeochemical criteria being less often employed. In the following, the most important structural, successional and biogeochemical criteria will be introduced and critically discussed.

2.2.1 Structural Definitions

2.2.1.1 Criteria

Structural old-growth criteria are based on data relating to age distributions, size distributions and spatial patterns of both live and dead trees, and they are basically formulated to identify stands with gap phase dynamics (Wells et al. 1998). Among these indicators, the data on age structure are the most valuable because they are directly linked with the birth and death events causing these dynamics. The following three criteria for age structure proposed by Mosseler et al. (2003) summarise the most important aspects: (1) uneven, multi-modal or inverse J-shaped age structure; (2) mean age of dominant species approaches half the maximum longevity for the respective species; and (3) some old trees are close to their maximum longevity. Diameter or height distributions are often used as a proxy for age distributions assuming that age and size are reasonably well correlated (but see below). An inverse J-shaped size distribution usually translates into a complex, multi-layered canopy structure (Franklin and Van Pelt 2004). Mortality of canopy trees is a prerequisite for gap phase regeneration. Large standing dead trees and coarse woody detritus on the forest floor are indirect evidence of this process, and their presence is often used as another structural indicator of gap phase dynamics (Harmon et al. 1986). A typical criterion is therefore the presence of large amounts of standing and downed dead wood in all stages of decay. Another indicative structural feature of old-growth forests is the pit-and-mound micro-topography that forms at the forest floor if large trees are uprooted (Lorimer and Frelich
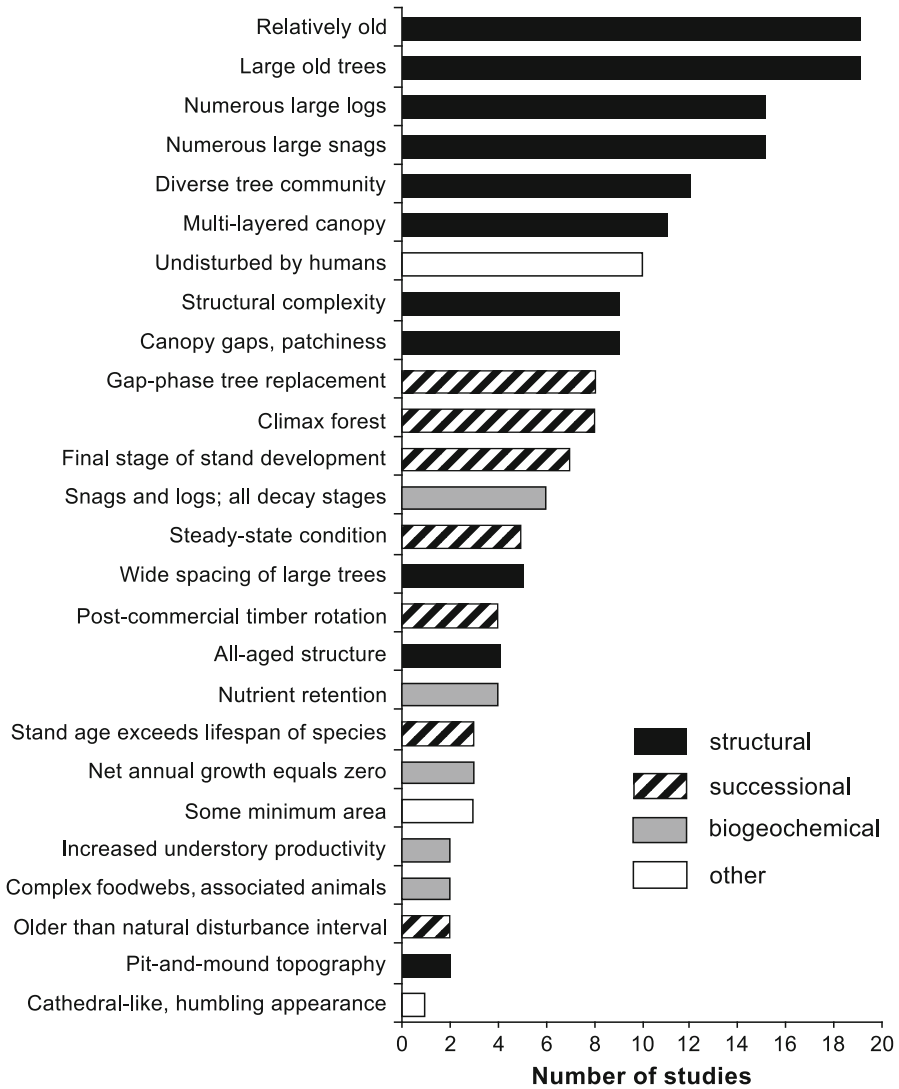
Fig. 2.1 Chart showing how often different criteria have been mentioned in a total of 39 publications devoted to the subject of defining old-growth forest (adopted from Table 1 in Kneeshaw and Burton 1998). The three main categories of old-growth criteria ("structural", "successional" and "biogeochemical") are indicated by the black and patterned bars; terms that fall into none of these three categories are shown as "other" (white bars)

1994; Liechty et al. 1997), but similar conditions can exist in young stands regenerating after major wind blow. Interestingly, spatial pattern analysis is rarely used as a means of quantifying the degree of 'gapiness' although stand maps are often available (but see, e.g. Getzin et al. 2006; Harper et al. 2006).

2.2.1.2 Limitations

The major limitation of structural indicators is that they have been developed to characterise old-growth appearance in a very limited set of forest types (Spies 2004). Many of the pivotal papers on old-growth definitions (Spies et al. 1988; Franklin and Spies 1991; Wells et al. 1998; Messier and Kneeshaw 1999; Kimmins 2003) have been written by scientists who worked in the Douglas-fir/Western hemlock forests of the Pacific North-West of the United States or British Columbia. The derived structural indicators are not easily transferred to other forest types – not even in qualitative terms. Bergeron et al. (Chap. 13, this volume) demonstrate the limited validity of typical old-growth indicators using a number of boreal forest types as examples.

As a more practical concern, the determination of tree ages for the establishment of age distributions is not without problems. First of all, it is very time-consuming. For example, in a pivotal study analysing 13 stands for old-growth characteristics, Kneeshaw and Burton (1998) determined the age of a total of 2,720 trees. Not only does this represent a substantial effort, but it is also prone to substantial error if not done correctly. This is especially true in old-growth forests where advance regeneration may be suppressed for up to a century, i.e. the pith of a core taken at breast height may have been the terminal shoot of a 100-year-old tree (Oliver and Larson 1996, pp 137–140). Even coring at base height does not solve the problem entirely because the oldest pith dates are often found well below the root collar. This is because many trees were bent down as saplings by snow or fallen logs, and have developed adventitious roots (Parent et al. 2002). Under these conditions, correct ageing requires sophisticated techniques such as cross-dating or pith node counting (Nilsson et al. 2002). If trees have regenerated through resprouting, only the ramet age can be determined but not the age of the individual tree (see Chap. 3 by Schweingruber, this volume). In the tropics, most tree species do not form annual rings and only a few species deposit annual parenchyma bands, which are difficult to identify under field conditions (Worbes 1999). Therefore, age determination often rests upon indirect methods based on size-growth rate relationships (Lieberman et al. 1985) or very expensive methods using radiocarbon dating (Horvitz and Sternberg 1999; Fichtler et al. 2003). Because of these problems, diameter distribution data are usually employed as a proxy for age distribution. However, this approach suffers from similar problems, because in datasets including suppressed saplings age and size are often poorly correlated, tending to follow a triangular relationship (Schulze et al. 2005).

Using the amount and size of deadwood as sole indicator may potentially be misleading (see also Chap. 8 by Harmon, this volume). First, dead wood stocks often exhibit a U-shaped pattern over succession (Harmon et al. 1986; Kimmins 2003). Since most stand-initiating disturbances (including fire) do not remove coarse woody material, early stages of succession are often characterised by high loads of large-sized legacy dead wood – both standing and downed – of all decay classes. The structural characterisation of dead wood in terms of size, abundance

and decay state is therefore not a good indicator of old-growth conditions unless accompanied by additional information on stand structure and history. For example, if age distribution data suggest a long period without stand-replacing disturbances, the presence of strongly decayed large-sized coarse woody detritus ensures that single tree mortality and gap opening has been a stand feature for an extended period of time.

Second, because of elevated decay rates in warm and humid climates, deadwood stocks in tropical forests are generally low. Using the coarse woody debris database compiled by Mark and Janice Harmon[1], we calculated that median coarse woody detritus (CWD) decomposition rates, k, in tropical regions below 25° latitude are 0.221 year^{-1} (10%–90% percentile: 0.053–0.607 year^{-1}, $n = 32$), i.e. a factor six higher than decay rates in the extra-tropics [0.038 year^{-1} (0.009–0.127 year^{-1}); $n = 179$]. These decay rates translate into deadwood lifetimes (time after which 95% of the original material has decayed) of 14 years in the tropics versus 80 years outside the tropics. With a given input of deadwood I and decay constant k, the equilibrium stocks of CWD can be simply calculated as I/k (Olson 1963). It follows that, even if we assume double input in the tropics, CWD stocks in the tropics are still lower by a factor of three than in temperate and boreal zones.

Finally, static structural definitions fail where changes in structural attributes are a characteristic feature of a particular forest ecosystem. Forests subject to recurring surface fires exhibit very different spatial patterns and size and age distributions depending on the timing of the last fire event (Sannikov and Goldammer 1996; Wirth et al. 1999; Spies 2004; Spies et al. 2006).

2.2.2 Successional Definitions

2.2.2.1 Criteria

An important criterion grounded in succession theory was given by Oliver and Larson (1996), according to which the term *true* old-growth "*describes stands composed entirely of trees which have developed in the absence of allogenic processes*". In its original meaning, the term *allogenic* refers to all external processes freeing available growing space, as opposed to *autogenic processes*, where changes in available growing space are caused by plant interactions (Tansley 1935). In the above definition – although not explicitly stated – *allogenic processes* refers to large-scale disturbances like fire, harvest or major wind-throw, which have the potential to reset secondary succession, but excludes external continuous forcing such as changes in climate. Secondary succession usually starts with pioneer species that possess a suit of traits enabling them to colonise and thrive on disturbed ground – high output of far-travelling seeds, seedlings with high desiccation and high-light

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[1]http://afoludata.jrc.it/carboinvent/cidb_cwdgdb.cfm

tolerance, high nutrient acquisition rates and growth rates, to name only a few (Horn 1974). Fast growth rates are often realised at the expense of chemical defence and/or mechanical stability, with the consequence that pioneers are mostly short-lived (Loehle 1998). One way to interpret the above criterion is to define true old-growth as the phase after which this first cohort of pioneers has disappeared and the stand is taken over by mid- and late-successional species that arrived later (true old-growth in Fig. 2.2a). Using the average life-time of temperate and boreal pioneer species given in Wirth and Lichstein (Chap. 5, this volume; see also Fig. 2.7), this is the case after about 100–150 years in the respective biomes. In the tropics, pioneers turn over even faster and the old-growth phase may be reached already after 80 years (Lieberman et al. 1985; Laurance et al. 2004). However, one could argue that mid-successional species are also "delayed pioneers" that profit indirectly from conditions created by allogenic processes, and that may not be able to persist under true old-growth conditions. With this interpretation, the true old-growth stage would commence much later. In any case, the successional concept of Oliver and Larson, (1996) clearly focusses on processes leading to old-growth, namely the replacement of early- (or mid-) by late-successional species. This concept ignores structural aspects and does not contain any statements about the absolute size and age of stands. To apply successional criterion data on forest composition and establishment, history of trees is required. Other successional definitions highlight processes that maintain old-growth, such as the type of prevailing disturbances (presence of small-scale and absence of stand-replacing disturbances), gap phase or nurse-log regeneration, or high shade tolerance of dominant species (Mosseler et al. 2003).

2.2.2.2 Limitations

Oliver and Larson's (1996) successional criterion for old-growth requires that the initial post-disturbance cohort of trees is replaced by tree species capable of gap phase regeneration. This definition is problematic in forest successions containing long-lived pioneer species. These share several features of typical pioneers (colonising ability, high light requirements and tolerance) but may well live for 300 years and more (Peet 1992; Lusk 1999; Spies 2004). Hence, they may still be present in old stands that meet most structural criteria for old-growth. They are often found in forest communities of xeric habitats (e.g. species of the genera *Pinus*, *Quercus, Juniperus*) but may also occur on mesic sites (e.g. species of the genera *Picea, Fraxinus, Liquidambar, Pseudotsuga, Nothofagus*). In boreal and high-elevation forests, late-successional species of the genera *Abies* and *Picea* often invade disturbed areas simultaneously with broad-leaved pioneers of the genera *Betula* and *Populus* (Schulze et al. 2005). Such late-successional species act as long-lived pioneers that undergo an initial phase of suppression and will eventually replace themselves. Under all these circumstances, stands would enter the true old-growth stage *sensu* Oliver and Larson (1996) only very late (>300 years) after the long-lived pioneers have also been replaced (true old-growth in Fig. 2.2b). An extreme case is presented by very old (~400 years), even-aged Scots pine stands
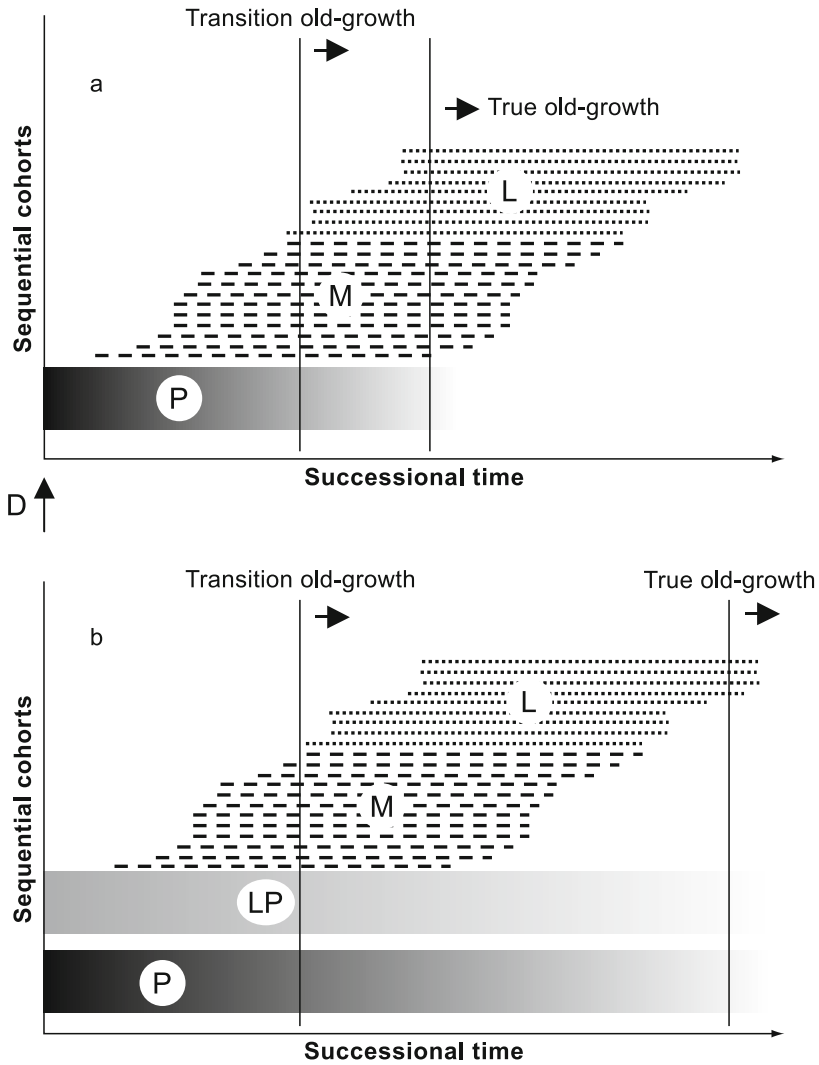
Fig. 2.2 a,b Conceptual illustration of successional criteria of old-growth. According to Oliver and Larson (1996), the true old-growth stage is reached when all individuals have regenerated in the absence of allogenic processes initiating stand development. **a** Immediately after a stand-replacing disturbance the site is colonised by pioneers (*P*). After some time the first individuals of mid-successional species (*M*) become established, followed by late successional species (*L*) later on. True old-growth conditions are reached when the regeneration wave of pioneers has disappeared. For transition old-growth, a minor component of pioneers is acceptable but late-successional are already an important component of the stand. **b** True old-growth conditions are reached much later if long-lived pioneers (*LP*) are present in the mixture. The onset of the transition old-growth stage is not affected

(a typical pioneer species) on sandy soils in boreal Eurasia where surface fires keep out fire-sensitive late-successional species (Wirth et al. 1999). As a 'soft' version of the successional definition, Oliver and Larson (1996) introduced the term *transitional* old-growth (Fig. 2.2a,b), which characterises the phase where a reduced number of pioneer individuals may coexist with mid- and late-successional species in advanced stages of succession. The application of this term mitigates some of the problems mentioned above, however at the expense of definitional clarity, because the start of the phase of transitional old-growth is difficult to determine.

2.2.3   Biogeochemical Definitions

2.2.3.1   Criteria

Biogeochemical criteria are undoubtedly the most difficult to apply and therefore also the least reported. Examples of biogeochemical criteria that have been listed as indicative of old-growth conditions are closed nutrient cycles, reduced tree net primary production (NPP), zero net accumulation of biomass, and increased understorey vegetation.

2.2.3.2   Limitations

Even if one were to agree that a decline in NPP, a biomass equilibrium and closed nutrient cycles are in fact indicative of old-growth conditions (but see Chap. 21 by Wirth, this volume), the quantification of almost all of these parameters is extremely labour-intensive and requires expensive instrumentation and extended observation periods (Sala et al. 2000). For example, the quantification of net primary productivity involves, as a minimum requirement, the measurement of tree ring widths and wood density of stems, branches and coarse roots, the estimation of foliage and fine-root biomass and turnover, a full stand inventory, and the development of suitable allometric equations for scaling up of sample tree information (Lauenroth 2000; Sala and Austin 2000; Clark et al. 2001). In short, biogeochemical criteria represent typical results of multi-year ecosystem studies and thus certainly do not qualify as easy measures for identifying old-growth forests.

Besides such practical considerations, there is a more philosophical objection against including functional attributes as part of a definition. In science, a definition is useful when it allows the scientist to unambiguously identify an object that, in a second step, may become subject to a more detailed characterisation. In the context of this book, biogeochemical functions represent 'response variables' (see below) and should not be confused with criteria defining the term 'old-growth'.

2.3   Use of the Term "Old-Growth" – a Literature Survey

According to the philosopher Karl Popper (1994) it is not the definition that dictates the application of a term, but rather the application of a term that shapes its definition. Thus, as an alternative to conducting a scholarly analysis of existing definitions as done above, it is also instructive to analyse how scientists and land-managers actually use the term *old-growth* and – most importantly – whether they use the term at all. Definitional problems are usually aggravated by the fact that there are related terms that are commonly used and confused. Scoping the ecological literature, we find a plethora of competing terms in the most diverse contexts: ancient, antique, climax, frontier, heritage, indigenous, intact, late-seral, late-successional, natural, original, over-mature, pre-settlement, primary, primeval, pristine, relict, untouched, virgin. This list is not exhaustive and there is neither the space nor the necessity to discuss each of these terms individually. Ignoring subtle differences they fall broadly into two groups (Fig. 2.3). The first group specifies forests or forest
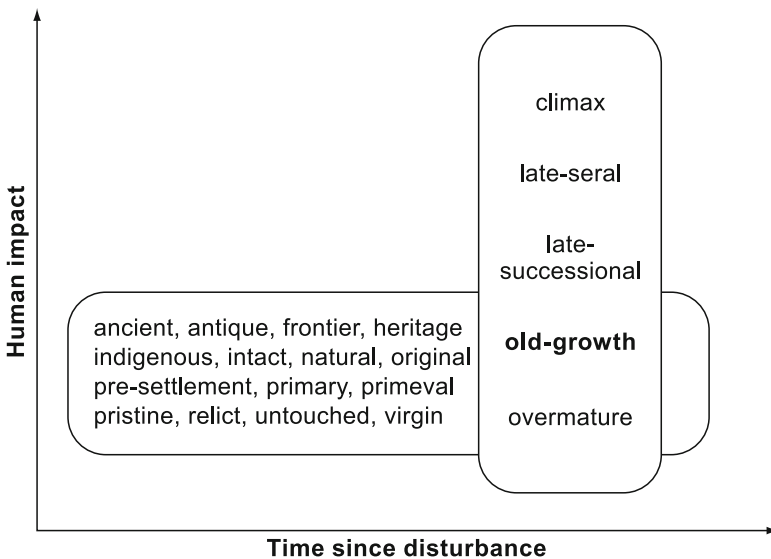
Fig. 2.3 The most important terms used in the context of forest conservation that may be used erroneously in place of 'old-growth'. The terms are arranged in a semantic space defined by two axes: degree of human impact (*y*-axis) and time since the last stand-replacing disturbance (*x*-axis). The majority of terms (*horizontal box*) describe stands that have been subject to very low levels of human impact for an extended period of time. This includes stands of any age and time since disturbance. On the other hand, the terms in the vertical box denote stands that have reached a certain age or late successional stage and that may or may not have been impacted by humans. For example, old-growth stands may originate from a planted stand developing after clear-cut. In this book we use the term 'primary' to characterise the former, and the term 'old-growth' to refer to the latter category

landscapes that have never or only rarely been impacted by humans. The second group is closer to the definition of old-growth and emphasises the fact that forests are relatively old. Whenever we want to refer to the former category we will use the term 'primary' in this book. We surveyed the Web of Science database to address the following questions: How often is the term old-growth used in relation to potentially competing terms? Has the terminology changed over time? Does the terminology differ between ecological sub-disciplines and scientific communities? Finally, how old are forests that were labelled 'old-growth' really?

Covering three time periods (1940–1960, 1970–1980 and 1995–2005), we searched for papers containing the keyword 'old-growth' (or 'old growth') and the seven most common competing terms: 'natural', 'pre-settlement', 'primary', 'primeval', 'pristine', 'relict', 'virgin'. Next, we screened all abstracts and selected only those studies that addressed the topics conservation, general ecology, and ecosystem science. This resulted in a total of 2,153 papers for the three periods. For each paper we recorded the home country of the main author based on the author's address. It should be noted that this is not necessarily the country where the study sites were located, but rather specifies which regional scientific community the main author belongs to. Where given in the abstract, forest ages associated with old-growth stands were recorded. Hereby, we distinguished between estimated stand ages and age thresholds. If a range of stand ages was given we calculated the central value as (min + max)/2. This analysis ignores studies that are not listed in the Web of Science and those published in languages other than English (e.g. the majority of European publications on forestry prior to 1950 were published in German, French, or Russian).

If we first look at the development of the total number of publications over time we observe a slight increase in the number of publications from 9 per decade between 1940 and 1960, to 46 per decade between 1970 and 1980, followed by a sudden jump to 2,089 per decade between 1995 and 2005 (Fig. 2.4a, top panel). This does not necessarily mirror the real trend in paper output as the Web of Science coverage of publications is certainly higher today than in the 1950s. However, the recent explosion in paper output is certainly not consistent with the general law of information science, according to which the body of literature in the natural sciences doubles every 10 years. We may thus speculate that this current boom can also be ascribed to a renewed interest in, and an increasing awareness of the threat to, old-growth forests.

In the 18 early studies published before 1960, the term old-growth was used only once in a paper on molluscs (Jacot 1935). The most common term in those days was 'virgin' forest ($n = 13$; Fig. 2.4a). Although in its original meaning 'virgin' merely means untouched by humans, most studied forests clearly qualify as old-growth in a contemporary sense (Morey 1936; Meyer and Stevenson 1943; Oosting and Billings 1951; Oosting and Reed 1952; Grier et al. 1992). In the 1970s the percentage of studies referring to old-growth increased to 39%, closely followed by 'natural' forests (37%); 13% used the term 'primeval' and only 9% referred to 'virgin' forests. Today (1995–2005) 'old-growth' has become the most widely used term, occurring in 62% of all publications; 13% still use the term 'natural' and all other
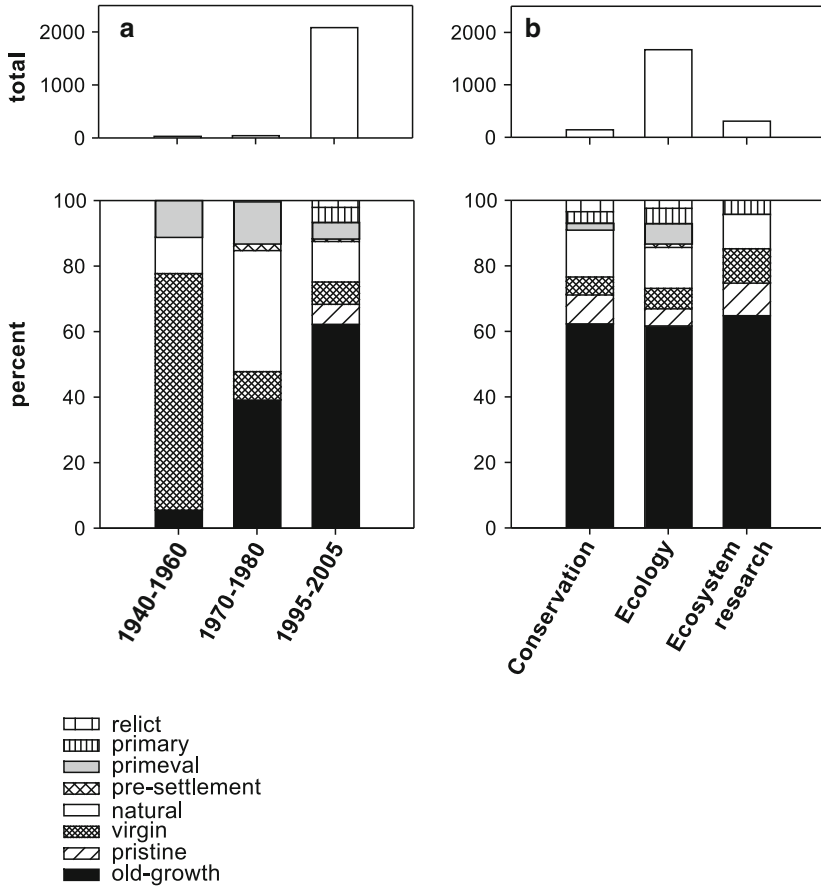
Fig. 2.4 Literature analysis based on 2,153 publication from three periods (1940–1960, 1970–1980 and 1995–2005). **a** Temporal development of the usage of the term 'old-growth' in relation to seven competing terms: 'natural', 'pre-settlement', 'primary', 'primeval', 'pristine', 'relict', 'virgin' (lower panel, see *key*). **b** Comparison of the three ecological sub-disciplines conservation, ecology and ecosystem research with respect to usage of the term 'old-growth' in relation to the seven competing terms. The top panels show the absolute numbers of publications

terms are used only occasionally. The increase in importance is probably due to the fact that many of the pivotal papers on the definition of old-growth were written only recently (Wells et al. 1998; Kneeshaw and Burton 1998; Mosseler et al. 2003; Gratzer et al. 2004).

While there were only subtle differences in the use of terms between the three disciplines conservation biology, general ecology and ecosystem science (Fig. 2.4b), the terminology spectrum depended strongly on the first author's nationality (Fig. 2.5). The great majority of North American publications (80%) used the term 'old-growth'. The same is true for Scandinavian countries (N-Europe), Australia and New Zealand, Chile, Argentina, and Japan – all countries with
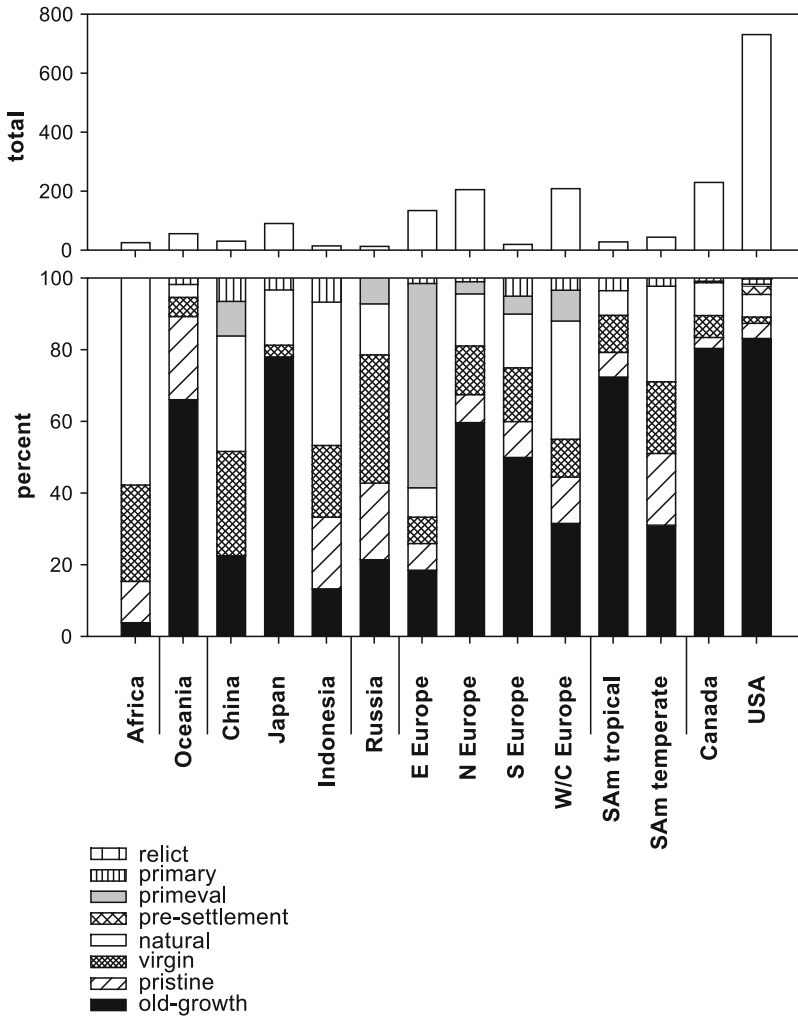
Fig. 2.5 Regional comparison of the usage of the term 'old-growth' in relation to the seven competing terms 'natural', 'pre-settlement', 'primary', 'primeval', 'pristine', 'relict', and 'virgin'. Regions were assigned based on the address of the first author, which may differ from the actual location of the study site. *E* Eastern, *N* northern, *S* southern, *W/C* western/central, *SAm* South America

close relationships to the United States scientific community. Taking Chile as an example, we find that out of the 17 relevant publications 13 were co-authored by United States scientists and the remaining 4 included Juan J. Armesto, who received his PhD in the United States, as a co-author. Authors from Central and Western European countries rarely used the term 'old-growth', most likely because forests meeting the criteria for old-growth barely exist here and can only be studied abroad (see Chap. 15 by Schulze et al., this volume). However, this is not true for the

Eastern European countries and Russia, which do possess remnants of 'old-growth' forest and yet do not use this term. Instead the term 'primeval' is preferred; this is clearly due to the fact that the famous Biatowieźa National Park in Poland carries the attribute 'primeval' in its name (Biatowieźa Primeval Forest). Of 135 Eastern European investigations, 91 were conducted in Biatowieža. Another region where the term 'old-growth' is rarely used is the tropics (Africa, tropical Latin America, and Indonesia). First of all, only a few studies ($n = 86$) exist where the first author resides in a tropical country. Of these 86 studies, only 17 used 'old-growth', while 33 used the term 'natural'. We speculate that this is because old-growth conditions are nothing special in the tropics and thus need not be emphasised (see Fig. 2.7).

Finally, we wanted to know the stand age of forests that were labelled as 'old-growth'. Altogether we identified 118 studies where ages of old-growth forests were reported, half of which were temperate or high-elevation coniferous forests and 25 were communities dominated by Douglas fir (*Pseudotsuga menziesii*), one of the classical 'majestic' old-growth species in the north-western United States. Old-growth forest ages ranged from 50 to 1,150 years (Fig. 2.6). The youngest 'old-growth' stand was a mangrove stand (Bird et al. 2004), and the oldest a montane
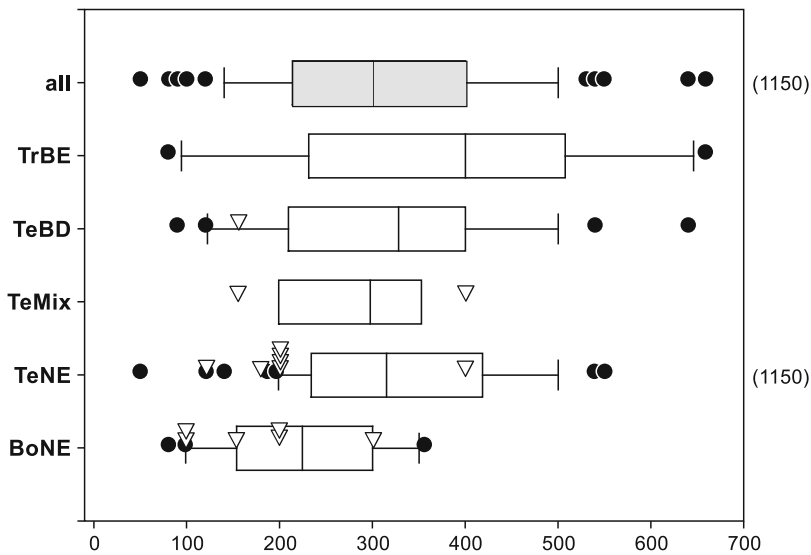
Fig. 2.6 Age range for forest stands reported to be in the old-growth stage separated according to forest type: *BoNE* boreal needle-leaved evergreen ($n = 14$), *TeNE* temperate needle-leaved evergreen ($n = 41$, this group contains also temperate rainforest and high-elevational conifer stands), *TeMix* temperate mixed forest ($n = 4$), *TeBD* temperate broad-leaved deciduous ($n = 14$), *TrBE* tropical broad-leaved evergreen ($n = 7$). *Boxes* interquartile range; *error bars* 10%- and 90%-percentile range for forest types with $n > 6$; *filled circles* outliers; *open triangles* papers making reference to age thresholds, e.g. claiming that any stand older than x years was considered old-growth; *values in brackets* extreme values

fir-hemlock forest on the coast of British Columbia (Parish and Antos 2004). The median age of all forests was 300 years with an inter-quartile range of 210–400 years. This corresponded to the old-growth ages of the three temperate forest types with median ages close to 300 years (temperate needle-leaved: 315 years; temperate mixed: 289 years; temperate deciduous: 313 years). Boreal old-growth forests were somewhat younger (median age 224 years, inter-quartile range 150–300 years), whereas tropical old-growth forests tended be older (median age 400 years, inter-quartile range 230–508 years). This is surprising as the analysis above suggested that tropical forests reach the old-growth stage much earlier, and they are also more common than boreal forests. To further examine why several studies ($n = 19$) identified stands younger than 200 years as old-growth we had a closer look at the species composition. Against our expectations, most stands were dominated by long-lived species. Extreme cases of suspiciously young 'old-growth' forests are 60- to 120-year-old oak stands (Laiolo et al. 2003), a 100-year-old boreal Norway spruce stand (Dahlberg et al. 1997), and a 110-year-old Balsam fir stand (Sturtevant et al. 1997). There seemed to be reasonable agreement between reported age thresholds and actual stand ages. The overall median threshold across forest types was 200 years, which corresponded quite well with the lower quartile range of 210 years. This is in agreement with the minimum age criteria developed for the western United States, which ranges between 150 and 200 years (Wells et al. 1998).

2.4 Old-Growth and the Disturbance Spectrum

The relationship between the disturbance regime and the occurrence of old-growth forest is so fundamental that it deserves a separate discussion. Depending on their severity, disturbances may promote or destroy old-growth. In the following, we will discuss the importance of both the temporal and spatial scale of disturbances on old-growth forest occurrence in the world's largest forest biomes.

2.4.1 Temporal Scale

In most forest types, irrespective of the definition applied, it may take several centuries before old-growth conditions develop. At the same time, forest landscapes are subject to stand-replacing disturbances such as wildfires, wind-throw, insect infestations or harvest, which terminate the old-growth stage or development towards it. Obviously, the potential of a forest region to host old-growth forests depends on two rates: (1) the time it takes for old-growth to develop, and (2) how often succession is set back by disturbances. In the following we will develop a simple theoretical framework to quantify this potential for different forest types based on data on species longevities and disturbance regimes obtained from the literature. Adopting the successional definition despite its limitations, we define the

time to reach true old-growth conditions, t_{og}, as the time it takes for the initial cohort to disappear. As an estimate of t_{og} we use the maximum longevity of typical pioneer tree species (Lieberman et al. 1985; Ellenberg 1986; Burns and Honkala 1990; Nikolov and Helmisaari 1992; Laurance et al. 2004). Imagine that we know the distribution of stand ages on the landscape. In this case the fraction of old-growth can be calculated as the fraction of stands older than t_{og}. The stand age distribution in turn depends on the typical recurrence of stand-replacing distur-bances (Johnson and Gutsell 1994). If each parcel of land is equally likely to be disturbed in any given year, the age distribution follows a negative exponential distribution. The cumulative probability distribution of stand ages is given by

$$F(t_{sd}) = 1 - \exp(-t_{sd}/t_{di}) \qquad 2.1$$

where t_{sd} is the time since the last stand-replacing disturbance, i.e. the forest age in years and t_{di} is the mean disturbance interval in years. The fraction of old-growth, f_{og}, is then calculated as

$$f_{og} = 1 - F(t_{sd} = t_{og}) \qquad 2.2$$

Figure 2.7 illustrates how the predicted old-growth fraction depends on the values of the time to reach the old-growth phase, i.e. in this case the pioneer longevity, and the mean interval of stand-replacing disturbances. Onto this response surface of f_{og} we projected a number of exemplary forest types with their specific median values and quartile ranges for t_{og} and t_{di} compiled from a range of studies (for references see legend of Fig. 2.7). Ideally, the estimates of t_{di} include all types of stand-replacing disturbances (fire, wind, insects, etc.). However, such compre-hensive estimates were available only for a limited number of studies (Frelich and Lorimer 1991; Lorimer and Frelich 1994; Zhang et al. 1999; Schulte and Mladenoff 2005). For the boreal and tropical forest regions, we had to rely on data on fire return intervals only, which leads to an overestimation of the fractional old-growth area.

The fraction of old-growth predicted by our simple model forest ranges from 92% in the tropical forest of Central Amazonia to less than 1% in light taiga forests of the boreal zone. There is a clear latitudinal trend of an increasing old-growth fraction from boreal to temperate to tropical forests. Within the temperate biome, broad-leaved deciduous forests are predicted to exhibit higher fractions of old-growth (50–70%) than coniferous forests (10–50%). Within the boreal biome, dark taiga forests dominated by spruce and fir species have higher fractions than Canadian light taiga forests dominated by Jack Pine (*Pinus banksiana*) (30% vs <1%; see Chap. 13 by Bergeron et al., this volume, for a more comprehensive analysis of the North American boreal forests). Across the range of chosen forest types there was a significant negative correlation between the disturbance interval and pioneer longevity. The high old-growth fraction in the central Amazon results
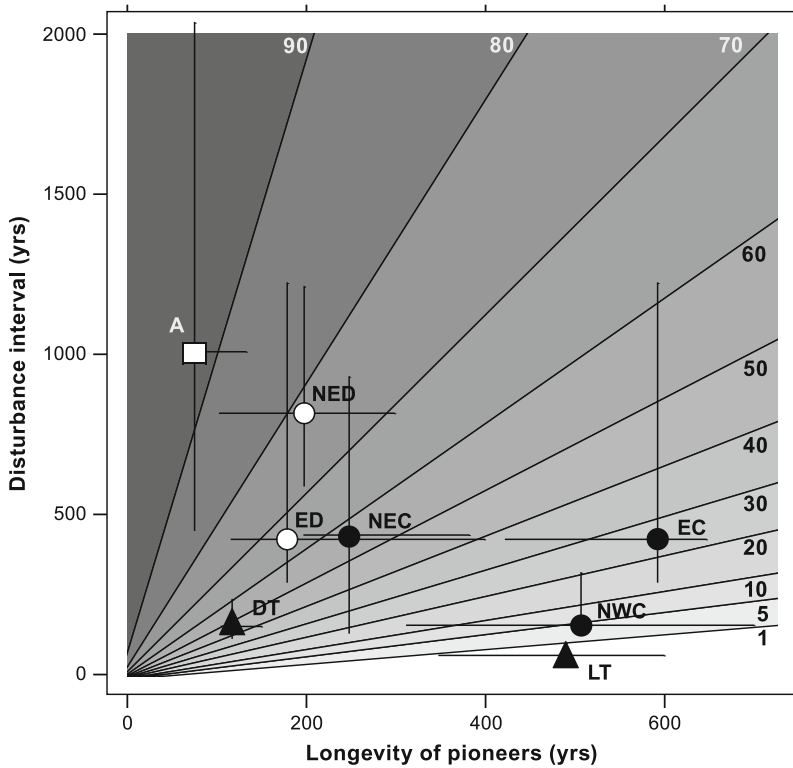
Fig. 2.7 Estimated percentage of old-growth forest under near-natural conditions (*shaded contours*) for a range of forest regions as a function of their characteristic stand-replacing disturbance regimes (*y*-axis) and the longevity of typical pioneer species (*x*-axis) as a measure of the time required to reach the old-growth stage. Individual regions: *A* Amazonia, *NWC* western coniferous forests of North America, *NED* eastern deciduous forest of North America, *NEC* eastern coniferous forest of North America, *ED* European deciduous forest, *EC* European coniferous forest, *DT* boreal dark taiga forests dominated by spruce or fir, *LT* boreal light taiga forests dominated by *Pinus banksiana*. Symbol colours indicate whether the late-successional stages are dominated by broad-leaved (*white*) or coniferous (*black*) tree species. Symbol types indicate the biome: *squares* tropical, *circles* temperate, *triangles* boreal. *Error bars* 20% and 80% percentiles of the literature data. Literature estimates of t_{og} and t_{di} were taken from the following sources: A (t_{og}: Laurance et al. 2004; Lieberman et al. 1985; $n = 12$; t_{di}: Sanford et al. 1985; Saldarriaga and West 1986; $n = 5$), *NWC* (t_{og}: Burns and Honkala 1990; $n = 18$; t_{di}: Wirth 2005; $n = 12$), *NED* (t_{og}: Burns and Honkala 1990; $n = 32$; t_{di}: Zhang 1999; Lorimer and Frelich 1994; Schulte and Mladenoff 2005; $n = 7$), *NEC* (t_{og}: Burns and Honkala 1990; $n = 11$; t_{di}: Zhang 1999; Schulte and Mladenoff 2005; $n = 13$), *ED* (t_{og}: Ellenberg et al. 1986; $n = 20$; t_{di}: FAO TBFRA 2000; $n = 5$), *EC* (t_{og}: Burns and Honkala 1990; $n = 7$; t_{di}: Burns and Honkala 1990; Wirth 2005; $n = 5$), *DT* (t_{og}: Ellenberg et al. 1986; Nikolov and Helmisaari 1992; $n = 5$; t_{di}: Wirth 2005; $n = 26$), *LT* (t_{og}: Ellenberg et al. 1986; Nikolov and Helmisaari 1992; $n = 6$; t_{di}: Wirth 2005; $n = 28$). Here, *n* refers to either the number of pioneer species (t_{og}) or the number of stand types or regions used to estimate the disturbance interval t_{di}

from a combination of very long natural disturbance intervals (>1,000 years) and the occurrence of short-lived pioneer trees with a mean longevity of 80 years. The other extreme is represented by light taiga forest dominated by *Pinus banksiana*. This species is a pioneer on fresh burns and may live for about 200 years, but the highly flammable forests it forms burn on average every 40–60 years (Lynham and Stocks 1991; Carroll and Bliss 1982). The fraction of old-growth in broad-leaved temperate forests ranges between 50% and 80%, with disturbance intervals and pioneer longevities of about 600 years and 200 years, respectively. The major simplification contained in these calculations is the assumption that each parcel of land is equally likely to be disturbed. In real complex landscapes this is never the case and Chap. 13 by Bergeron et al. (this volume) is devoted to illustrating the consequences of spatial and temporal variability of disturbance regimes for old-growth forests occurring in North American boreal forests. Nevertheless, the broad latitudinal gradient emerging for the three major forest biomes (excluding Savannah woodlands and Mediterranean forests), and the differences between coniferous and deciduous forests within the temperate biome, are probably robust. It is also important to realise that these findings are not dependent on the underlying successional definition of old-growth. Similar patterns would emerge if t_{og} was kept constant to represent a uniform age-threshold. For example, projecting all data points onto a vertical line at $t_{og} = 200$ years in Fig. 2.7 would still result in a latitudinal gradient.

2.4.2   Spatial Scale

The scheme of Oliver and Larson (1996) distinguishes only between stand-replacing disturbances and gap creation by single tree mortality. However, late-seral communities are often characterised by intervening partial disturbances, with gap sizes just large enough for successful re-colonisation of pioneer species (Lertzman and Fall 1998). Depending on which disturbance types and sizes are accepted under a given old-growth definition, these may become an important component of old-growth forest landscapes (Runcle 1981) or mark the start of a new secondary succession on patches. The spatial dimension may also become important in highly fragmented landscapes, where the natural course of succession is impeded by dispersal limitation of late successional species (e.g. Tabarelli and Peres 2002).

2.5   Identifying Old-Growth – the Conservation Perspective

According to a remote-sensing-based assessment initiated by Greenpeace, only 23% of the world's forests remain intact (see Chap. 18 by Achard et al., this volume), i.e. are not significantly impacted by humans and thus can be considered

primary forest (cf. Sect. 2.3, and Chaps. 17 and 18, this volume). It is primarily within these 23% of the world's forest area where we can expect to find contiguous parcels of old-growth forests. In the race against forest destruction and conversion, the need for practical solutions to old-growth identification arises for state agencies or non-governmental organisations (NGOs) engaged in forest protection seeking efficient methods to map old-growth forest remnants. Even if an all-encompassing, unambiguous definition was available, this would not necessarily lead to a fast and practical detection method. As shown above, obtaining a good estimate of a forest's age distribution – probably the most valuable type of data with which to identify old-growth conditions – is very labour-intensive and thus prohibitive if large areas are to be screened for old-growth forest. There are basically two options: (1) snapshot inventories of structural measures, and (2) remote-sensing (including aerial pictures). Structural features are easily quantified using standard forest inventory methods for live trees and standing dead trees, and fast methods are available for quantifying deadwood dimensions and stocks (van Wagner 1968). These data can be used to derive indicators of 'old-growthness', which can combine multiple thresholds of structural and successional criteria and weighting factors in a pragmatic way (Spies et al. 1988; Messier and Kneeshaw 1999). These become especially useful if data from more detailed studies are available for calibration. The few general principles depicted in such a rating scheme (relatively old, structure indicating gap-phase dynamics, presence of snags and logs resulting from single-tree mortality events – see the shortlist under Sect. 2.6 below) should hold everywhere, and it should be possible to adjust compositional criteria and dimensional thresholds to capture the variability in species pools[2], growth rates, gap persistence times and deadwood decomposition rates across the globe. While the use of simple measures is unavoidable for rapid screening, it is the consistent evaluation and interpretation of data that should be of prime concern. Unfortunately, work to harmonise existing old-growth inventories at an international level is yet to be done. For example, large inconsistencies emerged when several national datasets were compiled by the Taiga Rescue Network to quantify the spatial extent of the remaining old-growth forest in the Eurasian boreal zone (Aksenov et al. 1999). In Russia, old-growth forest is defined as "... *forests originated through natural successions unaffected by destructive human impact over a significant period of time ...*". According to the Scandinavian definition, they are characterised as "... *originating through natural succession with a significant contribution of old trees and dead wood often with a multi-layered stand structure ...*". Hence, according to the Russian definition every stand unaffected by human activity qualifies as old-growth, whereas the Scandinavian definition is closer to the structural definitions mentioned earlier and is thus more restrictive. As a consequence, in Russian provinces like the Komi Republic the 'old-growth' fraction is in the order of

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[2]See also Chap. 17 by Grace and Meir, this volume, in which they emphasise (Sect. 17.1) that many rainforests have the diagnostic characteristics mentioned above, in that they completely lack human impact. Therefore they distinguish old-growth secondary forests that have much of the general appearance of undisturbed forest, but lack some of the biodiversity.

15%, whereas in Scandinavia it is below 1% – despite the fact that the history, dynamics and composition of the forests are broadly similar. In comparison, remote-sensing-based estimates using satellite imagery are obviously unaffected by regional definitions and can be obtained globally using a consistent automated methodology. However, using satellite imagery it is not possible to identify old-growth forest per se but rather 'intact' forest regions with a high likelihood of hosting old-growth forests (see Chap. 18 by Achard, this volume). On a more regional scale, canopy structure can be resolved using aerial pictures, and old-growth forests can be identified based on the fraction and dimension of forest gaps (Piovesan et al. 2005).

2.6 Conclusions and Pragmatic Considerations

In Sect. 2.2 we introduced a range of criteria underlying existing old-growth definitions and highlighted – for heuristic reasons – some problems that arise when such definitions are confronted with methodological constraints as well as the structural and successional diversity one encounters in nature (cf. also Chap. 20, Sect. 20.3, this volume). It was decidedly not our goal to distil yet another 'better' definition of old-growth forests. Rather, we agree with Wells et al. (1998) who stated "… *that a single, precise definition of old-growth applicable to all forest types is neither possible nor desirable*". There seems to be an inevitable trade-off between the sharpness of the definition of old-growth and its general applicability. Attempts to identify clear quantitative thresholds after which a given forest succession enters the old-growth stage have failed (Hunter and White 1997). Recently, Spies (2004) presented a highly generic scheme that embraces the high diversity of old-growth forest characteristics with respect to development time, structure, grain size of patches and stability, but which – as is to be expected – does not provide a sharp definition. If we abandon the idea of one universal and unambiguous definition, the long list of criteria in Fig. 2.1 (this chapter) and Table 13.2 in Chap. 13 boils down to a few relative descriptors of true old-growth that are more or less captured by the list of Mosseler et al. (2003): (1) relatively old (existence of large old late-successional tree species with ages close to their life expectancy, and a mean age of half the longevity of the dominating trees), and (2) structural and compositional features witnessing self-replacement through gap-phase dynamics (uneven-aged, regeneration of shade-tolerant species, presence of canopy gaps, large snags and logs in varying stages of decay). Wherever necessary the individual chapter authors have further refined the definition to match their specific cases (Messier et al., Chap. 6, Bauhus et al., Chap. 10, Schulze et al., Chap. 15, Armesto et al., Chap. 16, Grace and Meir, Chap. 17, and Freibauer, Chap. 20).

   The literature analysis (Sect. 2.3) has shown that the ecological community seems to converge on preferring the term old-growth over related terms irrespective of the subdiscipline, but important regional differences remain. Recently, a number of reviews dealing with definitional aspects have been published and we can

anticipate that these accounts, together with our book project, will help avoid terminological confusion in future. The renewed interest in old-growth forests, especially in industrialised countries of the northern hemisphere has been sparked by an increasing awareness that land-use change and forest management have almost eradicated old-growth forest. In countries like the United States, Japan, China and European countries, true old-growth forests today make up less than 0.5% of the forest area, whereas the analysis in Sect. 2.4 suggested that under natural disturbance regimes we should expect about 50%. The same analysis has shown that, because of very long natural disturbance intervals and rapid successional change, old-growth conditions dominate in the tropics. Hence, deforestation in the tropics by and large means eradicating old-growth forest. Institutions and NGOs involved in the protection of old-growth or primary forests need fast and efficient survey methods and, given the land-use pressure on the remaining areas, they cannot afford to waste time with the laborious methods required to satisfy scientifically precise definitions (Sect. 2.5). Instead, they have to rely on proxy measures based on forest inventory data or remote-sensing imagery (see Chap. 18 by Achard et al., this volume). However, more detailed regional studies and ground-truth data are required to calibrate such proxies.

The central question pursued in this book is how forests in their late stages of succession differ from younger and/or managed forests in their functioning. The old-growth stage is the last in a series of four fundamental stages of forest development (stand initiation, stem exclusion, understorey reinitiation, old-growth; Oliver and Larson 1996) and thus serves as an important reference point for any analysis on age-related trends. However, there are two main reasons why in this book we do not focus exclusively on the old-growth stage:

1. Data on old-growth forests are generally scarce, especially when it comes to ecosystem processes. If we attempt to provide a comprehensive picture of old-growth forest functioning, we cannot afford to lose information by applying an overly strict definition. Many of the data presented in the following chapters will come from forest stands that are in advanced stages of forest succession, but do not qualify as old-growth in the strict sense. Whenever possible, we will therefore indicate whether the data come from mature, transition old-growth or true old-growth stands.
2. Another reason to adopt a broader definition and include transitional stages is to alleviate the 'time-axis' problem. If we want to quantify rates of biomass carbon accumulation or the dynamics of NPP over time, the stands have be arranged along an absolute time axis. However, it is inherent to the definition of true old-growth forests that signs of the event triggering stand initiation, which are needed to age the stand, have vanished. For example, in a chronosequence study on carbon dynamics in Douglas-fir stands, Janisch and Harmon (2002) were unable to determine the stand ages of old-growth stands and had to assign them an arbitrary high age of 500 years. Thus, including mature and transition old-growth stand of known stand ages gives us a better handle on depicting age-related patterns of important ecosystem functions.

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Chapter 3
Old Trees and the Meaning of 'Old'

Fritz Hans Schweingruber and Christian Wirth

3.1 Introduction

While the mere presence of 'old' trees does not automatically indicate old-growth conditions (see Chap. 2 by Wirth et al., this volume), it is fair to say that many old-growth forests contain a high number of trees close to their maximum longevity. Besides definitional aspects, tree longevity *per se* is a key demographic parameter controlling successional dynamics of species replacement, stand structure and biogeochemical cycles (see Chap. 5 by Wirth et al., this volume). This chapter takes a dendroecological perspective on tree longevity. The first part will explore differences in longevities between different life forms and will ask to what extent trees differ from herbs and shrubs and among each other (Sect. 3.2). The second part will discuss the mechanisms underlying the death of cells, tissues and whole plants (Sect. 3.3). It will be shown that the concept of death is problematic in the context of clonal plants, and that the inevitable presence of external mortality agents may bias our perception of biological limits of longevity.

3.2 Longevity of Conifers and Angiosperms

"After an individual becomes established, it must persist" (Weiher et al. 1999). The question remains: for how long? Undoubtedly, the oldest living beings on our planet are trees. The oldest trees look back on an individual history of almost 5,000 years, whereas most herbaceous plants persist for only a few years and some annuals die in the course of weeks. Apparently, longevity is highly variable among plants.

Reconstructing the age of an old tree is far from trivial because ring formation can be suppressed in stress periods or rings may be doubled in interrupted growing periods. In such cases, age determination requires the dendrochronological technique of cross-dating. As shown in Fig. 3.1, this simple method allows the
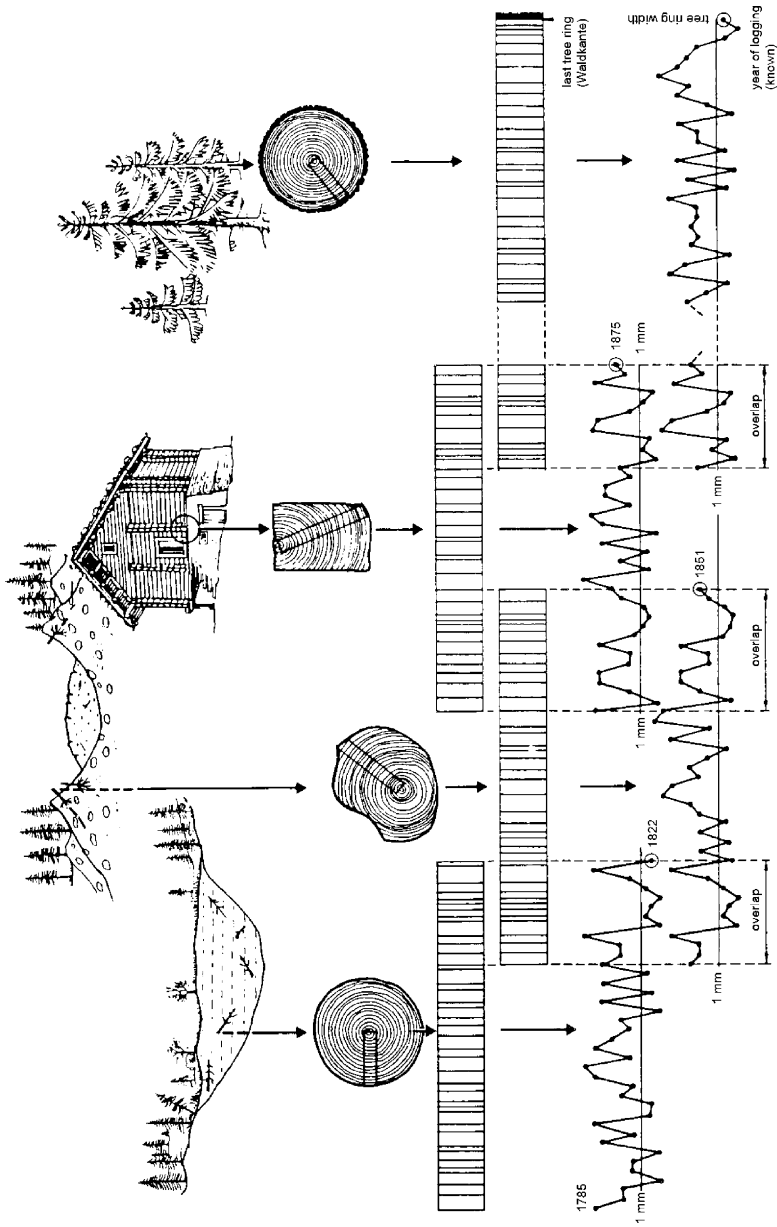
Fig. 3.1 Principle of dendrochronological cross-dating. The key to evaluating the calendar date of the last ring on a stem disk is the irregular distribution of extreme years, the so called pointer years (Schweingruber et al. 2006)

determination of felling dates of ancient woods as well as the age determination of living trees.

A selection of the maximum ages of some of the oldest trees (see Table 3.1) shows that the availability of data on tree longevity, determined by cross-dating, is not evenly distributed across the world. The list suggests that tree longevity itself is not strictly related to the climate. The hot spot of tree longevity is located in the mountain ranges of western North America, where many species reach an age of 2,000 years. In contrast, the Canadian boreal forest is characterised by remarkably short maximum longevities. Here, conifers rarely exceed an age of 400 years. The biogeochemical relevance of these differences in longevity is shown in the model study presented in Wirth et al. (see Chap. 5 by Wirth et al., this volume). However, low longevities are not a feature of boreal forests in general, as some larches in the Eurasian subalpine zones and the boreal taiga are over 1,000 years old. The Eurasian Stone pines (*Pinus cembra* and *Pinus sibirica*) can probably also reach that age, but relevant dendrochronological data are missing. Spruces, firs, and deciduous trees do not exceed a maximum lifespan of 500 years. In this context, it is interesting to note that the oldest *artificial* tree, a cross-dated tree ring sequence composed of different individuals of central European living and subfossil oaks and pines is 12,460 years old (Friedrich et al. 2004).

Information on the maximum longevity of shrubs is very limited, but it seems that they are generally shorter-lived than trees (Schweingruber 1995) and dwarf-shrubs (see below). The oldest known shrubs grow in Siberia. Hantemirov et al. (2003) found an 840-year-old *Juniperus sibirica*. Dendrochronological analyses in a dry temperate *Quercus pubescens* forest in the Swiss Jura mountains revealed that the age of the root stocks of several shrub species capable of resprouting is usually much higher than the age of the shoots. For *Cornus sanguinea* the ages of the root stock and the shoots were 35 years and 5 years, respectively; for *Ribes alpinum* the relationships was 62 vs 10 years; and for *Lonicera xylosteum* 48 vs 12 years.

More is known about the maximum longevities of dwarf shrubs. According to Kihlman (1890), Callaghan (1973) and Schweingruber and Poschlod (2005), the oldest individuals may reach maximum ages of up to 200 years (Table 3.2). Even a small, delicate plant such as *Dryas integrifolia* has been found to live for at least 145 years. In general, individuals of dwarf shrubs older than 50 years are not rare in subalpine and sub-Arctic environments.

Within the group of herbs, the age of the whole plant can be determined only in species that form a taproot – this being the only structure where all rings are preserved. In clonally growing rhizomatous plants, counting of annual rings in the rhizomes allows the age of currently present tissues to be determined, but not the age of the whole plant. The maximum ages of tap-rooted herbs are well known for western Europe (Schweingruber and Poschlod 2005). As for the dwarf shrubs, the herbaceous species with highest longevities grow in the subalpine and alpine zone. We found 50 annual rings in *Trifolium alpinum*, 43 in *Draba aizoides*, 40 in *Minuartia sedoides* and 32 in *Eritrichium nanum*. The maximum age of the majority of tap-rooted herbaceous plants in the lowlands is between 1 and 6 years.

Table 3.1 Selection of maximum (extreme) tree ages. Sources: Old-list, Rocky Mountain Tree-Ring Research (http://www.rmtrr.org/oldlist.htm), and tree-ring data-bank (http://www.wsl.ch), Dendrochronological laboratories of P. Gassmann, Neuchatel, Switzerland, and H. Egger, Boll, Switzerland

Species	Location	Maximum age (years)
Pinus longaeva	Wheeler Peak, Nevada, USA	4,844
Pinus longaeva	Methusela Walk, California, USA	4,789
Fitzroya cupressoides	Chile	3,622
Sequoiadendron giganteum	Sierra Nevada, California, USA	3,266
Juniperus occidentalis	Sierra Nevada, California, USA	2,675
Pinus aristata	Central Colorado, USA	2,435
Pinus balfouiana	Sierra Nevada, California, USA	2,110
Juniperus scopulorum	Northern New Mexico, USA	1,889
Pinus balfouriana	Sierra Nevada, California, USA	1,666
Pinus flexilis	South Park, Colorado, USA	1,661
Thuja occidentalis	Ontario, Canada	1,653
Pinus balfouriana	Sierra Nevada, California, USA	1,649
Taxodium distichum	Bladen County, North Carolina, USA	1,622
Thuja occidentalis	Ontario, Canada	1,567
Pinus flexilis	Central Colorado, USA	1,542
Juniperus occidentalis	Sierra Nevada, California, USA	1,288
Pinus albicaulis	Central Idaho, USA	1,267
Pseudotsuga menziesii	Northern New Mexico, USA	1,275
Juniperus occidentalis	Sierra Nevada, California, USA	1,220
Lagarostrobus franklinii	Tasmania, Australia	1,089
Pinus albicaulis	Alberta, Canada	1,050
Larix decidua	Valais, Alps[a]	1,081
Thuja occidentalis	Ontario, Canada	1,032
Cedrus atlantica	Atlas, Morocco[b]	1,024
Pinus edulis	Northeast Utah, USA	973
Pinus ponderosa	Wah Wah Mountains, Utah, USA	929
Pinus monophylla	Pine Grove Hills, Nevada, USA	888
Pinus albicaulis	Western Alberta, Canada	882
Pinus ponderosa	Central Utah, USA	843
Pinus nigra	Vienna, Austria[c]	833
Picea engelmannii	Western Alberta, Canada	780
Pinus cembra	Alps, Austria[d]	775
Larix sibirica	Ovoont, Mongolia	750
Pinus ponderosa	Northwest Arizona, USA	742
Pinus mugo ssp. *uncinata*	Pyrenees, Spain[e]	732
Larix lyalli	Western Alberta, Canada	728
Pinus ponderosa	Black Hills, South Dakota, USA	723
Pinus monophylla	White Pine Range, Nevada, USA	718
Pinus cembra	Carpathians, Romania[f]	701
Picea glauca	Klauane Lake, Yukon, Canada	668
Abies magnifica var. shastensis	Klamath Mountains, California, USA	665
Pinus siberica	Tarvagatay Pass, Mongolia	629

Pinus jeffreyi	Truckee, California, USA	626
Picea glauca	Aishihik Lake, Yukon, Canada	601
Pinus strobiformis	San Mateo Mountains, New Mexico, USA	599
Taxus baccata	Jura, Switzerland[a]	550
Picea abies	Jura, Switzerland[a]	576
Picea glauca	Norton Bay, Alaska, USA	522
Fagus sylvatica	Abruzzi National Park, Italy	503
Fagus sylvatica	Jura, Switzerland[a]	500
Abies lasiocarpa	Southern Yukon, Canada	501
Quercus petraea	Jura, Switzerland[a]	480
Acer pseudoplatanus	Jura, Switzerland[a]	460
Picea abies	Alps, Switzerland	455
Quercus petraea	Bern, Switzerland[g]	428
Quercus robur	Jura, Switzerland[a]	400

[a]Personal communication, P. Gassmann
[b]Personal communication, J. Esper
[c]Personal communication, M. Grabner
[d]Personal communication, K. Nicolussi
[e]Personal communication, U. Buentgen
[f]Personal communication, I. Popa
[g]Personal communication, H. Egger

3.3 What Limits the Life Span of a Tree?

Different aspects of ageing have been discussed in a number of reviews. A summary is given in Schweingruber and Poschlod (2005). Most studies to date focus on physiological aging processes and refer to parameters at the level of cells, tissues or organs, while processes relevant at the level of the whole plant are usually ignored (Thomas et al. 2003; Zentgraf et al. 2004; Schweingruber et al. 2006).

3.3.1 Programmed Cell Death

The process of secondary growth in trees involves the continuous formation and death of cells. Programmed cell death creates a diverse array of cell longevities. Taking the xylem as an example, tracheids and vessels formed very early in the growing season may live for only a few days, while the same cell types formed later may survive for months. In general, however, all water-conducting tissues die at the end of the growing season. Non-conducting fibres normally die after cell-wall thickening is finished. Their lifespan is short and rarely exceeds 1 year. In contrast, most parenchyma cells are longer-lived. Axial and vertical parenchyma cells in the sapwood may live for several years. The maximum age of living ray cells in *Robinia pseudoacacia* is 4–6 years and up to 130 years in *Sequoiadendron giganteum*.

Table 3.2 Selection of maximum ages of dwarf shrubs according Kihlman (1890), Callaghan (1973) and Schweingruber and Poschlod (2005)

Species	Location	Maximum age (years)
Rhododendron ferrugineum	Subalpine belt, Alps, Switzerland	202
Dryas octopetala	Banks Island, Canada	45
Loiseleuria procumbens	Subalpine belt, Alps, Switzerland	110
Vaccinium vitis-idaea	Heathland, Finland	109
Salix myrsinithes	Tundra, Kola, Russia	99
Arctostaphylos alpina	Tundra, Kola, Russia	84
Empetrum nigrum	Tundra, Kola, Russia	80
Helianthemum nummularium	Subalpine belt, Alps, Switzerland	66
Globularia cordifolia	South exposed rock, Switzerland	60

Trees face the problem that they can grow taller only by progressively putting on new cell layers around the entire surface of the stem. Over the years, this leads to the accumulation of a massive body of woody tissue, which, if containing live, respiring parenchyma cells (usually around 7% and 16% of the sapwood volume in conifers and hardwoods, respectively; White et al. 2000) would inevitably drain the energy resources of the tree even under the most favourable growing conditions due to the fact that the surface of assimilating foliage increases more slowly with size than the wood volume. To overcome this problem, old parenchymatic cells die and excrete fungicidal phenolic substances (Fig. 3.2). This protects the interior dead woody tissues from microbial decomposition, which is important in maintaining the mechanical stability of the tree [Fig. 3.3; but see Thomas (2000) for trees without true heartwood]. Often, this chemical impregnation of the heartwood goes along with a discoloration allowing us to distinguish macroscopically the coloured heartwood from the pale "living" sapwood.

The design of a tree crown is largely the product of cladaptosis, the die-back of twigs and branches. The process of cladaptosis is crucial for a trees ability to forage for light. It enables the tree to abscise branches that run into a negative carbon balance due to self-shading and light competition with neighbours. Some species, such as oaks and poplars, show a weak and almost unlignified zone at the base of the twigs, which acts as a predetermined breaking point (Fig. 3.4). Other species actively form a barrier zone at the base of their twigs to cut the twigs off from the water supply. As a consequence they dry up and drop off after a few months or years.

3.3.2 Whole Plant Longevity – Internal Versus External Factors

There is little literature about the endogenous processes controlling the longevity of whole plants (Ricklefs and Finch 1995) and, if discussed, the focus is either on genetic components or on the mere quantification of mortality rates as a demographic parameter.
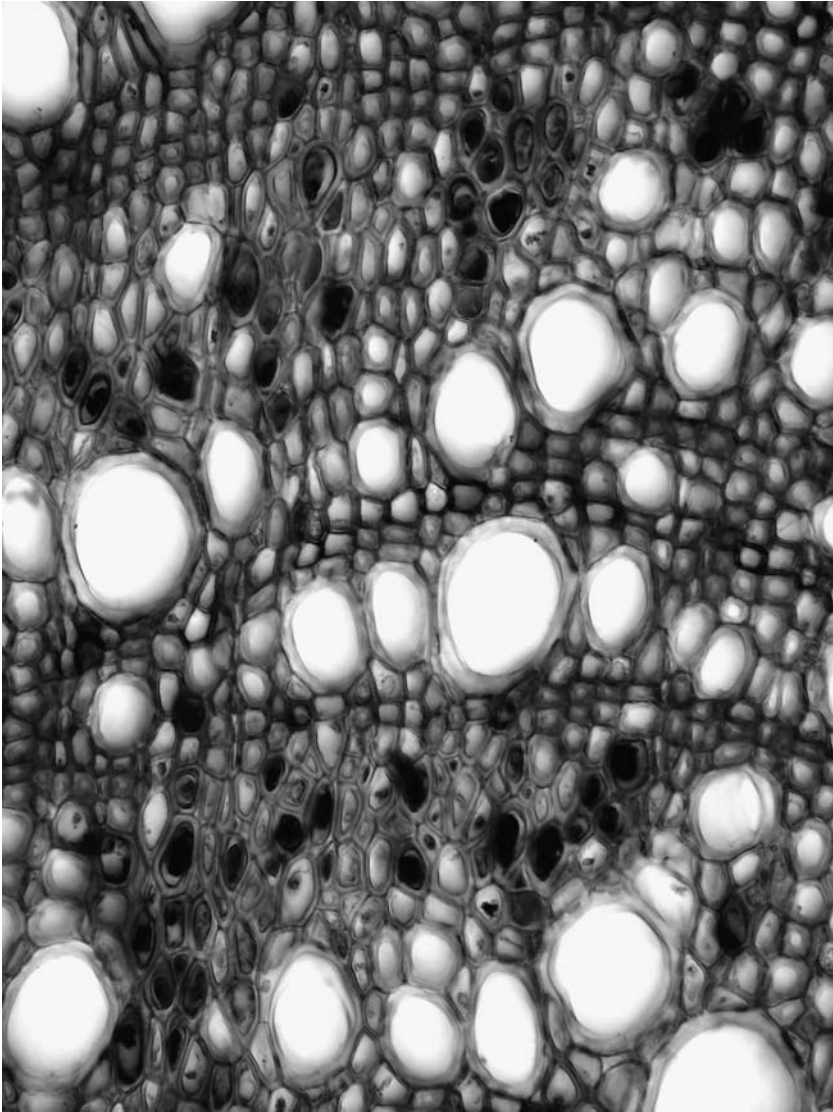
Fig. 3.2 Microscopic section through the heartwood of the dwarf shrub *Eriogonum jamesii*. Axial parenchyma cells contain dark substances, probably phenols

For herbs (with taproots – see above) the data allow us at least to distinguish between annual and perennial species (Schweingruber and Poschlod 2005). In addition, this latter study demonstrated that the life span of most herbs is definitely restricted to a few years, because the genetic potential excludes the possibility of reaching longevities in the order of decades (Fig. 3.5).
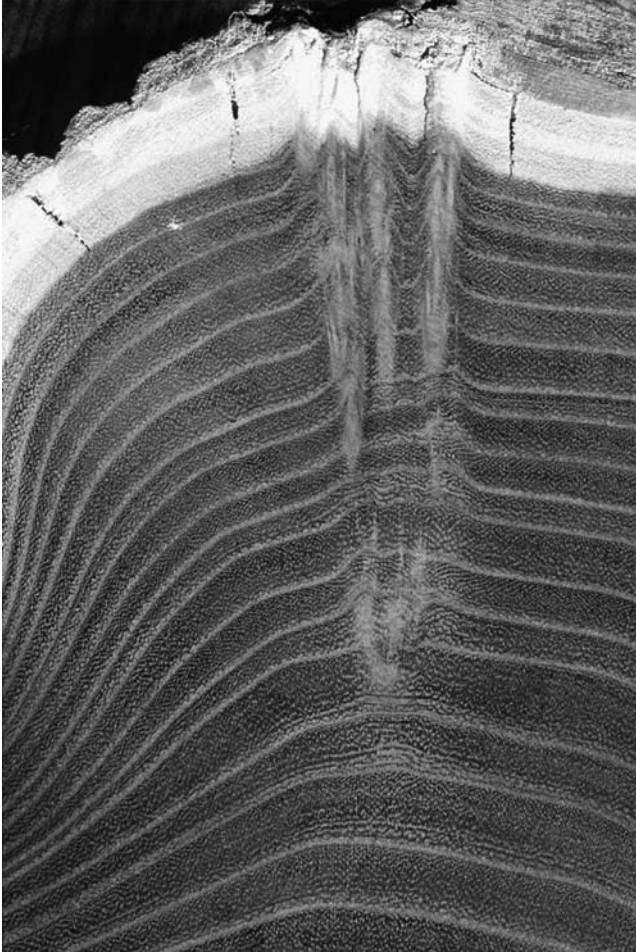
Fig. 3.3 Sapwood and heartwood in the xylem of a *Robinia pseudoacacia* stem. All cell types in the dark part (heartwood) of the stem are dead and contain phenolic, fungicide substances. Water transport and storage of assimilates occur in the light part (sapwood). Axial and vertical (ray) parenchyma cells are living

The genetic predisposition of whole plant death is difficult to evaluate in long-lived trees, because it would require long-term common garden experiments that would by far exceed human longevity. The collection of maximum tree ages given in Table 3.1 is rather arbitrary. Moreover, the available data probably underestimate maximum longevities. So-called "age hunters" tend to search for trees with particularly thick stems, but we know very well that size is an unreliable predictor for tree age. Quite on the contrary, maximum tree ages are much lower on sites with optimal environmental conditions. Dendrochronologists have often found

Fig. 3.4 Branches with scars of dropped twigs on *Quercus robur*. Crown formation is based on the existence of this process of cladaptosis

the oldest trees on marginal sites, where trees survive close to their ecological limit, e.g. in swamps or on shallow soils near the timberline. Such a negative relationship between site quality and longevity can be found in both 'annual' herbs and perennial trees. The 'annual' *Linum catharticum* completes its life cycle in 1 year only at optimal sites, but needs 3 years in the subalpine zone. The giant tree *Sequoiadendron giganteum* may grow for more than 3,000 years without any sign of senescence in its natural habitat in the Rocky Mountains, with ring widths remaining on average below 1 mm for centuries. In contrast, the same tree species grown in European plantations in a wet oceanic climate on deep soils has an average ring width of about 1 cm, but becomes very susceptible to wind storms. Thus, mortality seems to be correlated with size rather than absolute age.

Determination of maximum longevity becomes impossible in trees that reproduce clonally, such as poplars, willows and hornbeam. In these species, new ramets continue to sprout long after the initial stumps has decayed away. Even where the founder module is still present in the population of ramets, molecular methods may be required to actually identify it. This is illustrated by two examples: in the Canadian boreal forest, black spruce (*Picea mariana*) spreads vegetatively by
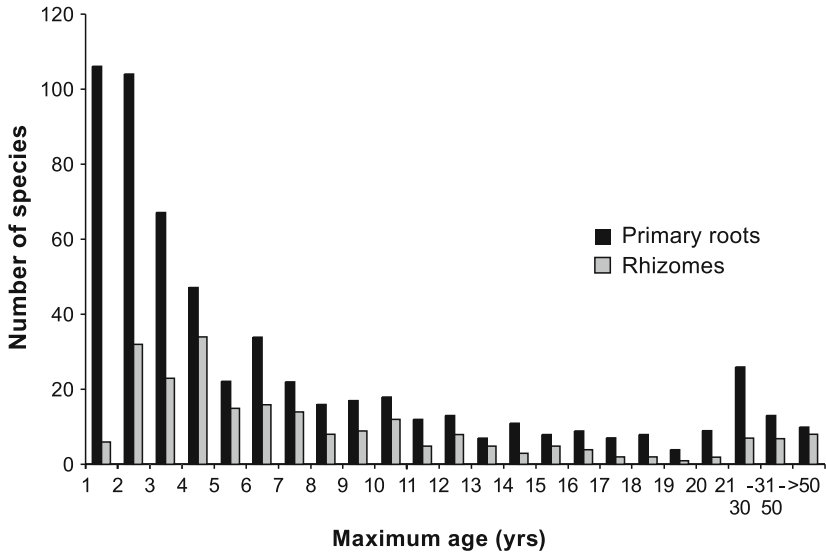
Fig. 3.5 Maximum ages of central European herbs and dwarf shrubs. *Black columns* Number of species with taproots roots (total of 603 species), *grey columns* species with rhizomes (total of 232 species); 63% of the species with taproots have a limited age between 1 and 6 years, and only of 8% of the plants have a lifespan that exceeds 20 years (Schweingruber and Poschlod 2005)

branch layering. A dendrochronological analysis revealed that a genet having regenerated from seeds after a forest fire may reach an age of at least 300 years (Legère and Payette 1981). However, molecular studies showed that a larger genet could even reach 1,800 years (Laberge et al. 2000). The oldest genet on earth is a polycormon of *Lomatia tasmanica* in Western Australia spread over 1.2 km^2. Charcoal buried next to fossilised leaves with the same genome as the contemporary trees was dated as being at least 43,600 years old (Lynch et al. 1998).

It remains an open question whether trees are in principal immortal or whether their genetic constitution limits their lifespan as is the case for herbaceous plants with taproots. The example of *Lomatia tasmanica* in fact suggests that clonal tree species are almost immortal. However, even for non-clonal trees we are unable to know for sure whether they would not live forever (or at least for much longer), if they were protected from disturbances and diseases. While we know very little about the endogenous controls of longevity, there are countless studies on how various external agents such as fire, wind, flooding, herbivory, pathogens, pollutants, etc. speed up senescence and reduce the lifespan of trees. In the following we can only briefly touch on this topic, and we do so only to emphasise that the influence of external mortality factors biases our view of tree longevity.

Based on the simple observation that ecological factors limit the existence of single trees, we have to accept the old idea that trees often die by exhaustion or starvation (Molisch 1938), e.g. due to a lack of light (Fig. 3.6) or energy (i.e. summer temperatures; Fig. 3.7) or a shortage of water (Bigler et al. 2006). This
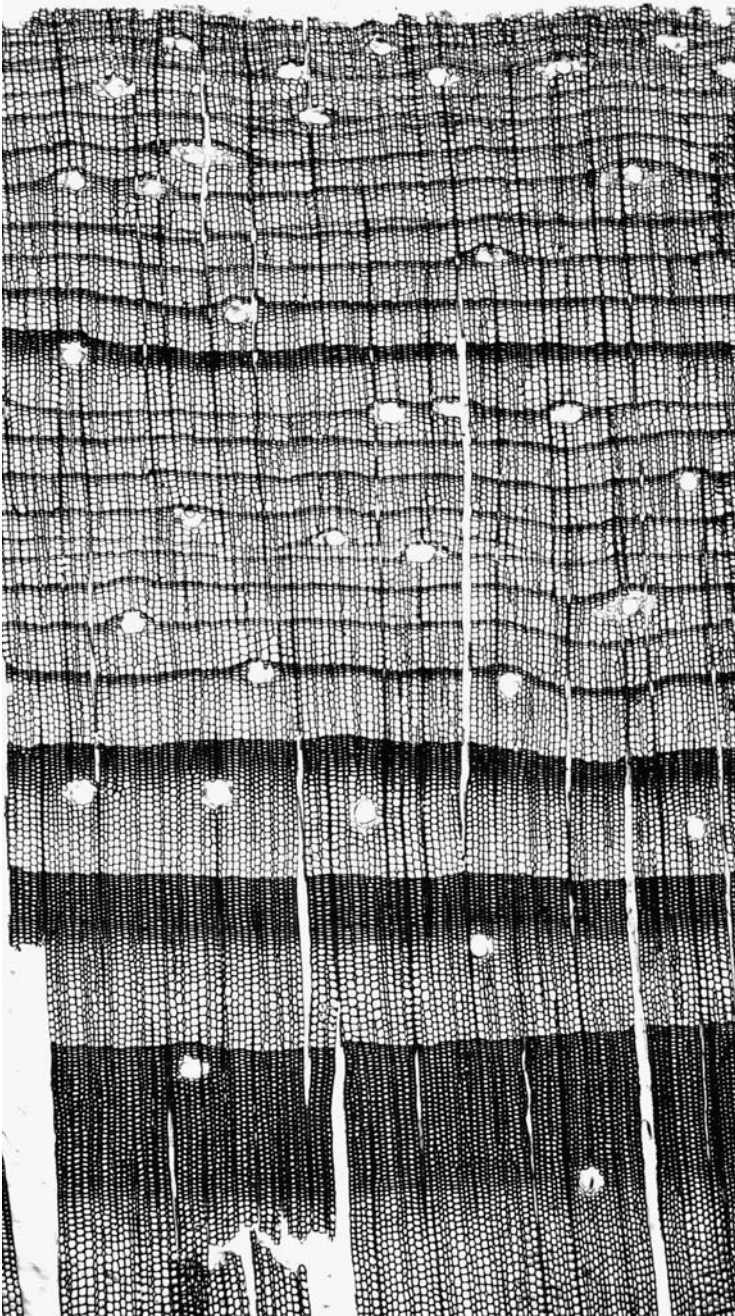
Fig. 3.6 Starvation due to light shortage. Competitive beeches have suppressed the crowns of pines (*Pinus sylvestris*) and induced their death. The starving period is indicated by the narrow rings with small latewood and the enhanced frequency of resin ducts in the pre-lethal period

Fig. 3.7 Dying at the beginning of the Little Ice Age between 1430 and 1450 AD. Stands of larches (*Larix sibirica*) died at the timberline in the Polar Ural. The stumps have remained and have been dated dendrochronologically (Shiyatov 1992)

may lead to false conclusions about the longevity of species. For example, maximum longevities reported in the literature for the Eurasian *Betula pendula* range between 120 and 140 years (Nikolov and Helmisaari 1992). However, Schulze et al. (2005) recently found individual trees older than 300 years. One reason for the low literature estimates may be that birches, as typical pioneer trees, tend to be outcompeted by tall-statured late-successional species already after about 100 years. Thus, the majority of birches dies early as a result of light starvation and not because they have reached their biological limit. Older individuals may simply have been overlooked. Another example was already mentioned above: old trees are very rare in the Canadian boreal forest. However, this is determined not only by the biological age limit of the tree species, but also by the circumstance that in the North American boreal forest lethal crown fires recur on average every 100 years (see Chap. 13 by Bergeron and Harper, this volume, and Wirth 2005). Toxic substances, for example, sulphur dioxide from anthropogenic pollution sources can kill trees, but we have also found that the reaction to poisonous agents depends on the species and may vary even between individuals. Trees at the borderline of the catastrophic sulphur contamination in the downwind area of Norilsk (Siberia) clearly show species-, individual-, and site-dependent mortality: larches (*Larix sibirica*) in all ecological situations were dead, whereas spruces (*Picea obovata*) and birches (*Betula pendula*) growing at the same ecological sites were either dead, or had reduced foliage or even looked healthy. Spruces in the most intensive contaminated regions survived as dwarfs in moist riverbeds between healthy looking sedges (Schweingruber and Voronin 1996, see Fig. 3.8).

Biological degradation caused by mammals, insects, nematodes and fungi affects different species in different ways (Thomas and Sadras 2001). A morphological expression of the different sensitivities towards herbivory of pathogen

Fig. 3.8 Death due to anthropogenic pollution near a smelter in Central Siberia (Norilsk). Extremely high SO_2 content in the air leads to selective tree death. The most sensitive species are larches (*Larix sibirica*); spruces (*Picea obovata*) and birches (*Betula pendula*) are less sensitive. Within Siberian spruce there are also intra-specific differences in sensitivity: some individuals die, but some manage to survive high doses of toxic gases

attack is the formation of barrier zones (Schweingruber 2001, see Fig. 3.9). Longitudinal barriers are, for example, weak in birch and ash, but very effective in beech and maple (Dujesiefken and Liese 1991).

A few years ago there was a great hope that tree-ring curves would allow the prediction of individual lifespan. Indeed, there is strong evidence that the risk of mortality is negatively correlated with growth and that the shape of this relationship differs between trees with low and high shade tolerance (Kobe et al. 1995). However, it is too simple to assume that a reduced growth period in adult trees

Fig. 3.9 Formation of a barrier zone after mechanical wounding of the cambial zone. The zone below the wound was laterally compartmentalised by the formation of a toxic barrier zone. Fungal decay occurs only in the part below the wound, all other parts are protected by the barrier zone. *Arctostaphylos uva-ursi*. 40x

would indicate senescence. Very narrow ring sequences simply indicate a transient period of starvation and, as such, are a reversible feature of tree growth (Fritts 1976). Moreover, tree death may occur abruptly or gradually. Rapid death has often been observed in shade-intolerant species, whereas shade-tolerant species literally

Fig. 3.10 Mammoth trees (*Sequoiadendron giganteum*) represent tremendous carbon stocks and may live for 3,000 years
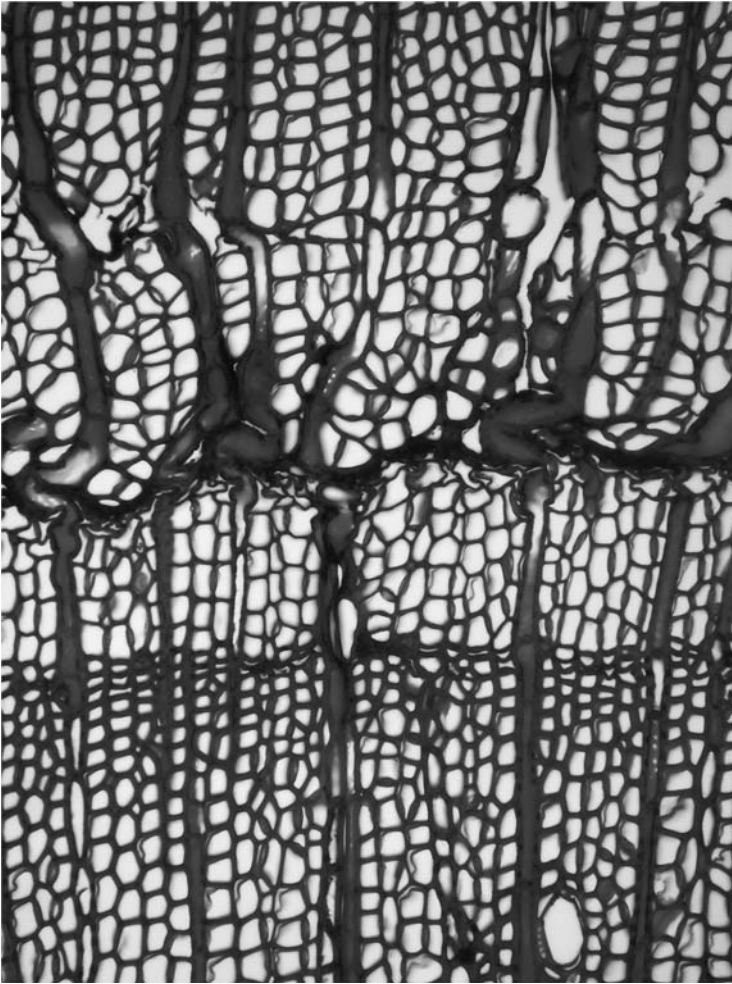
Fig. 3.11 Frost ring. The reaction to extreme low temperatures at the beginning of the growing season at the end of June 1601 in the Polar Ural was the formation of a frost ring. *Larix sibirica* (100x)

shrink to death on a branch-by-branch basis over decades to centuries. This variability in behaviour makes it impossible to use tree ring sequences to infer estimates of tree longevity or even to predict the expected duration until death.

In summary, the large range of longevities realised by trees makes it likely that a genetic predisposition in general determines longevity, but the real lifespan will always be modified by the environment. Thus, separating 'nature and nurture' in their effect on longevity will remain a difficult task.
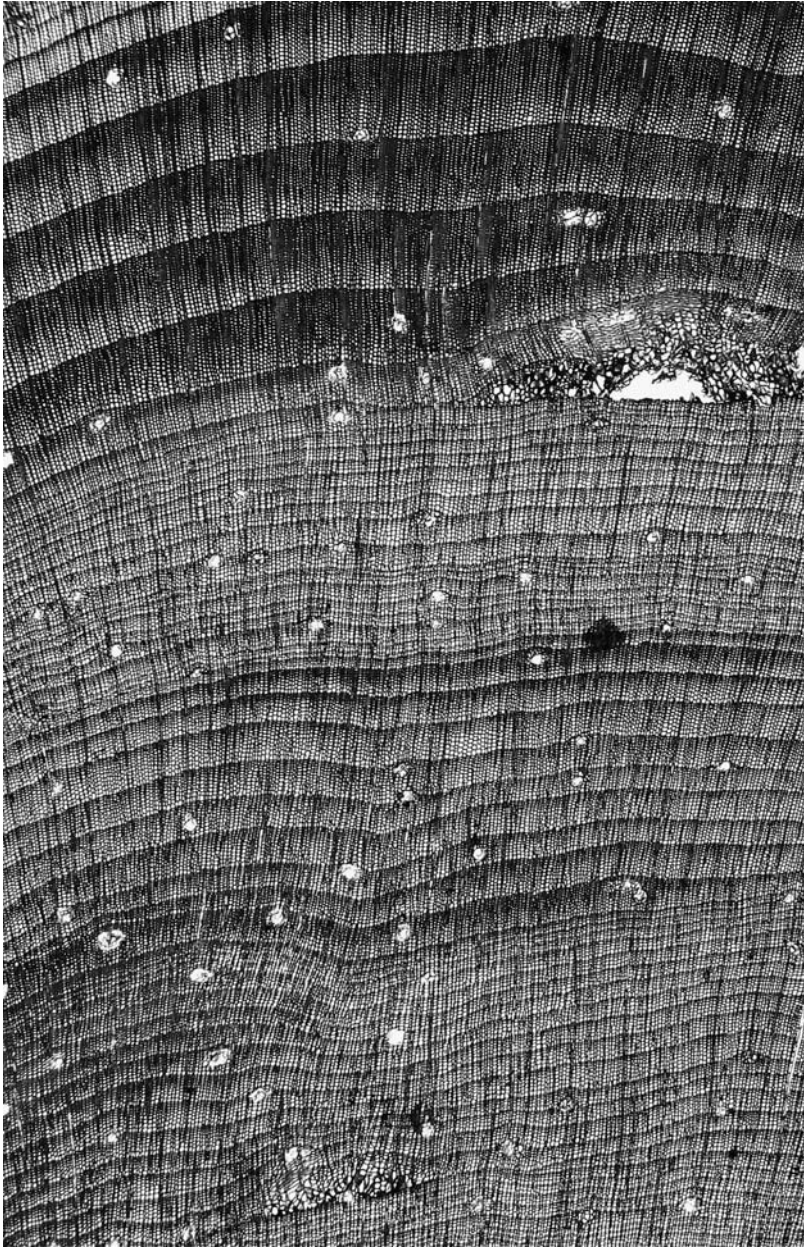
Fig. 3.12 The reaction to an extreme change in the position of a branch after being hit by a stone was the formation of a callus and compression wood. *Pinus mugo*. (20x)
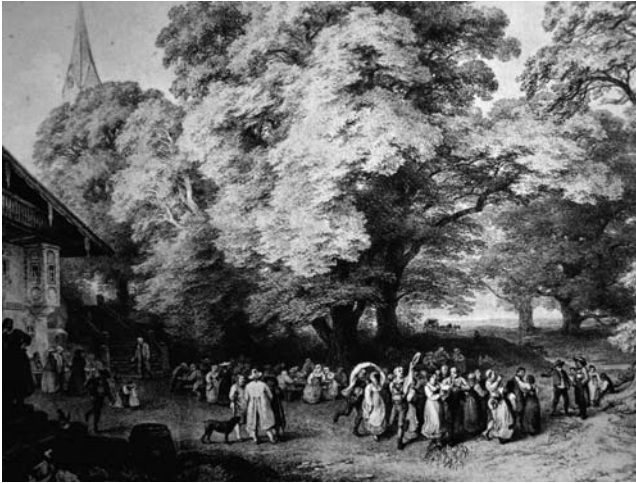
Fig. 3.13 People celebrating under the canopy of an old lime (Fischbach und Masius 1879)

3.4 Concluding Remarks

Within the plant system, and within the range of life forms, trees are very special. Thanks to their high longevity, trees may accumulate enormous amounts of biomass. The largest tree on earth, a *Sequoiadendron giganteum* contains 1,470 m^3 wood with a dry weight of 800 tons. One single tree contains approximately 400 tons carbon. These 'biological monsters' would not exist if they were not perfectly designed to resist extreme mechanical stress (Fig. 3.10).

The potential age of physically existing trees exceeds that of all other life forms. Old trees tend to be perfectly adapted to specific sites. In Europe, many old larches and stone pines at the alpine timberline germinated at the beginning of the Little Ice Age in the thirteenth century. They have survived many stress periods and are now benefitting from the current warming period. Since these 'living fossils' maintain the potential to regenerate generatively and, in many cases, also vegetatively, these trees are an indispensable genetic resource. Old trees do not lose their capacity to respond to the environment. Variations in the size of their cells and in the width of their tree rings demonstrate that even millennium-old trees maintain their biological sensitivity and their potential to react to environmental stress and favourable periods. Expressions of this reaction potential are e.g. scars, callus formation (Fig. 3.11), reaction wood (Fig. 3.12) and growth variations such as abrupt growth changes and pointer years.

Thanks to their longevity and their sustained sensitivity, old trees represent important archives of past climates. Dendrochronological techniques allow the reconstruction of annual climatic patterns and the occurrence of extreme weather events at both local and global level. In doing so, they provide a means of placing

the contemporary man-made climate warming into a historical context (Fritts 1976; Schweingruber 1995; Fig. 3.11).

Old trees have always fascinated people. Gollwitzer (1984) has summarised the evidence for the human fascination with old trees, which goes back at least 3,000 years: old trees were the seats of the gods. They stood at the centre of world religions and embodied myths. People celebrated and mourned under the canopy of old trees (Fig. 3.13). During the period of enlightenment in the seventeenth century, people began to study trees scientifically. Today, we still have not solved the puzzle of why trees become as old as they are. Only one thing is certain: the circumstance that so many tree species have gone extinct tells us that even trees do not live forever – as palaeontology shows us (Zimmermann 1959).

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Part II
Aboveground Processes

Chapter 4
Ecophysiological Characteristics of Mature Trees and Stands – Consequences for Old-Growth Forest Productivity

Werner L. Kutsch, Christian Wirth, Jens Kattge, Stefanie Nöllert, Matthias Herbst, and Ludger Kappen

4.1 Introduction

Trees increase their relative fitness to competing trees or to other life forms both directly and indirectly, by growing tall, as increased light interception increases photosynthesis (direct) and simultaneously making this resource unavailable to competitors (indirect). Consequently, trees that grow taller, larger, or have greater shading power may dominate smaller trees with less shading power. However, as trees become older and grow taller they face constraints that differ drastically from those experienced by smaller species or early ontogenetic stages. Falster and Westoby (2003), who used game-theoretic models to learn about the evolutionary background of tree height, summarised thus: '*height increases costs as past investment in stems for support, as continuing maintenance costs for the stems and vasculature, as disadvantages in the transport of water to height and as increased risk of breakage*'. No wonder that trees do not grow infinitely high. In general, absolute and relative growth rates tend to decrease with age and height. This decline in productivity – observed at both the tree and stand level – has been attributed to a range of processes, e.g., increasing respiratory demand and limitation of photosynthesis on the tree level, and, on the stand level, increasing sequestration of nutrients in slow-decomposing litter and ecophysiological differences between early-, mid- and late-successional canopies. This chapter will review these current hypotheses, first on the tree level, then the stand level, as well as in the context of successional changes of community composition.

4.2 Increased Respiratory Demand

A widespread hypothesis about the decrease in growth with tree age is based on the idea that higher respiratory demand limits resources for wood growth. Kira and Shidei (1967) first developed this hypothesis from empirical data over 10 years. It

became well accepted that forest production declines with age because woody respiration increases while gross primary productivity (GPP) remains constant or even decreases slightly. This idea was adopted by Odum (1969) in his well-known theory of ecosystem succession, which predicts that ecosystem respiration increases with community age and balances a slightly decreasing GPP until the difference approaches zero at steady state.

The net carbon yield of a tree depends on the ratio of assimilating organs to that of respiring tissues. Old and tall trees usually have a leaf-to-mass ratio (LMR = leaf mass per total tree biomass) of between 5% and 20%, with the remaining biomass in the stem, branches, and roots (Bernoulli and Körner 1999). The cost for maintaining these non-productive tissues may increase when trees grow taller. Especially for trees growing at high elevation, Wieser et al. (2005) have argued that, besides low temperatures and a short vegetation period, an imbalance in carbon-accumulating foliage versus respiring tissues might upset the carbon balance (see also Hättenschwiler et al. 2002). However, even though integrative studies have shown that the fraction of net photosynthetic production consumed by autotrophic respiration can vary between 30% and 70% (Sprugel et al. 1995; Luyssaert et al. 2007), no significant age effects on this ratio were revealed. The reason for this might be a decrease in activity (biomass-specific respiration rate) of accumulated woody tissue. Such observations oppose the traditional view that tree production decreases with age due to increasing respiratory demand. Moreover, several more studies have shown that a decrease in net primary productivity in old-growth forests – if it occurs – is related more to decreasing photosynthesis in old and tall trees (as well as in old-growth forest canopies) than to increasing respiratory demand (Ryan and Yoder 1997).

4.3 Limitations of Photosynthesis

The mechanisms that could lead to decreased photosynthetic income in high trees and old-growth forests are still unclear. The widespread hypothesis of hydraulic limitation will be discussed in the first part of this chapter. This more source-related mechanism will then be compared to the more sink-related mechanisms that have been introduced recently. At the end of the chapter we will return to the reduction of photosynthesis in the context of community composition, as late-successional species may show an imperfect acclimatisation to full sunlight.

4.3.1 Hydraulic Limitation

The basic assumption of the hydraulic limitation hypothesis (HLH) is that, as trees grow taller, gravitational potential, which increases by 0.01 MPa per metre of height (Fig. 4.1), and increased path length decrease leaf water potential (Fig. 4.2a)
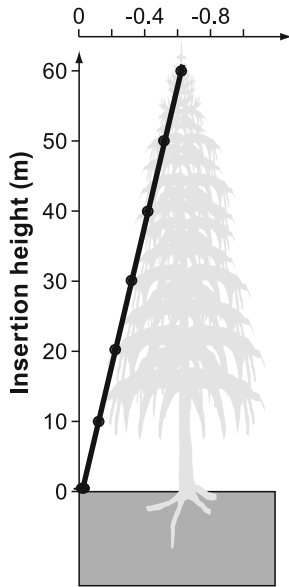
Fig. 4.1 The hydraulic limitation hypothesis (HLH) proposes decreased leaf-specific hydraulic conductance as trees grow in height. The figure shows the increase in gravitational potential with tree height. Trees have to overcome this potential to transport water to the leaves.
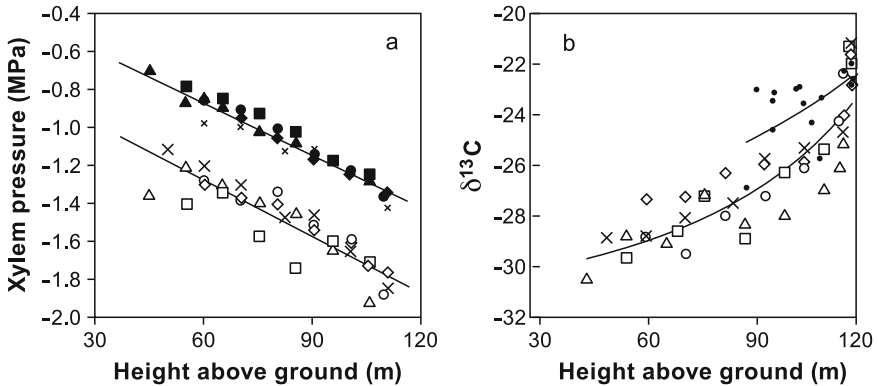
Fig. 4.2 a Xylem pressure of small branches measured at predawn (*upper group*) and midday (*lower group*) of redwood trees at Humboldt Redwoods State Park, California during September and October 2000. **b** Foliar carbon isotope composition ($\delta^{13}C$) of redwood trees at Humboldt Redwoods State Park, California increases with height within the crowns of 5 trees over 110 m tall, and among the tops (*filled circles*) of 16 trees from 85 to 113 m tall. Different symbol types denote different trees and are consistent in **a** and **b** (from Koch et al. 2004, with permission).

and, consequently, stomatal conductance. Promoters of the HLH usually employ a simplified Ohm's law analogy (Tyree and Ewers 1991) to provide a mathematical description of differences in stomatal conductance with height:

$$G_C = \frac{K_L \cdot \Delta\Psi}{D} \qquad\qquad 4.1$$

where G_C = canopy conductance for water vapour, K_L = hydraulic conductance from soil to leaf, $\Delta\Psi$ = soil-to-leaf water potential difference, and D = leaf to air saturation deficit. Since decreased stomatal conductance reduces photosynthetic uptake, Ryan and Yoder (1997) proposed the HLH as a mechanism to explain the slowing of height growth with tree size and the maximum limits to tree height. Barnard (2003) and Ryan et al. (2004) refined the HLH and stated that five necessary components have to be fulfilled: *'(1) stomata must close to maintain Ψ_{LEAF} above a minimum, critical threshold and this threshold must be the same for all tree heights; (2) stomata must close in response to decreased hydraulic conductance; (3) hydraulic conductance must decrease with tree height; (4) stomatal closure promoted by reduced hydraulic conductance must cause lower photosynthesis; and (5) reduction in photosynthesis in older, taller trees must be sufficient to account for reduced growth.'* The HLH has been widely discussed and has inspired a huge number of studies on tall trees during the past decade.

4.3.1.1 Empirical Evidence for the Hydraulic Limitation Hypothesis

4.3.1.1.1 Calculation of Hydraulic Conductance

The hydraulic conductance can be calculated either for a single leaf in a certain position in a tree or for the whole tree. In the first case, the hydraulic conductance is related to the insertion height of the leaf, in the second to the total height of the tree. In both cases the hydraulic conductance is related to the leaf area.

For a single leaf, the specific hydraulic conductance can be calculated from the following equation:

$$k_I = \frac{E_I}{\Psi_{\text{soil}} - pgh - \Psi_{\text{leaf}}} \qquad\qquad 4.2$$

where E_1 is the transpiration ; Ψ_{leaf} and Ψ_{soil} are leaf and soil water potential, respectively; ρ is the water density; g the acceleration due to gravity (9.81 ms^{-2}); and h the insertion height of the leaf (m). E_1 can be regulated by stomatal aperture. In order to compensate for the gravitational component, the leaf has to decrease its potential by the value of ρgh. Gradients of leaf water potential with tree height were indeed found in several studies (Waring and McDowell 2002; Koch et al. 2004).

Predawn measurements of Ψ_{leaf} during periods with high soil moisture reflect the gravitational potential very well (Koch et al. 2004), and therefore can be used to partition total water potential into 'gravitational' and 'non-gravitational' fractions (Waring and McDowell 2002; McDowell et al. 2002a, 2002b, 2005; Delzon et al. 2004). Correcting Ψ_{leaf} for the gravitational component ($\widetilde{\Psi}_{leaf}$, according to Delzon et al. 2004) allows direct calculation of $\Delta\Psi$ between soil and leaf and – in combination with transpiration measurements – of k_l. Whole tree hydraulic conductance (K_L) is usually estimated by relating sap flow measurements to water potential (e.g. Hubbard et al. 1999). Delzon et al. (2004) measured sap flow about 1 m below the live crown, and Ψ_{leaf} on leaves in the upper crown. Several studies have shown that K_L decreases as trees grow taller and age (Hubbard et al. 1999; Delzon et al. 2004).

4.3.1.1.2   Gas Exchange

Direct measurements of leaf gas exchange by means of infrared gas analysers with leaf-scale cuvettes may support the HLH if lower values of leaf net photosynthesis (A) and stomatal conductance (g_s) are associated with lower values of k_l. In most cases, neither photosynthetic capacity (A_{max}) nor leaf or needle nitrogen was reduced but increased stomatal closure caused a more sensitive response of A to reduced air humidity at greater heights in at least some studies (Yoder et al. 1994; Hubbard et al. 1999; McDowell et al. 2005). A decrease in stomatal conductance or increased stomatal sensitivity with height, which was also observed by Delzon et al. (2004), is commonly interpreted as a result of reduced hydraulic conductance.

4.3.1.1.3   Stable Isotopes

Another approach utilises the stable carbon isotope ratio ($\delta^{13}C$) of foliage, which is closely related to leaf gas exchange (Farquhar et al. 1989; Ehleringer et al. 2002). The discrimination against $^{13}CO_2$ by the CO_2-fixing enzyme increases with the leaf-internal CO_2 concentration. In conditions of low stomatal conductance the leaf-internal CO_2 concentration is reduced and, consequently, the $\delta^{13}C$ of assimilates is enhanced (Meinzer 1993; Flanagan and Ehleringer 1998). Accordingly, an increase in foliage $\delta^{13}C$ with tree size for individuals of the same species grown in similar environments (Fig. 4.2b) can be related to hydraulic constraints to gas exchange, and has been observed in many studies (Yoder et al. 1994; Hubbard et al. 1999; Waring and McDowell 2002; Phillips et al. 2003; Koch et al. 2004; McDowell et al. 2005; Schoettle 1994).

Overall, the results from these approaches indicates that height, and the resulting gravimetrical and hydraulic strain can burden photosynthetic uptake and possibly further growth of old and tall trees. However, it remains unclear whether hydraulic limitation is exclusively the reason for growth cessation in trees, in particular in trees that remain shorter than the theoretically calculated maximum tree height of about 120 m (Koch et al. 2004). Therefore, several reservations about the HLH have been formulated.

4.3.1.2   Reservations Against the Hydraulic Limitation Hypothesis

The most important argument against the HLH is the fact that trees can compensate for increased path length by changes in xylem structure, such as the production of xylem vessels with increased conductivity (Pothier et al. 1989). Xylem architecture varies between species and is very plastic within species or even within a single tree. Weitz et al. (2006) claimed that there is a general trend of tapering of conduit dimensions that might be regulated by a hormonal signal originating in the apices of tree branches. However, they described single vessel dimensions, whereas Mencuccini and Grace (1996), who worked on whole trees, reported a proportional increase of branch over stem wood sapflow area with age in Scots Pine, which can also be seen – at least partially – as hydraulic compensation. The formal hydraulic model of Whitehead et al. (1984) predicts compensation by a homeostatic balance between transport capacity and transpiration demand. Consequently, it was argued by Becker et al. (2000), that *'any path-length effects on water transport could be fully compensated if this was advantageous* to the plant'.

Another way of compensation is to decrease transpiring leaf area relative to xylem conductive area with height (Vanninen et al. 1996). Cochard et al. (1997) found for *Fraxinus excelsior* L., that the xylem resistance of single branches was correlated to their leaf area, thus keeping the leaf-area-specific conductivity constant. Several other studies showed adaptations in the leaf area to sapwood area ratio (A_L:A_S) in order to compensate for hydraulic or gravitational limitation (Waring and McDowell 2002; Delzon et al. 2004; McDowell et al. 2005) which results in a decrease in productivity, but on a whole plant or stand level.

Furthermore, trees can compensate by increasing the fine-root:foliage ratio (Sperry et al. 1998; Magnani et al. 2000) or by decreasing the minimum leaf water potential and consequently increasing the water potential gradient between soil and leaf (Hacke et al. 2000). In addition, a role in increased water storage in the stem for compensation is discussed (Phillips et al. 2003). Nevertheless, all these compensating reactions of tall trees are not 'for free' but are paid for by increased respiration costs.

4.3.2   Reduced Sink Strength

An alternative to the HLH and other theories that support source regulation, reduction of photosynthesis may also be induced by product inhibition of photosynthates. This kind of sink regulation can be explained by at least two mechanisms:

(1) Phloem transport may be reduced in tall trees because the resistance between source and sink also increases with distance. In-vivo whole-plant measurements have demonstrated that carbon flow rates are dependent not only on the properties of the sink, but also on the properties of the whole transport system (Gould et al. 2004; Minchin and Lacointe 2005).

(2) There is some evidence that old and tall trees cease later growth genetically. Given the fact that genetic programs were generated over thousands of generations, the cessation of height growth in old trees may be explained by the development of several mechanisms inducing a high risk/advantage-ratio when trees grow taller. The advantage is high-light supply for the highest trees, whereas the risks comprise mechanical damage due to windthrow or snowbreak, or climatic damage by frost or desiccation. As soon as a tree has grown taller than its neighbours, these risks will exceed the advantages of growing even taller. Understanding the evolution of height growth of trees in terms of risk (or cost)-to-advantage assessment in an uncooperative game (Falster and Westoby 2003), results in a high probability of genetic cessation of height growth and resulting sink reduction.

It is well known from leaf-level measurements that a reduction in sink strength results in an increase in starch and soluble sugars within the leaves followed by down-regulation of photosynthetic capacity (Equiza et al. 2006). Hoch et al. (2003) and Körner et al. (2005) showed that whole trees also exhibit high concentrations of storage carbohydrates, which suggests that growth is limited by the availability of sinks but not carbon supply (Day et al. 2001, 2002). Whether this lack of growth stimulus is related to an intrinsic genetic programme or progressive nutrient limitation is not known. The strong growth response of mature forests towards atmospheric nitrogen deposition in Europe may indicate the latter (Schulze 2000; Mund et al. 2002; Magnani et al. 2007).

4.4 Stand-Level Controls

Irrespective of the underlying mechanism, old and tall trees eventually reach a point where they become less efficient in assimilating carbon for growth per unit leaf area. To what extent this physiological response translates into individual-level growth performance, and eventually into stand-level decline in productivity, is still subject to debate (Gower et al. 1996; Ryan et al. 1997; Magnani et al. 2000; Weiner and Thomas 2001; Binkley et al. 2002). As pointed out in a seminal review by Ryan et al. (1997), stand-level net primary production could theoretically decline because of (1) a decline in assimilation rate at a given leaf area, or (2) a decline in total leaf area at a given assimilation rate. In the first case, the decline is driven purely by physiological changes (see above); in the latter purely by structural changes of the canopy, e.g. resulting from leaf abrasion or tree mortality. The 13 chronosequences presented by Ryan et al. (1997) clearly exhibited age-related decline of productivity at the stand-level. Stem growth peaked at the time of maximum leaf area, which, in this case, was after 29 ± 22 (SD) years. It is important to note that this very early onset of observed growth reduction rules out the notion that a physiological reaction to 'majestic' size or high age is the major driver of the stand-level decline in productivity sensu Ryan et al. (1997). In at least some chronosequences there was a post-peak decline in growth efficiency (i.e. stem-growth per unit leaf area), which

is why the authors argued that age-related decline results from both structural and physiological changes. However, the chosen chronosequences were by no means representative of the world's forests; all were even-aged monocultures, most of them were managed, and there was a strong bias towards shade-intolerant coniferous pioneers. These grow up quickly in a monolayer and respond strongly to crowding by down-regulating the stand-level leaf area. With productivity being closely related to leaf area index (LAI), the productivity peak may thus merely reflect the 'over-shooting' leaf area prior to the onset of self-thinning.

Recently, a new global database of forest productivity that comprises data from both chronosequences and individual stands has become available (Luyssaert et al. 2007). In addition to stand-level estimates of net primary productivity, the database contains details on the methodology, and a wide range of site descriptors that can be used as covariates or to filter and stratify the data. We used the database to model the aboveground and total net primary productivity (abbreviated ANPP and total NPP, respectively) as a linear function of LAI and stand age per se, thus separating physiological and structural effects. Because productivity and age are often confounded with site variables (stands become older on sites with more adverse growing conditions), we included two climate variables, mean annual temperature and annual precipitation, as additional predictors. All predictor variables were standardised to a mean of zero and a standard deviation of one. With this transformation, the intercept of the models is the productivity at the means of all predictors, and the absolute values of the coefficients reflect the explanatory strength of the respective predictors. For model simplification, we applied backward selection based on the Akaike Information Criterion. The best candidate models are presented in Table 4.1. The analysis was done separately for coniferous and broadleaved forests of the northern hemisphere. Mixed stands and stands subject to fertilisation or irrigation were excluded.

All four variables were significant predictors of ANPP in conifers. ANPP at the covariate means was 324 g C m^{-2} year^{-1}. Temperature had the strongest influence, followed by LAI (Fig. 4.3a) and precipitation. The negative effect of stand age, which was significant (at $\alpha = 0.05$) but relatively weak, indicated a slight decline in aboveground growth efficiency with age. In original units, this translates to 30 g C m^{-2} year^{-1} in 100 years. In comparison with ANPP, the total NPP was 1.6 times higher (intercepts 324 and 510 g C m^{-2} year^{-1}, respectively) and the four variables explained a higher fraction of the variance in total NPP (adjusted $R^2 = 0.50$ and 0.74, respectively). The importance of predictors decreased in the same order (temperature > LAI > precipitation > age, Fig. 4.3b again shows LAI as an indicator of ANPP). The similarity of the models for ANPP and NPP suggest that shifts in allocation from above- to below-ground NPP are of little relevance. For broadleaved forests, stand age was not a significant predictor of ANPP. The overall level of ANPP as reflected by the intercept was 506 g C m^{-2} year^{-1} and thus higher than in coniferous forests. The 'minimum model' contained only LAI and precipitation as predictors; the latter was not significant. The minimum model for total NPP was structurally similar, but the influence of precipitation was significant and the intercept was 1.35 times higher. The lower ratio of total to aboveground NPP

Table 4.1 Coefficients, significance level and indicators of model performance for the statistical analysis of aboveground and total net primary productivity (ANPP and NPP, respectively). Because all predictors were z-transformed prior to analysis, the absolute magnitude of the coefficients is indicative of their relative importance. *df* Degrees of freedom, *Std.err* standard error, *p* probability that coefficient equals zero, *LAI* leaf area index, P precipitation sum, T mean annual temperature, Age stand age

	Parameter	Std.err	t-Value	p	Parameter	Std.err	t-Value	p
ANPP		Coniferous forests				Deciduous forests		
Intercept	324.8	11.7	27.63	<0.001	506.8	21.2	23.9	<0.001
LAI	99.7	13.8	7.25	<0.001	93.1	21.6	4.3	<0.001
P	−81.9	17.1	−4.79	<0.001	32.9	21.6	1.5	0.131
T	137.4	16.5	8.33	<0.001	–	–	–	–
Age	−35.5	12.0	−2.96	0.0035	–	–	–	–
df	168				76			
Residual	154.6				188.2			
Adjusted R^2	0.510				0.216			
NPP		Coniferous forests				Deciduous forests		
Intercept	510.94	15.30	33.38	<0.001	697.9	25.2	27.7	<0.001
LAI	176.26	18.28	9.64	<0.001	97.7	25.7	3.8	<0.001
P	−55.39	25.92	−2.14	0.0348	93.0	25.7	3.5	<0.001
T	198.80	23.87	8.33	<0.001	–	–	–	–
Age	−43.68	16.00	−2.73	0.0075	–	–	–	–
df	109				75			
Residual	163.4				222.4			
Adjusted R^2	0.7385				0.287			

illustrates that broadleaved forests allocate less carbon to belowground productivity than coniferous forests, which dominate under harsher (drier, colder) growing conditions. In summary, differences in ANPP and NPP – when controlled for climate – were driven mostly by leaf area. This result suggests that structural changes leading to reduced displays of leaf area are more important than a deterioration in photosynthetic performance.

4.5 Community and Ecosystem Constraints on Age/Size-Productivity Relationships

Thus far we have been discussing the ecophysiological consequences of tree stature and age. Besides these two aspects of being a tall tree, major drivers of productivity, such as light, nutrient and water availability, may change significantly and predictably throughout the development of a single tree. Another aspect is that secondary successions usually involve species turnover, which in turn introduces a shift in the spectrum of relevant ecophysiological and morphological traits. In the following, we discuss these two aspects in more detail.
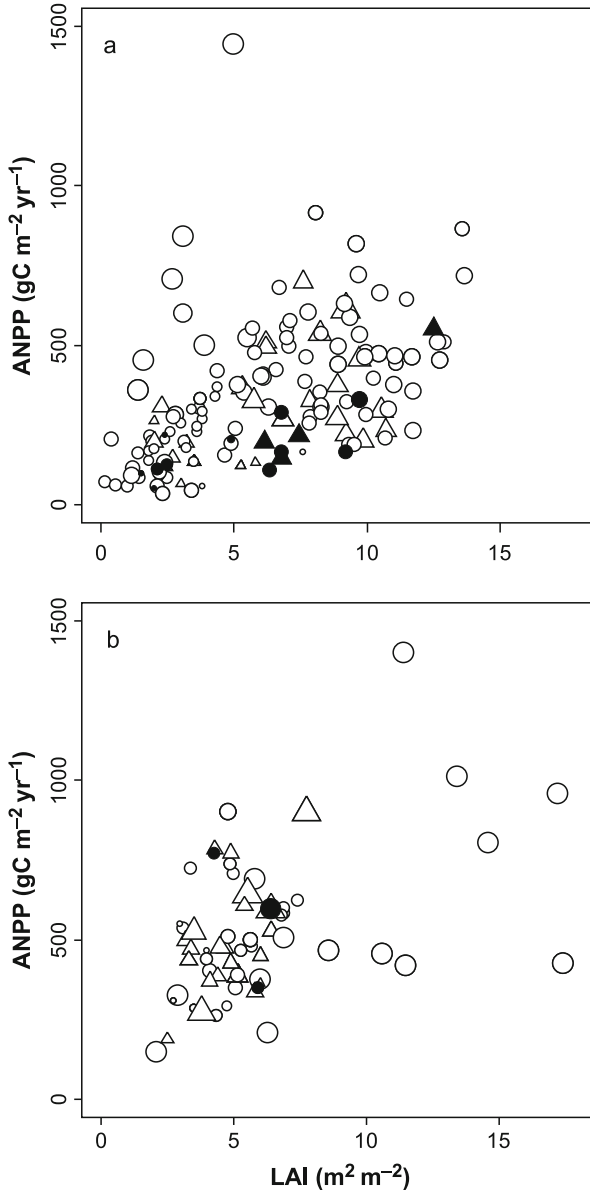
Fig. 4.3 Relationship between aboveground primary productivity (ANPP; g C m^{-2} year^{-1}) and leaf area index (LAI; m^2 m^{-2}) for coniferous (**a**) and deciduous (**b**) forests of the temperate and boreal biome. The symbols denote stand age classes: *open circles* 1–100 years, *open triangles* 101–200 years, *filled circles* 201–400 years, *filled triangles* >400 years. The size of the symbols is proportional to the mean annual temperature (without scale)

4.5.1 Light, Water and Nutrient Availability

In the struggle for light, trees have developed different strategies. Light-demanding pioneer species arrive early after stand-replacing disturbances, establish well, and grow fast. They dominate the early stages of succession, but are then gradually overgrown by more shade-tolerant species. Shade-tolerant species usually start their development in the understorey and reach the canopy after a long period of suppression. Shade-avoiding gap-phase species take an intermediate position. As a rule of thumb, size and age at the population level are negatively correlated with light availability in pioneers and positively correlated in shade-tolerant species. The sign of the correlation tends to aggravate size-/age-related decline in pioneers, but mitigates it in shade-tolerant species.

Water availability may also change with size, and the sign of the response varies with site conditions and root architecture in a predictable fashion. A positive correlation between individual tree structure and water availability is expected to emerge when trees protrude through a dry topsoil into subsoil aquifers by means of long tap roots (Irvine et al. 2004). A negative correlation usually occurs during stand development on shallow soils where root competition intensifies with stand age and biomass, often inducing stagnation of growth (Oliver and Larson 1996). Post-fire regeneration on permafrost soils represents an extreme example where the available unfrozen soil volume, the *active layer*, even shrinks during the course of stand development. This usually induces a cessation of tree growth after about 60 years in boreal larch and black spruce stands irrespective of tree size (Abaimov et al. 1997; Abaimov and Sofronov 1996). There are often pronounced changes in nutrient availability with succession. Most disturbances leave behind soils that are temporarily enriched in nutrients due to the decomposition of the newly available dead plant material and also, in the case of fire, thermal mineralisation (Neary et al. 1999). In secondary succession forest, re-growth progressively locks up nutrients (Vitousek and White 1981; see Chap. 9 by Wardle, this volume). Furthermore, litter quality, and thus remobilisation of nutrients, decreases as the proportion of woody litter increases over time. This led Gower et al. (1996) to hypothesise that the so-called 'age-related' decline in forest productivity can be explained by the temporal dynamics of nutrient availability (cf. Sect. 4.3.2 above). Wardle (Chap. 9, this volume) discusses additional mechanisms evoking the phenomenon of reduced nutrient availability in old versus young forests.

4.5.2 Shifts in Ecophysiological Traits with Changes in Community Composition

Secondary forest succession usually involves species turnover (see Chap. 5 by Wirth and Lichstein, this volume). In other words, tree species constituting old-growth stands are not likely to be the same as those that founded the community a

few hundred years ago, and they exhibit a different set of functional traits. Here, we will concentrate on the ecophysiological and morphological traits known to govern productivity (shift in demographic traits are discussed in Wirth and Lichstein, Chap. 5, this volume). Analysis of growth has identified four key traits with major relevance for productivity (Lambers and Poorter 1992): area-based maximum photosynthesis rates ($A_{max,a}$), mass-based dark respiration rates ($R_{d,m}$), specific leaf area (SLA), and relative biomass allocation to leaves (leaf-mass-ratio, LMR). In the following, we attempt to demonstrate how three of these quantities ($A_{max,a}$, $R_{d,m}$ and SLA) vary with shade-tolerance for temperate and boreal tree species. In this context, we use shade-tolerance as a proxy for a species' successional niche. According to Niinemets and Valladares (2006), a ranking of shade-tolerance (τ) ranges from 1 (=shade intolerant) to 5 (=highly shade tolerant). These rankings were used to form three guilds: early-successionals ($\tau = 1$ or 2), mid-successional ($\tau = 3$), and late-successionals ($\tau = 4$ or 5).

The trait data were assembled as part of the FET (functional ecology of trees) database project (Kattge et al. 2008). The sources for the physiological data are the same as those used in Kattge et al. (2009) for temperate and boreal tree species. Due to space limitations, references for the extensive specific leaf area database are not listed here. We applied the following filter criteria for all variables: Only sun-exposed leaves under ambient CO_2 concentration from mature trees or saplings, but not from seedlings, were used; data from measurements in conditioned chambers were excluded; for one-sided specific leaf area only data from natural vegetation or outside sample plots were used. To avoid pseudo-replication, we used the mean species values per study as the basic observation unit. The statistical analysis was done in a hierarchical Bayesian framework using the software WinBUGS (Spiegelhalter et al. 2003). The generic model had the following structure:

$$\log y_{ij} \sim N(\beta_{j[i]} + \sum_{k=1}^{k=p} \alpha_{k[i]} C_{k[i]}, \sigma^2) \qquad 4.3$$

where y is the trait variable of observation i from tree species j. The natural logarithm of y is normally distributed around a mean prediction - defined by the first term inside the brackets - and variance σ^2. Vector C denotes the covariates that were standardised to a mean of zero and a standard deviation of one prior to the analysis. Then, the βs become the species-specific (across-study) intercepts at the means of the $k = 1,\ldots,p$ covariates C with their respective coefficients β, which we assume to be constant across species. This controls for the variability induced by the numerous covariates, which were light levels and temperature at the time of measurement for $A_{max,a}$, growth temperature prior to and during the measurement for $R_{d,m}$ and potential evapotranspiration of the site for SLA. On the next higher level, the βs per shade-tolerance group are modelled simultaneously in an ANOVA design as

$$\beta_j \sim N(\gamma_{ST[j]}, \sigma_{ST}^2) \qquad 4.4$$

where γ is the mean value of the three shade-tolerance groups ST. The variance is allowed to vary between these groups. The posterior distributions of the parameters β and γ were monitored, as well as the pair-wise differences between the γ-values. Two groups are referred to as significantly different when the credible interval of the monitored differences excludes 0. Unlike a simple step-wise calculation, this multi-level modelling approach ensures proper error propagation and thus realistic credible intervals of the differences. The individual data points in Fig. 4.4 represent the back-transformed posterior means of the β-values, and the error bars indicate the mean and 95% credible interval of the respective γ-values. Posterior means, credible intervals and pair-wise comparisons were calculated only if the number of species per shade-tolerance group was at least three. In general, the combination of the aggregation strategy (one species per study = one observation in the lower level model) and the hierarchical statistical approach (one species = one observation in the higher level model) represents a conservative approach.

For the 41 broad-leaved deciduous tree species ('broad-leaved' for short) in our database we observed a significant decline in the predicted $A_{max,a}$ with increasing shade tolerance, from 11.4 mol CO_2 m^{-2} s^{-1} in early-successional to 7.5 µmol CO_2 m^{-2} s^{-1} in late-successional species (Fig. 4.4b). The majority of species belonged to the early- and mid-successional groups, only five were late-successional, with *Acer saccharum*, *Acer pensylvanicum*, and *Fagus sylvatica* as dominants and *Cornus florida* and *Cornus racemosa* as typical understorey species. A similar trend was observed for the 24 conifers, but the picture was less clear (Fig. 4.4a). No significant differences in $A_{max,a}$ between the successional guilds were found. The data for early-successional species were confined to a narrow range between 8 and 10 µmol CO_2 m^{-2} s^{-1}, but varied widely in the late-successionals; some studies revealed rates higher than 11 mol CO_2 m^{-2} s^{-1} (*Picea abies* and *Taxus baccata*) while others exhibited rates below 5 µmol CO_2 m^{-2} s^{-1} (*Abies lasiocarpa* and *Picea engelmanni*). Here, we would like to note that the high uncertainty in estimating the one-sided leaf area of conifers may contribute substantially to the observed high scatter of $A_{max,a}$ data. In general, we observed slightly higher values of $A_{max,a}$ in broad-leaved species than in conifers. Less data are available for mass-based dark respiration. We observed a non-significant trend of decreasing respiration rates with increasing shade tolerance from 0.005 to 0.0035 µmol CO_2 g^{-1} s^{-1} in conifers (Fig. 4.4c), and from 0.011 to about 0.005 µmol CO_2 g^{-1} s^{-1} in broad-leaved species (Fig. 4.4d). The respiration rates of the latter were twice as high as those of the conifer species, which is most likely related to differences in SLA (see below). As expected, SLA was generally higher in broad-leaved species (Fig. 4.4f). There was no difference between successional guilds within conifers (Fig. 4.4e); the overall mean of SLA for conifer needles was close to 100 cm^2 g^{-1}. The high scatter within the early-successional conifers is due to the presence of the deciduous genus *Larix*, with SLA values of around 150 cm^2 g^{-1}. The broad-leaved late-successional species had an SLA (230 cm^2 g^{-1}) that was significantly higher than both early- and mid-successional species (152 and 163 cm^2 g^{-1}, respectively).

To summarise, all three traits, $A_{max,a}$, $R_{d,m}$ and SLA were higher in broad-leaved species than in conifers. Broad-leaved species revealed significant differences
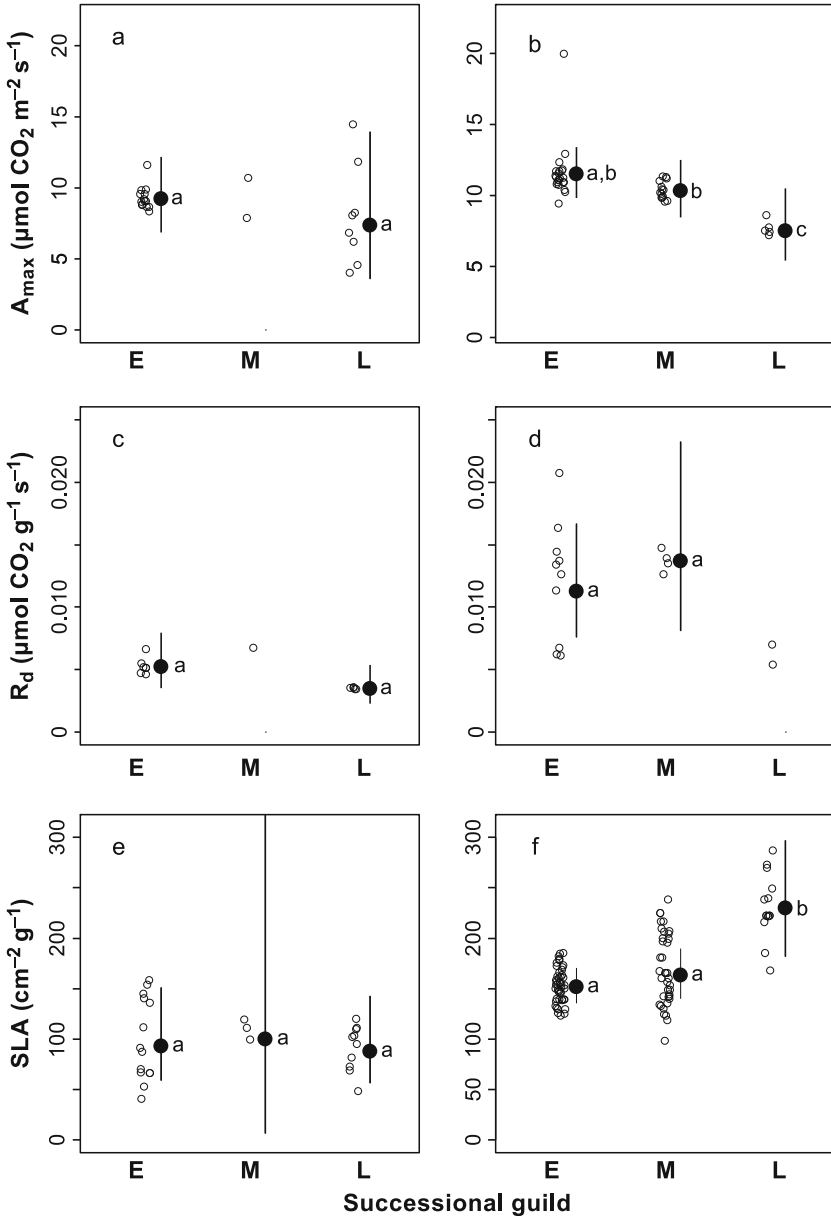
Fig. 4.4 Differences in maximum photosynthetic capacity (A_{max}), dark respiration rate (R_d) and specific leaf area (SLA) for conifers (**a**, **c**, **e**) and broad-leaved deciduous tree species (**b**, **d**, **f**). The species are further grouped into successional guilds according to their shade-tolerance scores: *E* early-successional, *M* mid-successional, *L* late-successional. The individual data points (*open circles*) represent posterior means per species and study. A slight random scatter was added to increase the visibility. The adjacent *filled circles* represent the posterior mean across species and studies and the corresponding 95% confidence intervals

between successional guilds because late-successional species had lower $A_{\mathrm{max,a}}$ and higher SLA than early-successional species. The data for $R_{\mathrm{d,m}}$ were insufficient, but suggest lower rates in late-successional species. Similar, but non-significant trends for $A_{\mathrm{max,a}}$ and $R_{\mathrm{d,m}}$ were found for conifers. At this point, we can state that there are differences between successional guilds, and that typical old-growth species are likely to have lower $A_{\mathrm{max,a}}$ and $R_{\mathrm{d,m}}$, but higher SLA. Pronounced shifts in mean trait values are expected if the succession involves a succession from broad-leaved deciduous to conifers and vice versa. It is difficult to say, however, how these successional trends translate into differences in growth performance. This comparison is justified if we assume a fixed carbon allocation to leaf biomass. Accordingly, late-successional broad-leaved trees would be able to produce a higher leaf area than their early-successional counterparts (higher SLA), but this could be compensated for by lower assimilation rates per unit area. However, if the mass-based dark respiration rates were taken to be lower, the net carbon gain would be higher in late successional species. Our findings contradict a similar study on seedlings by Walters and Reich (1999), who report for broad-leaved winter deciduous trees a decrease in SLA, no differences in $A_{\mathrm{max,a}}$ and – similar to our findings – a decrease in $R_{\mathrm{d,m}}$ with increasing shade tolerance. In the latter study, the trait shifts compensated each other such that relative growth rates were similar across the shade-tolerance gradient, while our results suggest higher growth rates for late-successional shade-tolerant species of both broad-leaved and coniferous tree species. The comparison between conifers and broad-leaved deciduous trees needs to take into account the fact that, due to differences in leaf longevity, foliage biomass is at least three times higher in conifers. With the relative differences in SLA (conifer to broad-leaved ratio 1:1.7), $A_{\mathrm{max,a}}$ (1:1.25) and foliage biomass (3:1) this translates into a relative difference in net carbon gain of 1:0.7. This simple calculation suggests that a successional change from broad-leaved to conifer would therefore induce 40% higher productivity. This confirms data reported by Schulze et al. (2005) showing that both GPP and NPP of a spruce forest are higher than in an otherwise comparable beech forest, although $A_{\mathrm{max,a}}$ was two times lower in the conifer.

By and large, we may state that species shifts from early- to late-successional within conifers and broad-leaved species operate against an 'age-related' decline in productivity, as does a change in composition from broad-leaved species to conifers. This was well illustrated by Carey et al. (2001), who showed for a long-term chronosequence in the Rocky Mountains that the contribution of *Abies lasiocarpa* undergrowth below the pioneering *Pinus albicaulis* is even able to increase the overall productivity when the productivity of the pine trees declines beyond a stand age of 250 years. A succession from coniferous to broad-leaved trees, however, may result in a combination of ecophysiological traits likely to exert a lower net productivity. In addition, the common tendency in many (but not all!) forest successions that species composition shifts towards tree species with a taller stature and a higher longevity, as discussed in Wirth and Lichtstein (Chap. 5, this volume), allows the community to progressively explore more growing space – a phenomenon that, again, operates against a stand-level decline in productivity.

4.5.3 Imperfect Acclimatisation of Late-Successional to Full Sunlight: A Case Study on European Beech (*Fagus sylvatica*)

Studies on leaf traits of early- and late-successional can describe only general trends that do not include specific site properties (e.g. nutrient availability) or the changes in physiology required in order to adapt to changing constraints throughout the lifetime of a tree. European Beech (*Fagus sylvatica*), being a typical late-successional, is an appropriate example to demonstrate these mechanisms. Beech has a high competitive performance in old-growth forests due to the extremely high shade tolerance of its seedlings and saplings (Burschel and Huss 1964; Schulze 1970, 1972; Saxe and Kerstiens 2005). Under optimum conditions, beech is able to out-compete every other tree species during undisturbed succession in many parts of Europe. Niinemets (2006) emphasises the importance of understanding temporal changes in leaf traits beyond the seedling stage, because young trees sometimes have to grow in the deep shade for decades before gap formation occurs. As it is well known that beech seedlings are sensitive to full sunlight (e.g. Valladares et al. 2002), the question arises of how old and tall beech trees cope with full sunlight once they have become the dominating tree species in a forest. Schulze (1970) found that sun-exposed leaves decrease their chlorophyll content during sunny periods and start to senesce as early as the end of July or beginning of August.

More detailed vertical observations of leaf traits through a beech canopy in northern Germany by Kutsch et al. (2001) indicate the existence of at least three physiologically different layers in beech canopies. The sun layer – according to Schulze (1970), one homogeneous layer – is actually composed of two sub-layers: the most peripheral part of the crown – called Sun-1-layer in this study – and a Sun-2-layer with leaves more inserted into the inner part of the canopy but still receiving 40–60% of the incoming radiation. These leaves of the Sun-2-layer are temporarily receiving high irradiance but are sheltered from direct sunlight for most of the day. It is noteworthy that Sun-2-layer leaves have higher photosynthetic capacities and nitrogen contents than those of the Sun-1-layer. In contrast, specific leaf weights and chlorophyll-a/b-ratios are slightly lower than in the Sun-1-layer. A third layer consists of inner leaves, which receive low light levels. These shaded leaves have, according to Schulze (1970), typically very low specific leaf weights, chlorophyll-a/b-ratios, A_{max}, and nitrogen contents. Figure 4.5 shows gradients of some leaf properties through the canopy.

The fact that the leaves of the Sun-2-layer have a fairly high nitrogen content and high photosynthetic capacity is contrary to the common hypothesis that nitrogen within single plants and within plant canopies is regulated by relative light supply, with leaves of highest light supply showing the highest nitrogen content (Field 1983; Werger and Hirose 1991). Model calculations showed that this pattern maximises the total photosynthetic income of the canopy (Anten et al. 1995, 1998).

The question arises why beech trees do not allocate the highest amounts of nitrogen to the most peripheral leaves of the Sun-1-layer. The following observations may explain this: besides the already discussed early senescence, Sun-1-layer leaves showed that the stomatal conductance of these leaves was low and gradually
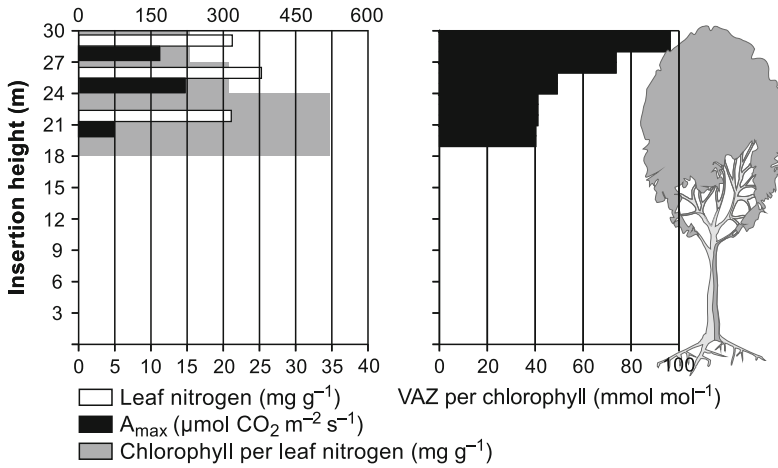
Fig. 4.5 Vertical distribution of leaf properties in a Beech canopy in the Bornhöved Lake district in northern Germany. *Left panel* Leaf nitrogen content, area-related photosynthetic capacity ($A_{max,a}$) and chlorophyll per nitrogen content for three layers. Data are mean values of four leaf samples per layer that were taken during a sunny period in July 1999. The right part shows the continuous decrease of the xantophyll content (violaxanthin + antheraxanthin + zeaxanthin, *VAZ*) from the top inside the canopy. Data are mean values of three leaf samples per layer taken following a sunny period on 4 August 1999

decreasing during the growing season (Kutsch et al. 2001). Since the layers do not differ very much in height, hydraulic limitation can be excluded as the reason for the observed reduction in stomatal conductance in the Sun-1-layer; their performance must be due to specific microclimatic conditions. It may be inferred here that the energy budget of a fully sun-exposed leaf results in a higher demand for transpiration compared to a shaded leaf at the same vapour pressure deficit of the air (Jarvis 1976). However, when stomata are closed during periods of high irradiance, the incoming energy has to be otherwise dissipated in order to avoid damage to the foliage. The xanthophyll content is an indicator of the ability of leaves to dissipate excessive light and protect the photosystems from damage (Bjoerkmann and Demming-Adams 1995). Xanthophyll (violaxanthin + antheraxanthin + zeaxanthin, henceforth "VAZ") content per unit chlorophyll was lower in Sun-1-leaves of beech than those of ash or oak leaves of a nearby forest containing two-to-three times the amount of VAZ per chlorophyll (Fig. 4.5). Consequently, the low VAZ per chlorophyll of the Sun-1-layer indicates their lower physiological adaptability to high sun irradiance and also explains their early senescence.

Respecting the decreased acclimation potential to full sun irradiance and the resulting multiple stress situation of the beech leaves, a high allocation of nitrogen to the Sun-1-layer could be considered a misinvestment. This hypothesis was tested by a model study. The goal of this model study was to find out whether the dynamics of eco-physiological properties throughout the growing season explain the pattern of nitrogen distribution in European beech. The temporal dynamic of $A_{max,a}$ in the model runs was followed according to field measurements that showed that Sun-1-layer leaves lost their photosynthetic capacity due to senescence much earlier than those of the Sun-2-layer (Figs. 4.6, 4.7a). Also, the increase in sensitivity of the
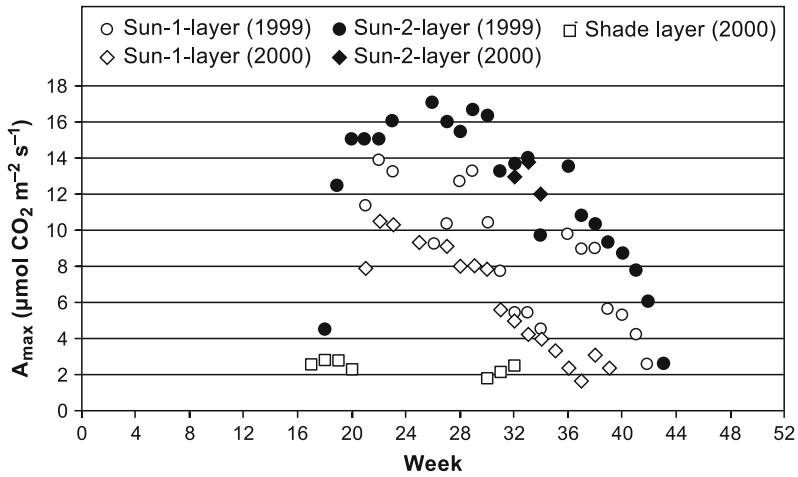
Fig. 4.6 Annual courses for the years 1999 and 2000 of photosynthetic capacity ($A_{max,a}$) for different layers within a Beech canopy in the Bornhöved Lake district in northern Germany. Data points were derived weekly from continuous field measurements
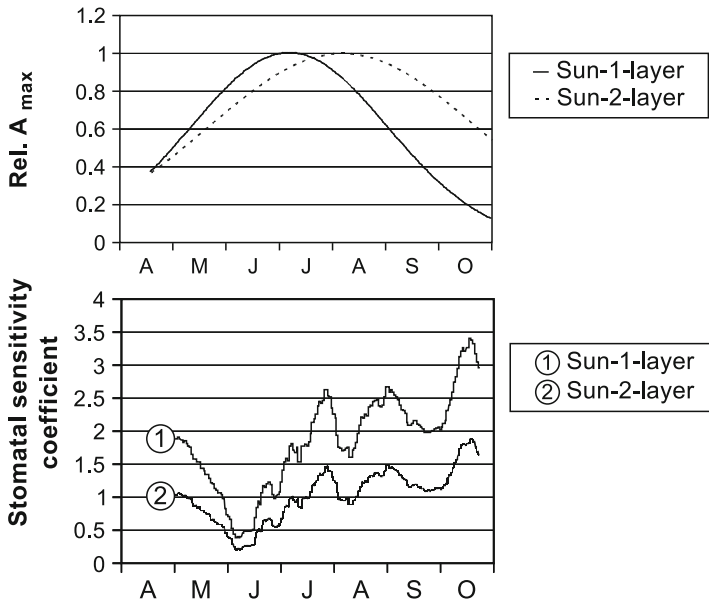
Fig. 4.7 Annual courses of photosynthetic capacity, $A_{max,a}$, and coefficient c describing stomatal sensitivity to leaf-air vapour pressure deficit (VPD) (Kutsch et al. 2001) used in the model study for the two uppermost layers in a beech canopy. An early senescence of the Sun-1-layer results in an earlier decline of $A_{max,a}$ and an earlier increase in c, which means that the stomatal conductance decreases more with increasing VPD
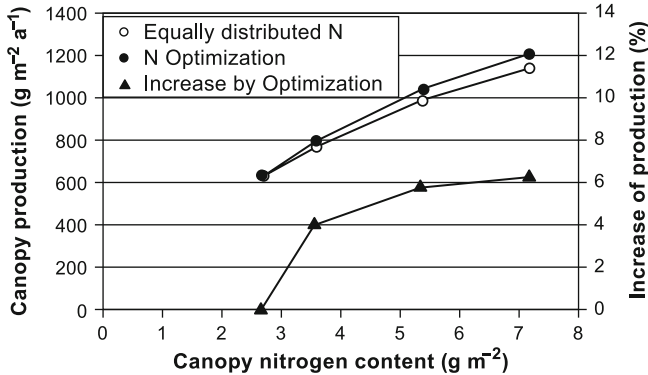
Fig. 4.8 Modelled annual gross primary production (GPP) of a Beech forest in relation to the nitrogen content of the whole canopy. *Open circles* GPP of a canopy with equally distributed nitrogen, *black circles* canopy with optimised nitrogen distribution, *triangles* relative increase due to nitrogen optimisation

stomata to low air humidity in the Sun-1-layer as a consequence of strong irradiance (symbolized by the coefficient *c* according to Kutsch et al. 2001; Fig. 4.7b) was incorporated into the model.

During several model runs the foliage nitrogen concentration was constantly increased. We used two scenarios: nitrogen was either distributed equally throughout the whole canopy or optimised to gain highest canopy photosynthetic production. Both scenarios showed that the photosynthetic income was increased with increasing nitrogen content, but to a higher extent when the nitrogen distribution was optimised (Fig. 4.8). The distribution of foliage nitrogen in the tree crown according to the modelled optimisation was equal to that found in the field (Kutsch et al. 2001): highest overall production was gained when more nitrogen was allocated to the Sun-2-layer than to the Sun-1-layer.

The results can be summarised with the hypothesis that even the tall and dominating beech tree maintains its character of a shade-adapted plant as it needs to shelter the highly productive inner parts of the crown against full sun irradiance by means of peripherically inserted leaves.

4.6 Conclusions

Tall and old trees face unique environmental challenges. Height, and the resulting gravimetrical and hydraulic strain, can burden, but not completely limit, further growth of tall trees in most cases. The slowing of height growth with tree size and the levelling off or decrease of GPP and NPP in old forests seems rather to be a consequence of the complex interaction between environmental constraints, physiological compensation, evolutionary adaptation, population- and community-level

processes and ecosystem development. Therefore the development of a single hypothesis by reducing this complex fabric of interaction to a single mechanism is inappropriate. In the debate about 'age-related decline' the pitfalls of mono-causality are manifold:

- Confounding the effects of 'height' and 'age': These variables are highly correlated and their effects are thus difficult to separate. Clearly, 'height' plays a dominant role in the context of hydraulic limitation of photosynthesis. However, the idea of genetically induced reduction in either source capacity or sink strength as well as shifts between different sinks may shift the perspective rather towards age than towards height effects (Day et al. 2001; Bond et al. 2007).
- Direct scaling from the tree- to the stand-level: Tree-level responses to either height or age can be fully compensated, partly buffered or exaggerated at the population-level by processes acting on the amount of displayed leaf area, the most important of which are changes in stand density and canopy architecture. Our reanalysis of the Luyssaert dataset suggested that structure is more important than physiology.
- Negligence of temporal covariates: Both the environmental drivers and the actors (the tree species themselves) may change substantially with secondary succession. As shown, these changes may work in the direction of an 'age-related decline' of productivity, but also against it.

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Chapter 5
The Imprint of Species Turnover on Old-Growth Forest Carbon Balances – Insights From a Trait-Based Model of Forest Dynamics

Christian Wirth and Jeremy W. Lichstein

5.1 Introduction

Succession is the process that eventually transforms a young forest into an old-growth forest. Describing and analysing plant succession has been at the core of ecology since its early days some hundred years ago. With respect to forest succession, our understanding has progressed from descriptive classifications (i.e. identifying which forest types constitute a successional sequence) to general theories of forest succession (Watt 1947; Horn 1974, 1981; Botkin 1981; West et al. 1981; Shugart 1984) and simulation models of forest dynamics that are capable of predicting successional pathways with remarkable precision (Urban et al. 1991; Pacala et al. 1996; Shugart and Smith 1996; Badeck et al. 2001; Bugmann 2001; Hickler et al. 2004; Purves et al. 2008).

Although the importance of different factors in controlling successional changes in species composition is still debated – particularly in speciose tropical forests (Hubbell 2001) – a large body of evidence implicates the tradeoff between shade-tolerance and high-light growth rate as a key driver (Bazzaz 1979; Pacala et al. 1994; Wright et al. 2003). In contrast, there is no well-accepted mechanism to explain successional changes in forest biomass, much less other components of ecosystem carbon. A range of biomass trajectories have been observed (e.g. mono-tonic vs hump-shaped curves), and some basic ideas have been proposed to explain these patterns (Peet 1981, 1992; Shugart 1984). However, we are aware of only one systematic, geographically extensive assessment of biomass trajectories (see Chap. 14 by Lichstein et al., this volume). In this data vacuum, it has been difficult to assess the relative merits of different theories or mechanisms. This is especially true for later stages of forest succession, and in particular for old-growth forests.

With respect to biomass dynamics, there are at least four non-mutually exclusive hypotheses: (1) the 'equilibrium hypothesis' of Odum (1969); (2) the 'stand-breakup hypothesis' of Bormann and Likens (1979) and its generalisations (e.g. Peet 1981, 1992; Shugart 1984); (3) the hypothesis of Shugart and West (1981), which we term the 'shifting-traits hypothesis'; and (4) the 'continuous accumulation hypothesis' of Schulze et al. (Chap. 15, this volume). Because some of these

hypotheses are discussed in greater detail in later chapters of this book (e.g. Lichstein et al., Chap. 14), we will only briefly summarise their main features here.

The equilibrium hypothesis of Odum (1969) states that, as succession proceeds, forests approach an equilibrium biomass where constant net primary production (NPP) is balanced by constant mortality losses. These losses are passed on to the woody detritus compartment, which will itself equilibrate when mortality inputs are balanced by heterotrophic respiration and carbon transfers to the soil. This logic may be extended to soil carbon pools, but the validity of the equilibrium hypothesis for soil carbon is challenged by Reichstein et al. (Chap. 12, this volume); this is therefore not addressed in the present chapter. Odum makes no strict statements about how ecosystems actually approach the assumed equilibrium, but views a monotonic increase to an asymptote as typical. In addition, it follows from Odum's hypothesis that, once equilibrium is reached, an 'age-related decline' in NPP would induce a biomass decline given a constant mortality (see Chap. 21 by Wirth, this volume).

The 'stand-breakup hypothesis' assumes synchronised mortality of canopy trees after stands have reached maturity. As the canopy breaks up, the stand undergoes a transition from an even-aged mature stand of peak biomass to a stand comprised of a mixture of different aged patches and, therefore, lower mean biomass (Watt 1947; Bormann and Likens 1979). Peet (1981) generalised this hypothesis by allowing for lagged regeneration (formalised in Shugart 1984), which may result in biomass oscillations. In any case, the mortality pulse at the time of canopy break-up would result not only in declining biomass, but also in an increase in woody detritus.

The 'shifting traits hypothesis' states that biomass and woody detritus trajectories reflect successional changes in species traits, which follow from successional changes in species composition. Relevant traits, which are also typically used in gap models of forest succession, include maximum height, maximum longevity, wood density, shade tolerance, and decay-rate constants of woody detritus (Doyle 1981; Franklin and Hemstrom 1981; Shugart and West 1981; Paré and Bergeron 1995). The reasoning is straightforward: The maximum height defines the upper boundary of the total aboveground ecosystem volume that can be filled with stem volume. Shade tolerance and wood density modulate the degree to which this volume can be filled with biomass. The combination of these three parameters thus determines the maximum size of the aboveground carbon pool for a given species. Tree longevity controls how long a species' pool remains filled with biomass carbon. Similarly, wood decay-rate affects the dynamics of the woody detritus carbon pool.

Finally, the 'continuous accumulation hypothesis' of Schulze et al. (Chap. 15, this volume) states that, by and large, natural disturbance cycles in temperate and boreal systems are too short for us to make generalisations about the long-term fate of aboveground carbon pools, and that during the comparatively narrow observational time-window, accumulation is the dominant process.

It is one of the goals of this book to review empirical evidence for carbon trajectories predicted by these different hypotheses. Successional trajectories of aboveground carbon stocks can, in principle, be derived from large-scale forest inventories (see Chaps. 14 and 15 by Lichstein et al. and Schulze et al., respectively;

Wirth et al. 2004b). However, in those countries where extensive and well-designed inventories are available, little old forest remains; and even large inventories do not provide a comprehensive picture of old-growth carbon trajectories (see Chap. 14 by Lichstein et al., this volume). Alternatively, long-term chronosequences could be used. As we discuss below (see Sect. 5.7), the number of chronosequences extending into the old-growth phase is limited and by no means representative. It appears that the empirical evidence for old-growth carbon trajectories is insufficient to differentiate between the extant hypotheses and to assess their relevance for natural landscapes.

In this chapter, we present a model that was designed to assess the potential contribution of the 'shifting-traits' mechanism to forest carbon dynamics. The model was tailored to work with two unusually rich sources of information: the abundant trait data available for nearly all United States (US) tree species, and detailed descriptions of successional species turnover in different US forest types. The work presented in this chapter constitutes, to our knowledge, the first systematic evaluation of the 'shifting traits hypothesis'.

Specifically, the model uses four widely available tree traits (maximum height, longevity, wood density, and woody decay rates) to translate qualitative descriptions of succession for a vast number of forest types into quantitative predictions of aboveground carbon stock trajectories. We focused on US forests because only here could we find sufficient information for both model parameterisation and validation (see Chap. 14 by Lichstein et al., this volume). We first describe the model parameterisation and simulations. Next, we characterise how the input trait data for the 182 tree species relate to successional status. After validating the model with data from the old-growth literature, we use the model to calculate aboveground carbon trajectories, including woody detritus, for 106 North American forest types. The results provide insights into the factors controlling the shapes of forest carbon trajectories and the capacity of the biomass and deadwood pools to act as carbon sinks in old-growth forests.

5.2   A Trait-Based Model of Forest Carbon Dynamics

5.2.1   Successional Guilds

One of the most obvious features of forest succession is a gradual change in species composition. The dominant tree species in old-growth stands are not likely to be the species that dominated when the community was founded a few hundred years before. Depending on when species tend to dominate in the course of succession, we refer to them as early-, mid- or late-successional. The mechanism by which these three guilds replace each other may vary (West et al. 1981; Glenn-Lewin et al. 1992). The model developed in this chapter does not attempt to capture the mechanisms leading to species turnover, but rather takes this

turnover as given and prescribes it according to empirical descriptions (see below). Therefore, we mention the mechanisms of species turnover only briefly here.

Most commonly, it is assumed that species turn over via gap-phase dynamics; i.e. succeeding species arrive and grow in canopy gaps created by the death of individuals of earlier successional species. Alternatively, all species may arrive simultaneously, and differences in longevity or maximum size may allow the successor species to either outlive or outgrow the initially dominant species (see Fig. 15.8 in Schulze et al., Chap. 15, for an example).

The three guilds differ in many ways but most prominently with respect to their tolerance of shading. Forest scientists have grouped tree species according to shade tolerance (Niinemets and Valladares 2006). Usually, an ordinal scale with five levels is employed, ranging from 1 (very intolerant) to 5 (very tolerant), and these classes are often used to infer a species' successional niche. The physiological and demographic underpinnings of shade tolerance have been intensively studied (see Chaps. 4 and 6 by Kutsch et al. and Messier et al., respectively), and there is a long list of associated physiological and morphological traits (Kobe et al. 1995; Lusk and Contreras 1999; Walters and Reich 1999; Henry and Aarssen 2001; Körner 2005). In this chapter we apply the concept of shade tolerance to sort species into early-, mid- and late-successional species.

5.2.2   Model Structure

We first describe the model structure. The data used to parameterise the model are described in Sect. 5.2.3. We simulated a stochastic patch model with an annual time-step. Each patch is 10×10 m and contains a single monospecific cohort that grows in height and simultaneously accumulates biomass. Thus, the model simulates the dynamics of volume and biomass of cohorts, not individuals. Each patch experiences stochastic whole-patch mortality (see below), after which a new cohort of height zero is initiated. At the beginning of the simulation, each patch is initialised with the pioneer species of a given successional sequence (see Sect. 5.2.3), which, upon whole-patch mortality, are replaced by mid-successional species, which in turn are replaced by late-successional species. From then on, late-successional species replace themselves. We simulated the dynamics of 900 independent patches for each forest type and report the ensemble means of the bio- and necromass-dynamics.

In each patch i, the cohort increases in height H (m) according to a Michaelis-Menten-type curve:

$$H_i(t') = \frac{h_{\max}t'}{(h_{\max}/h_s) + t'} \qquad\qquad 5.1$$

where t' (years) denotes the time since cohort initiation, $h_{\max}$ the asymptotic height, and h_s the initial slope of the height-age curve of a given species. Cohort height is converted to stand volume V (m^3 m^{-2}) as

$$V(t') = \underbrace{(\beta_0 + \beta_1\tau)}_{\beta_0{}^*} H(t')^{\beta_2} \qquad 5.2$$

where the coefficient $\beta_0{}^*$ depends on a species' shade-tolerance τ (from 1 = very intolerant to 5 = very tolerant). Values of β were estimated separately for conifers and hardwoods using European yield tables (Wimmenauer 1919; Tjurin and Naumenko 1956; McArdle 1961; Assmann and Franz 1965; Wenk et al. 1985; Dittmar et al. 1986; Erteld et al. 1962). These yield tables were constructed from long-term permanent sample plots and thinning trials and provide data on canopy height (mean height of dominant trees) and merchantable wood volume for a range of site conditions for a total of 21 European and North American species. Because the yield tables represent monospecific, even-aged stands, Eq. 5.2 does not include sub-canopy cohorts. For both taxonomic groups, the values of β_1 were positive; i.e. for a given canopy height, stands of shade-tolerant tree species contain more stem volume than stands of light-demanding tree species. This probably reflects the fact that shade-tolerant species are better able to survive under crowded conditions.

Volume is converted to biomass carbon C_b (kg m^{-2}) as

$$C_b(t', H) = V(t') \cdot \rho \cdot c \cdot \theta \cdot e(H) \qquad 5.3$$

Here, ρ is the species-specific wood density, and c is the carbon concentration of biomass (Table 5.1). The tuning parameter θ corrects for several biases in our model and/or parameterisation: (1) the yield-table parameterisation (see above) ignores sub-canopy trees present in natural forests; (2) advanced regeneration may survive canopy mortality events, so that patch height may not, in reality, start at a height of 0 as assumed in our model; and (3) stand densities in forest trials used to construct the yield tables tend to be lower than in natural forests. The value of θ was adjusted to maximise the overall fit to the validation dataset (Sect. 5.4). Because θ was set constant across all species, it corrects for overall bias of modelled carbon stocks but does not influence the shapes of the carbon-stock trajectories over time. Finally, the crown biomass expansion factor e (the ratio of total aboveground biomass to stem biomass) decreases with patch height as

$$e(H) = \varepsilon_1 + (\varepsilon_2 - \varepsilon_1) \cdot \exp(-\varepsilon_3 H) \qquad 5.4$$

where ε_1 and ε_2 are the minimum and maximum expansion factors, respectively, and ε_3 controls the rate of decline in e with patch height. We used the parameters ε_1 and ε_2 for conifers and hardwoods given in Wirth et al. (2004a).

We distinguish two types of mortality resulting in woody-detritus production: self-thinning and whole-patch mortality. Self-thinning is represented as a carbon

Table 5.1 Model parameters, values (C conifers; H hardwood) and units

Parameter	Meaning	Value	Unit
h_{max}	Maximum height	Species-specific	m
h_s	Initial slope of height–age curve	0.6	m year^{-1}
β_0	Baseline coefficient of height–stem volume allometry	C: 2.14, H:1.26	m^3 ha^{-1}
β_1	Control of shade–tolerance over β_0	C: 0.53, H: 0.15	m^3 ha^{-1}
β_2	Exponent of H-volume allometry	C: 1.47, H: 1.59	m^3 ha^{-1}
c	Carbon concentration of biomass	0.5	kg C kg^{-1} dw[b]
ρ	Wood density	Species-specific	kg$_{dw}$ m^{-3} fv[c]
θ	Tuning parameter	2	Unitless
ε_1	Maximum ABEF[a] at zero height	C: 5.54, H: 1.71	kg kg^{-1}
ε_2	Shape factor for ABEF decline	C: 0.22, H: 1.80	Unitless
ε_3	Lower positive asymptote of ABEF	C: 1.31, H: 1.27	kg kg^{-1}
λ	Longevity	Species-specific	year
k_d	Woody detritus decay constant	C: 0.03, H: 0.10	year^{-1}
δ_1	Fraction of h_{max} where μ equals 0.5	0.5	Unitless
δ_2	Fraction of h_{max} where μ equals f	0.75	Unitless
f	Fraction of μ^* at 0.75 h_{max}	0.95	Unitless

[a]Aboveground biomass expansion factors
[b]dw = dry weight
[c]fv = fresh volume

flux to the woody detritus pool that is set proportional to biomass accumulation. Specifically, in accordance with data from forest trials with low thinning intensity, the rate of woody-detritus production resulting from self-thinning was assumed to be one-half that of biomass accumulation (Assmann 1961). This implies that, in mature stands with little net biomass accumulation (which approaches zero in our model as patch height approaches h_{max}, see Eqs. 5.1 and 5.2), self-thinning is minimal and woody detritus production results primarily from whole-patch mortality. Although this scheme ignores branch-fall in mature stands, it provides a reasonable approximation to reality. Unlike self-thinning, whole-patch mortality (which resets cohort height, and thus aboveground biomass, to zero) is stochastic and occurs at each annual time-step (in each patch independently) with probability μ. We assume that μ can be approximated by the individual-tree mortality rate μ^*, which we estimate from maximum tree longevity λ, as is commonly done in gap models (Shugart 1984). Longevity can be viewed as the time span after which the population has been reduced to a small fraction $\phi \equiv (1 - \mu^*)^\lambda$, where we set $\phi = 0.01$; i.e. we assume that 1% of individuals survive to age λ. The annual individual mortality rate is thus $\mu^* = 1 - \sqrt[\lambda]{0.01}$. Note that we are applying this per-capita rate to a whole patch of 10×10 m. Therefore, it shall become effective only for patches that are occupied by a single large tree. To accomplish this, we assume that μ is size dependent, such that it is near zero in young patches (where most mortality occurs due to self thinning), and increases asymptotically to μ^* as

patch height approaches h_{max}. Specifically, we assume that μ is equal to the product of μ and a patch-height-dependent logistic function (Fig. 5.1):

$$\mu = \mu^* \cdot \frac{e^{\vartheta(H)}}{1 + e^{\vartheta(H)}} \qquad 5.5$$

where

$$\vartheta(H) = \frac{\ln(f/(1-f))}{h_{max}(\delta_2 - \delta_1)}(H - \delta_1 h_{max}) \qquad 5.6$$

According to Eq. 5.5, μ is $0.5\mu^*$ when H is $\delta_1 h_{max}$, and μ is $f\mu^*$ when H is $\delta_2 h_{max}$. We assigned δ_1, δ_2, and f the values 0.5, 0.75, and 0.95, respectively. This parameterisation yields a monotonically increasing approach to μ^*, with $\mu = 0.5\mu^*$ when $H = 0.5h_{max}$, and $\mu = 0.95\mu^*$ when $H = 0.75h_{max}$ (Fig. 5.1). In our simulations, these parameter values yield a smooth upward transition (no hump-shaped trajectory) to an equilibrium biomass, although other values result in a biomass peak followed by oscillations (results not shown). This complex behaviour (which was avoided in the simulations presented in this chapter) results from synchronised mortality across patches when there is a sudden transition from $\mu \approx 0$ to $\mu \approx \mu^*$.

Finally, note that as μ increases to its asymptote, mortality due to self-thinning declines to zero (see above); thus, the total mortality rate in a patch is constrained to reasonable values at all times.

Both self-thinning and whole-patch mortality result in a transfer of biomass to the woody detritus pool C_d, creating input $I_d(t)$. Woody detritus input from branch shedding by live trees is not taken into account. Decay of woody detritus is modelled according to first-order kinetics (Olsen 1981). The change in woody detritus carbon stocks is modelled as a discrete time-step version of the differential equation

$$\frac{dC_d}{dt} = I_d(t) - k_d C_d(t) \qquad 5.7$$

where k_d is the exponential annual decomposition rate constant.

5.2.3   Input Data

Trait data were assembled as part of the *Functional Ecology of Trees* (FET) database project (Kattge et al. 2008). To conserve space, we mention only the main data sources here. Maximum heights and longevities were obtained from Burns and Honkala (1990) and the *Fire Effects Information System* database (http://www.fs.fed.us/database/feis/). Shade tolerances were taken from Burns and
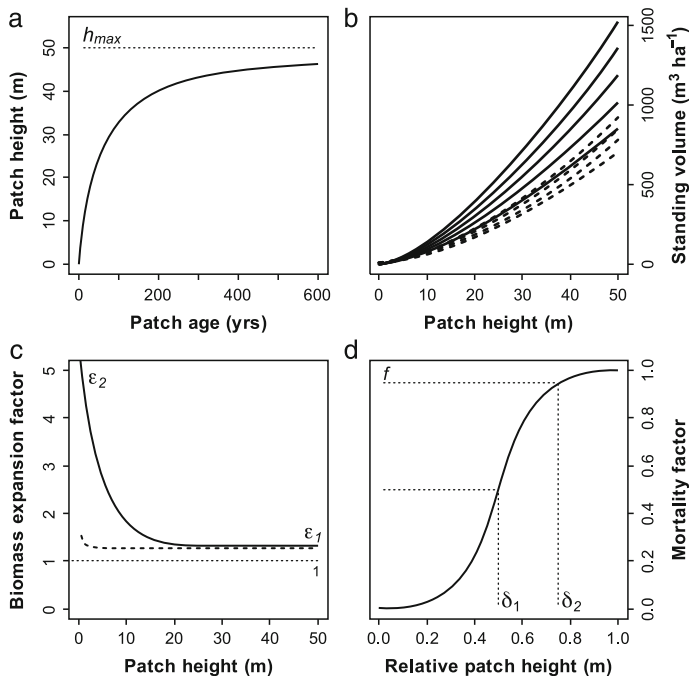
Fig.5.1a–d Illustration of main functions used in the model. **a** Height-age curve governed by the parameters maximum height h_{max} (*dotted line*) and initial slope h_s (Eq. 5.1). **b** Allometric relationship between patch height and stem volume (Eq. 5.2) for conifers (*solid line*) and hardwoods (*dashed line*) for different shade-tolerance classes (lowermost curves = very intolerant; uppermost curves = very tolerant), fitted from volume yield tables. **c** Relationship between the aboveground biomass expansion factor e and patch height for conifers (*solid line*) and hardwoods (*dashed line*) (Eq. 5.4). **d** Whole-patch mortality rate (proportion of asymptotic value) as a function of patch height (Eqs. 5.5, 5.6)

Honkala (1990) and Niinemets and Valladares (2006). The majority of wood density data were obtained from Jenkins et al. (2004). Decomposition rates of coarse woody detritus for conifers and hardwoods were derived from the FET database comprising over 500 observations of k_d from 74 tree species in temperate and boreal forest (C. Wirth, unpublished).

Species-specific parameters were assigned for maximum height h_{max}, maximum longevity λ, shade-tolerance τ, and basic wood density ρ. Due to data limitations, the following parameters were assigned at the level of angiosperms (hardwoods) vs gymnosperms (conifers): decomposition rates for woody detritus, the base-line allometric coefficients relating cohort height to cohort volume, and parameters controlling the size-dependency of the biomass expansion factors (see below). All other parameters were constants across all species (Table 5.1).

Successional sequences of species replacements were based on detailed descriptions of North American forest cover types (FCT) published by the Society of

American Foresters (Eyre 1980). Each FCT is described qualitatively in terms of its species composition, geographic distribution, site conditions, and dynamics. For each FCT, we noted which species were classified as dominant, co-dominant, or associated/admixed. We did not include species listed as 'additional', 'occasional', 'rare' or 'subcanopy'. We then classified each species in each FCT as pioneer-, mid-, or late-successional. In many cases, these assignments were explicitly stated in the *ecological relationships* section of the description. Otherwise, we used shade-tolerances to assign species successional status as follows: pioneer ($\tau = 1$ or 2), mid-successional ($\tau = 3$), and late-successional ($\tau = 4$ or 5) . Long-lived pioneer species ($\lambda > 400$ years) were assigned to all three successional guilds. Finally, for each FCT we calculated the weighted mean of the species-specific traits h_{max}, λ, τ and ρ. Dominant species were given triple weight, co-dominant species double weight, and admixed species single weight. Conifer or hardwood trait values for k_d, ε_1, ε_2, and ε_3, were used for successional stages dominated by either conifers or hardwoods. Mean values were used for mixed stages.

5.2.4 Model Setup

We simulated 2,000 years of succession for each of the 106 forest types. To isolate the importance of differences between conifers and hardwoods in woody detritus decay rates, we ran two sets of simulations, the first with $k_d = 0.05$ year^{-1} for both conifers and hardwoods, and the second with the standard parameterisation (Table 5.1), i.e. different k_d values for conifers and hardwoods. For each forest cover type, we report time-dependent means across the 900 patches for C_b, C_d, and their sum, C_a. In addition, we calculated aboveground net ecosystem productivity (ANEP) as the mean annual change in pool sizes, ΔC_x, for the following periods: (1) 0–100 years, (2) 101–200 years, (3) 201–400 years and (4) 401–600 years. We refer to these periods as 'pioneer', 'transition', 'early old-growth' and 'late old-growth' phases. Equilibrium biomasses in Fig. 5.4 were calculated as mean stocks from single-species runs between 1,000 and 2,000 years.

5.3 The Spectrum of Traits

Before we turn to the model predictions, we ask how the species-specific parameters influencing aboveground carbon stocks (h_{max}, λ and ρ) vary with shade tolerance ('intolerant': $\tau = 1$ or 2; 'intermediate': $\tau = 3$; and 'tolerant': $\tau = 4$ or 5; Fig. 5.2). Recall that, in our model, these three shade-tolerance classes correspond to the pioneer, mid- and late-successional guilds, respectively.

Intolerant conifers and hardwoods reached similar maximum heights (means of 27 m and 31 m, respectively; Fig. 5.2a,b). As shade tolerance increased, conifers
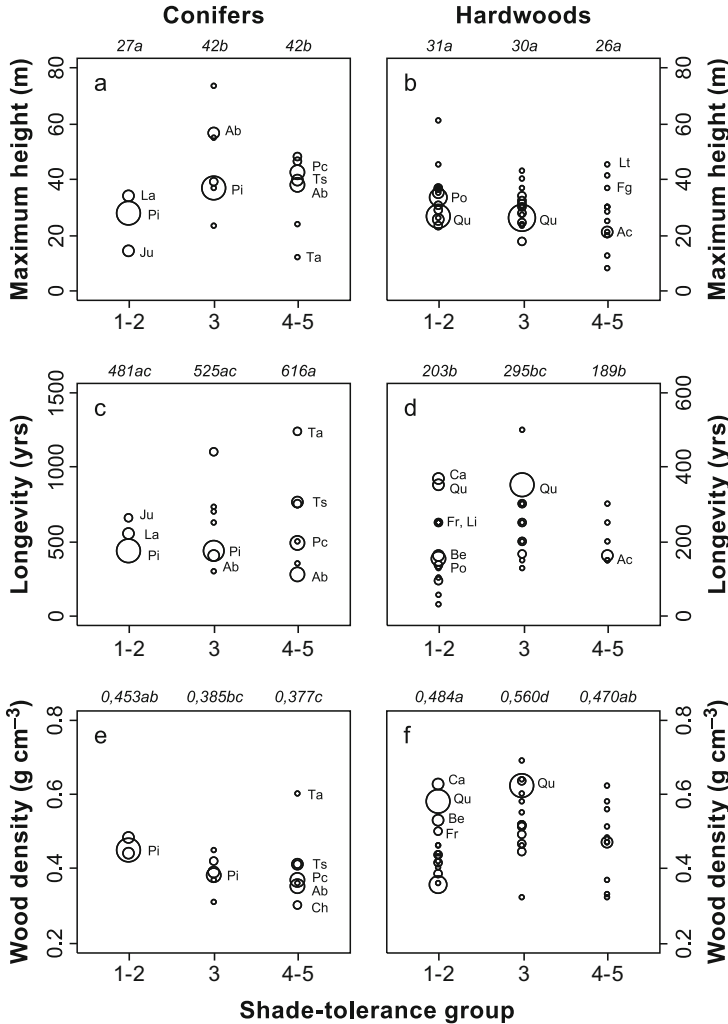
Fig. 5.2 Maximum height h_{max} (**a**, **b**), maximum longevity λ (**c**, **d**) and wood density ρ (**e**, **f**) for coniferous and hardwood species (*left* and *right panels*, respectively) as a function of shade-tolerance class (*1–2* intolerant, *3* intermediate, *4–5* tolerant) based on data for 182 North American tree species. Individual data points represent mean values for genera. The area of the *circles* is proportional to the number of species per genus. Figures at the top of the panel are means for each shade-tolerance class. The *lower case letters* indicate groups that are not significantly different (Tukey's HSD post-hoc comparison including both conifers and hardwoods). Specific genera mentioned in the text are abbreviated as follows: Ab *Abies*, Ac *Acer*, Be *Betula*, Ca *Carya*, Ch *Chamaecyparis*, Fg *Fagus*, Fr *Fraxinus*, Ju *Juniperus*, La *Larix*, Lt *Lithocarpus*, Li *Liriodendron*, Pc *Picea*, Pi *Pinus*, Po *Populus*, Qu *Quercus*, Ta *Taxus*, Ts *Tsuga*, Tx *Taxodium*, Ul *Ulmus*

increased in h_{max} to 42 m, but hardwoods decreased to 26 m. As a result, both intermediate and tolerant conifers were significantly taller by about 14 m than their hardwood counterparts. The high variance in h_{max} in the tolerant groups is due to the existence of two functional groups: (1) relatively tall canopy species;

and (2) relatively short sub-canopy species, such *Acer pensylvanicum* and *Carpinus caroliniana* in the hardwoods, and *Taxus brevifolia* in the conifers. As mentioned above, sub-canopy trees were not included in the model simulations.

Tree longevity was not related to shade tolerance within either conifers or hardwoods but, for a given shade-tolerance class, conifers were about 300 years longer-lived than hardwoods (Fig. 5.2c,d). This difference between conifers and hardwoods was significant for the intolerant and tolerant classes. The intolerant hardwoods include two subgroups: short-lived species dominated by poplars (*Populus* spp.) and birches (*Betula* spp.) with longevities up to 150 years, and 'long-lived pioneers' (see Chap. 2 by Wirth et al., this volume), such as oaks (*Quercus* spp.) and hickories (*Carya* spp.), with longevities over 300 years. Nearly all intolerant conifers are long-lived, and most belong to the genus *Pinus*. Longevities of intolerant conifers range from 100 years (*Pinus clausa*) to 1,600 years (*Pinus aristata*) with a mean longevity of 480 ± 370 years ($\pm$ standard deviation). The tolerant conifers are a particularly diverse group, with longevities ranging from 150 years (*Abies fraseri*) to 1,930 years (*Chamaecyparis nootkatensis*). True firs (*Abies* spp.), which tend to be shade tolerant, have among the lowest longevities of all conifers.

Wood density of conifers declined with increasing shade-tolerance, from about 0.45 g_{dw} cm^{-3} in intolerant genera (e.g. *Pinus*, *Larix* and *Juniperus*) to about 0.35 g_{dw} cm^{-3} in tolerant genera (Fig. 5.2e). The one outlier is again the understorey tree *Taxus brevifolia* (0.6 g_{dw} cm^{-3}). Both the mean and variance of wood density was higher in hardwoods than in conifers (Fig. 5.2e,f). Within the intermediate and tolerant classes, hardwood wood densities exceeded those of conifers by a factor of about 1.5. Within the hardwoods, the long-lived pioneers (*Carya* and *Quercus*) had the highest wood densities. It is important to note that shade-tolerance is partly confounded with water availability, as intolerant species tend to occur on drier sites where wood density is often elevated.

In summary, conifers reach higher maximum heights than hardwoods in the intermediate and tolerant classes, and conifers live substantially longer than hardwoods irrespective of shade-tolerance. However, conifers have a lower wood density compared to hardwoods.

5.4 Model Performance and Lessons from the Equilibrium Behaviour

We validated our model against the observed biomass of 41 old-growth stands of known age (see Table 14.3 in Chap. 14 by Lichstein et al., this volume), representing a wide range of forest types and stand ages (60–988 years; median age = 341 years). We assigned each of these 41 validation stands to one of the 106 forest types described above (Sect. 5.2.3). The forest type determined the prescribed species succession for each validation model-run, which was terminated at the actual age of

the validation stand. As in the standard setup (Sect. 5.2.4), we used the mean biomass across 900 patches to characterise the behaviour of the model. Despite the simplicity of the model, and the fact that it ignores edaphic and climatic controls, the model explained 63% of the variation in the old-growth biomass data (Fig. 5.3). This relatively high R^2 suggests that our model should be a useful tool for studying forest carbon stocks. After tuning θ (see Eq. 5.3), the regression line relating observed and predicted values was close to the 1:1 line (Fig. 5.3). Note that this tuning is not species-specific, and therefore has little effect on the R^2 of the validation exercise, but merely ensures that, on average, our model produces reasonable biomass values.

The general behaviour and sensitivity of the model is best understood by examining equilibrium carbon stocks ($C_{x,eq}$) in relation to two key species-specific parameters: maximum height, h_{max}, and longevity, λ (Fig. 5.4). All other parameters in Fig. 5.4, including wood density, were kept constant at the mean conifer or hardwood values.

The biomass equilibrium is controlled mainly by the maximum attainable biomass (which is largely a function of the height-age-curve defined by h_{max}) and the whole-patch mortality rate (which is a function of λ). Within both conifers and hardwoods, $C_{b,eq}$ increases with h_{max} in a slightly concave fashion but with λ in a strongly convex fashion (Fig. 5.4a,b); i.e. the sensitivity of $C_{b,eq}$ to h_{max} is highest for high values of h_{max}, whereas the sensitivity to λ is highest for low values of λ. Our analysis suggests two mechanisms leading to higher $C_{b,eq}$ in coniferous, compared to hardwood, old-growth: (1) Firstly, in North America, conifers occupy higher $C_{b,eq}$- regions of the two-dimensional h_{max}-λ space compared to hardwoods (cf. Figs. 5.4e–f). (2) A second, more subtle, effect is that, for given values of h_{max} and λ, conifers have higher $C_{b,eq}$ than hardwoods due to conifers having higher stand density (which is captured by the volume–height allometries in our model; Fig. 5.1b) and higher biomass expansion factors (Fig. 5.1c). These two factors more
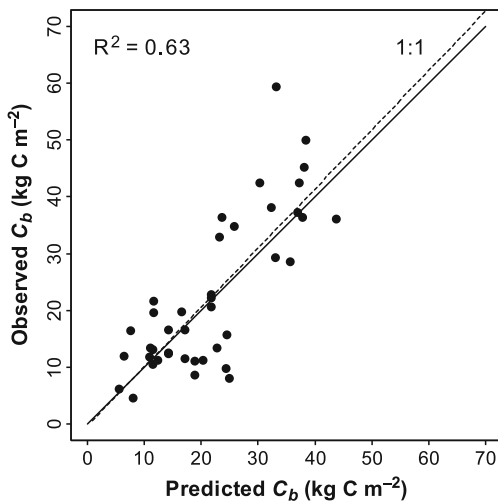
Fig. 5.3 Validation of the model against biomass data from old-growth stands with a known age (see Table 14.3 in Chap. 14 by Lichstein et al., this volume). The 1:1 relationship is shown as a *solid line* and the linear regression between observed and predicted biomasses as a *dashed line* ($C_{b,obs} = -0.34 + 1.04\ C_{b,pred}$)

than compensate for the fact that conifers have lower mean wood density than hardwoods.

The equilibrium woody detritus pool, $C_{d,eq}$, is controlled by woody detritus input and the decay rate k_d. Like $C_{b,eq}$, $C_{d,eq}$ increases with h_{max} because tall-statured
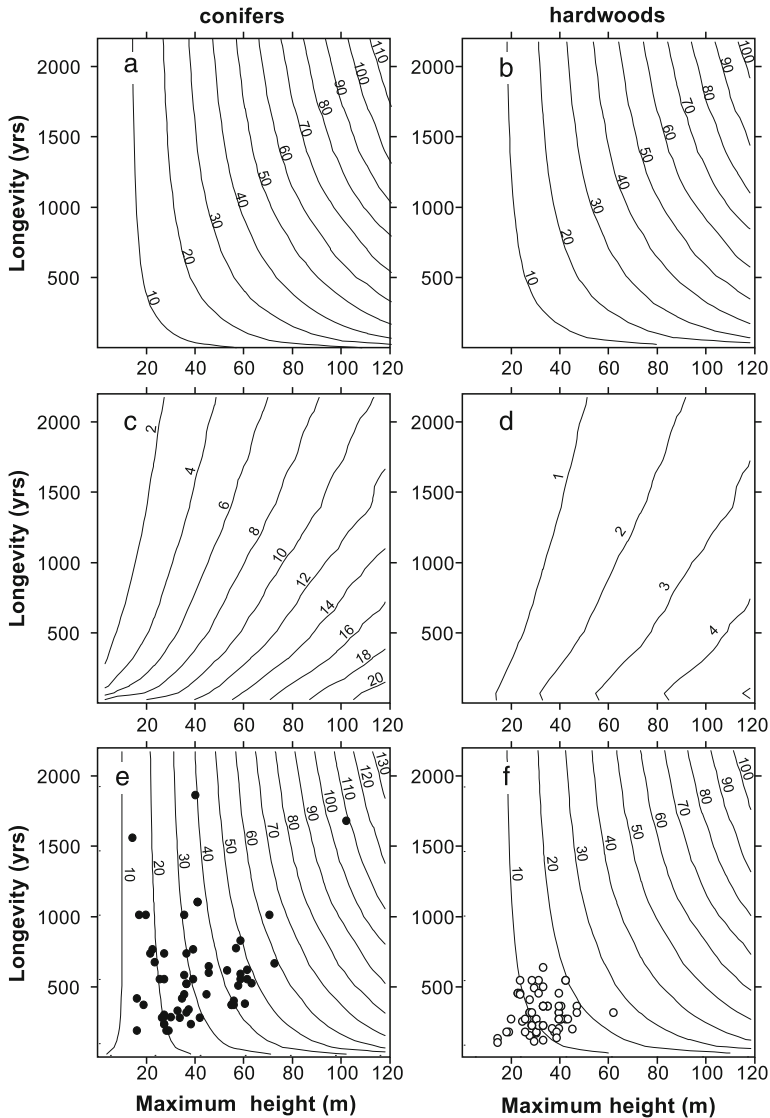
Fig. 5.4 Equilibrium stocks of biomass (**a**, **b**), woody detritus (**c**, **d**) and total aboveground carbon (**e**, **f**) as a function of maximum height (*x-axis*) and longevity (*y-axis*) shown separately for coniferous and hardwood monocultures (*left* and *right columns*, respectively). Isolines are labelled with carbon stocks in units of kg C m^{-2}. The spectrum of combinations of maximum height and longevity as realised in the tree flora of North America is displayed in panels **e** and **f** (*filled* and *open dots*, respectively)

forests reach higher biomass levels and therefore – for a given λ – produce more woody detritus (Fig. 5.4c–d). However, unlike $C_{b,eq}$, $C_{d,eq}$ decreases with λ because higher λ implies a lower biomass turnover rate (i.e. slower transfer from biomass to woody detritus). For given values of h_{max} and λ, $C_{d,eq}$ is about four times higher in conifers than in hardwoods (Figs. 5.4c–d) due to the decomposition rates (k_d of 0.03 year^{-1} in conifers versus 0.1 year^{-1} in hardwoods).

Total aboveground equilibrium carbon, $C_{a,eq}$, has a similar relationship to h_{max} and λ as $C_{b,eq}$, because $C_{b,eq}$ is much greater in magnitude than $C_{d,eq}$ (Fig. 5.4). However, the difference between conifers and hardwoods (for given values of h_{max} and λ) is greater for $C_{a,eq}$ than for $C_{b,eq}$ due to the additional contribution of $C_{d,eq}$. As with $C_{b,eq}$, conifers advance into regions of higher $C_{a,eq}$ due to their greater size and longevity and due to their steeper equilibrium surface (Fig. 5.4e–f). It is tempting to visualise successional carbon trajectories by moving from one circle (i.e. species) to another across the surfaces in Fig. 5.4. For example, moving from an average hardwood to an average conifer would imply a gain in carbon. Although this equilibrium approach is useful heuristically, it provides only limited insight into successional dynamics because it does not explicitly account for temporal dynamics. Succession, rather than progressing from one equilibrium state to the next, is most likely dominated by transient dynamics. In the next section, we use our model to examine the temporal (i.e. successional) dynamics of carbon stocks.

5.5 The Spectrum of Carbon Trajectories in North American Forests

The spectra of carbon stock changes (ΔC_x) across all 106 FCT during the four successional stages (pioneer, transition, early old-growth, and late old-growth) are shown in Fig. 5.5. Distributions of stock changes during the two earlier stages have substantial spread and are right-skewed. Changes in total aboveground carbon (ΔC_a) during the pioneer stage range from 60 (*Pinus clausa*) to 498 g C m^{-2} year^{-1} (*Sequoia sempervirens*). During the transition phase, the total spread of ΔC_a increases to 340 g C m^{-2} year^{-1}, with values ranging from a loss rate of -69 (coastal *Pinus contorta*) to an accumulation rate of 262 g C m^{-2} year^{-1} (transition from *Pinus contorta* to *Pseudotsuga menziesii*). During the early old-growth stage, ΔC_a ranges from carbon losses of -59 g C m^{-2} year^{-1} (*Picea mariana* to *Abies balsamea* in boreal Canada) to a gain of 93 g C m^{-2} year^{-1} (*Pinus monticola* to *Pseudotsuga menziesii*). Absolute values and ranges of biomass change (ΔC_b) were always greater than those of woody detritus (ΔC_d).

Despite the variability, there was a consistent decline in ΔC_a from the pioneer stage to the late old-growth stage (Fig. 5.5). Nevertheless, mean ΔC_a remained positive throughout the first 400 years of succession (126, 58, and 13 g C m^{-2} year^{-1} during the pioneer, transition, and early old-growth stages, respectively), and approached zero only during the late old-growth stage. This
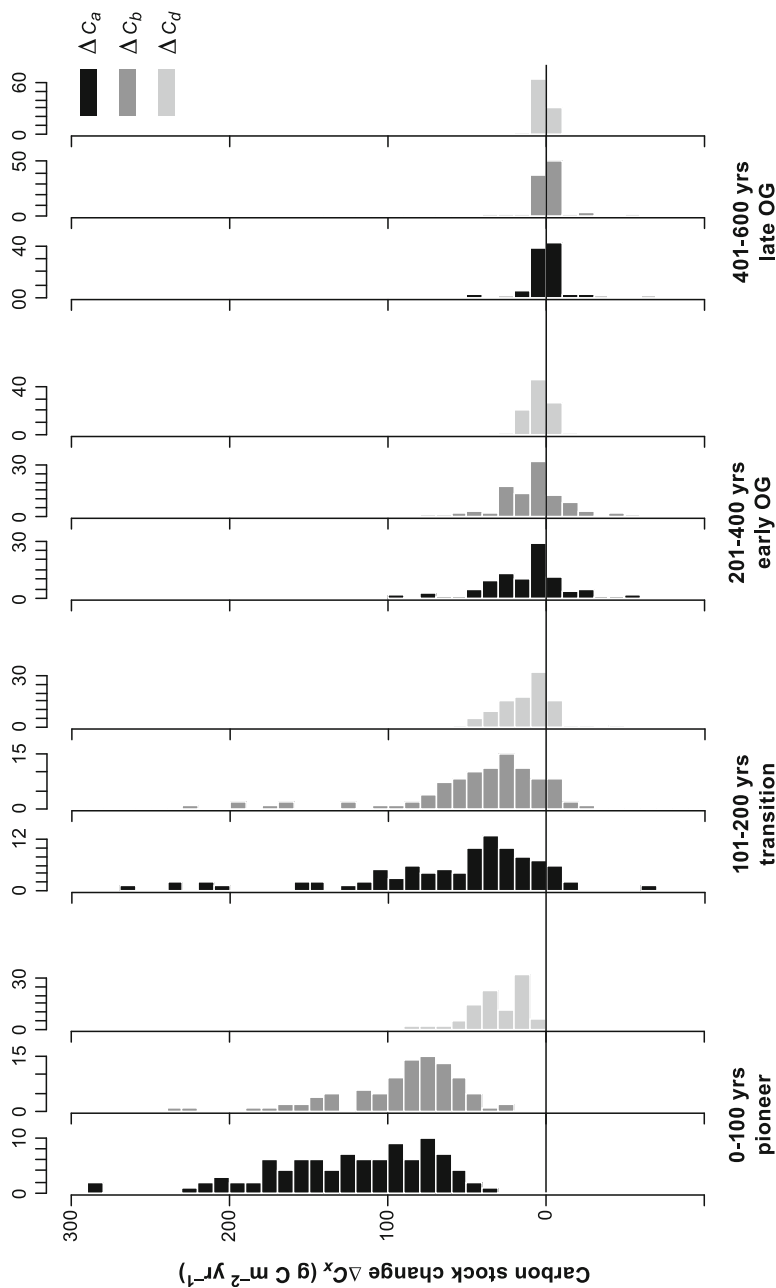
Fig. 5.5 Histograms of aboveground carbon stock changes (ΔC_x) in units of g C m^{-2} year^{-1} for 106 North American forest successions for four successional stages (pioneer: 0–100 years, transition: 101–200 years, early old-growth (*OG*): 201–400 years and late OG: 401–600 years). The different levels of *grey shading* indicate the different pools: C_a = Total above-ground carbon (biomass plus woody detritus), C_b = Aboveground biomass carbon, C_d = aboveground woody detritus carbon

result suggests that, on average, shifting traits produce an increase to a late-old-growth asymptote for aboveground carbon stocks in North American forests. Although shifting traits result in late-successional declines in some successions (see below), the results presented here suggest that this is not the typical case. We emphasise that these results represent the effects of shifting traits in isolation of other mechanisms (e.g. synchronised mortality) that may also affect biomass trajectories. The relative contribution of woody detritus to ΔC_a increased over time: From the transition to the early old-growth stage, mean ΔC_b decreased by a factor of 5.5 (from 44 to $8 \, \mathrm{g \, C \, m^{-2} \, year^{-1}}$), while mean ΔC_d decreased by a factor of 3 (from 12 to $4 \, \mathrm{g \, C \, m^{-2} \, year^{-1}}$).

5.6   Determinants of Old-Growth Carbon Stock Changes

The previous section examined patterns of aboveground carbon stock changes across the four successional stages. In this section, we focus on the early old-growth stage (201 to 400 years), and ask why certain sequences continue to accumulate carbon while others remain neutral or even lose carbon from the aboveground compartments during this period.

Given that equilibrium carbon stocks were higher in coniferous than in hardwood forests (Fig. 5.4), we might hypothesise that ΔC_a in the carbon balances of old-growth forests is driven by compositional changes that involve transitions between conifers and hardwoods. To test this hypothesis, we classified the 106 successions according to which species groups dominate in the pioneer and late-successional stages. We focus on the seven combinations represented by at least three cover types: (1) conifer to other conifer ($c_i c_j$), (2) conifer to same conifer ($c_i c_i$; i.e. no compositional change), (3) conifer to hardwood (ch), (4) hardwood to conifer (hc), (5) hardwood to other hardwood ($h_i h_j$), (6) mixed conifer-hardwood type to other mixed type ($m_i m_j$), and (7) mixed type to same mixed type ($m_i m_i$).

Substantial carbon accumulation occurred (on average) when conifers were replaced by other conifers ($c_i c_j$). Carbon stock changes were close to zero for all other cases that lacked a shift between conifers and hardwoods ($c_i c_i$, $h_i h_j$, $m_i m_j$, $m_i m_i$). As expected, the change from conifers to hardwoods was associated with carbon losses, while the reverse, a change from hardwoods to conifers, was associated with carbon gains. The above patterns held for total aboveground carbon (ΔC_a; Fig. 5.6a), biomass (ΔC_b; Fig. 5.6b), and woody detritus (ΔC_d; Fig. 5.6d) when group-specific decay rates were used ($k_d = 0.03$ and 0.1 for conifers and hardwoods, respectively). In contrast, ΔC_d was close to zero when the same mean decay rate was used for both conifers and hardwoods (Fig. 5.6c). Thus, accounting for phylogenetic differences in decay rates leads to a predicted loss of woody detritus when conifers (with relatively slow-decomposing detritus) are replaced by hardwoods (with relatively fast-decomposing detritus), and an accumulation of woody detritus when hardwoods are replaced by conifers. The biomass accumulation
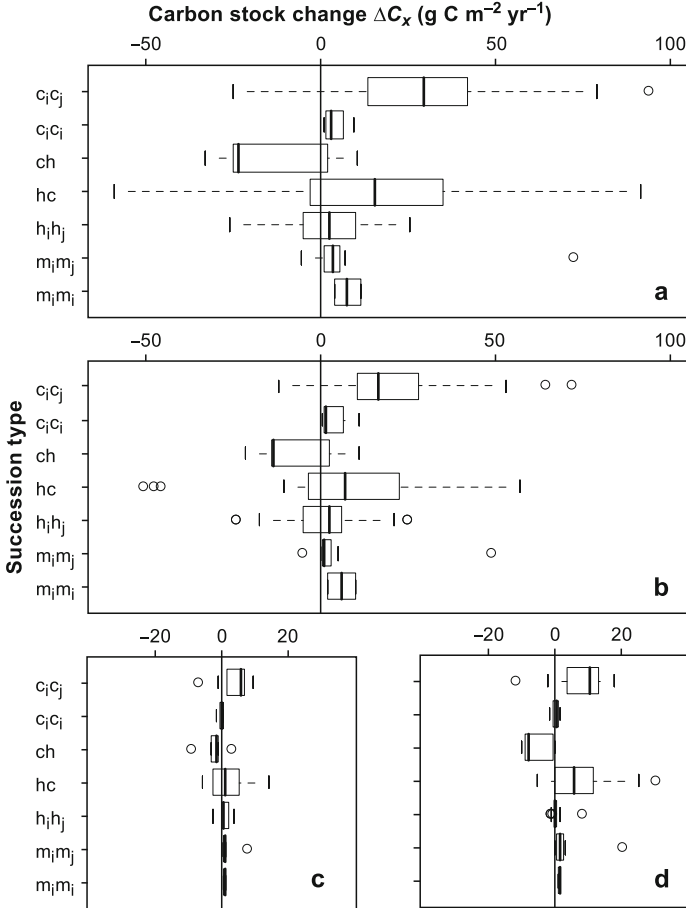
Fig. 5.6 Changes in the total aboveground carbon (**a**), biomass carbon (**b**), and wood detritus (**c, d**) during the early old-growth phase for different types of successional trajectories. In panel **c** a constant value of k_d of 0.05 year^{-1} was used for all forest types, and in panel **d** different values of the decay constant k_d were used for conifers and hardwoods (cf. Table 5.1). The successional trajectories are coded as follows (see also text): c dominated by conifers, h dominated by hardwoods, m mixed. The suffixes i and j indicate differences in species composition within the three groups. For example, a conifer sequence without species turnover is labelled '$c_i c_i$' whereas one involving species turnover is labelled '$c_i c_j$'

effect of changes in species groups is thus amplified by the woody detritus dynamics when phylogenetic differences in decay rates are accounted for. This is partly responsible for the positive correlation between ΔC_b and ΔC_d during the early old-growth stage ($r = 0.70$; Fig. 5.7).

When we compare how changes in the input parameters h_{max}, ρ, and λ between successional stages correlate with carbon stock changes during the early old-growth stage, we see indeed that height differences exhibit the highest degree of correlation
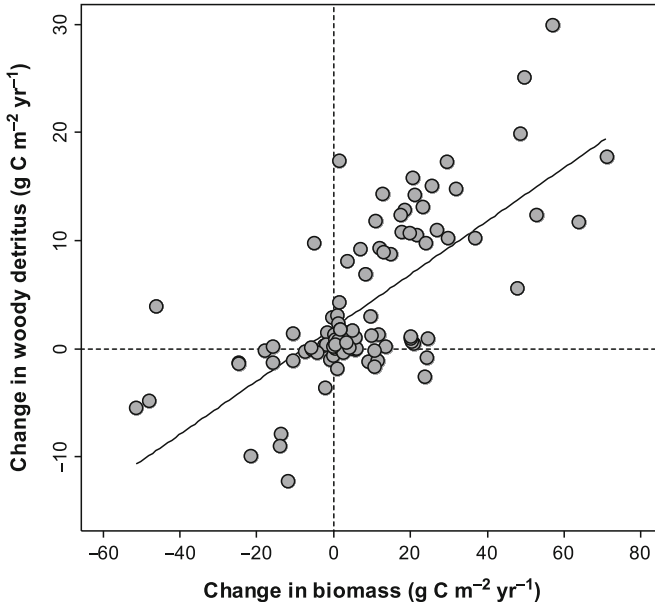
Fig. 5.7 Relationship between changes in biomass and woody detritus carbon stocks during the early old-growth phase in the 106 successions (*grey circles*) derived from the forest cover type descriptions

Table 5.2 Matrix of Pearson's correlation coefficients. Carbon stock changes (ΔC_a = total aboveground; ΔC_b = biomass; ΔC_d = woody detritus) refer to the early old-growth stage (201–400 years). Differences in the species-specific parameters h_{max}, ρ, and λ are between the late-successional and the pioneer stages (L−P) and the late-successional and mid-successional stages (L−M)

Δh_{L-M}	$\Delta \rho_{L-P}$	$\Delta \rho_{L-M}$	$\Delta \lambda_{L-P}$	$\Delta \lambda_{L-M}$	ΔC_a	ΔC_b	ΔC_d	
0.429	−0.279	−0.058	−0.004	0.003	0.531	0.515	0.471	Δh_{L-P}
	0.066	0.072	−0.042	0.176	0.354	0.422	0.11	Δh_{L-M}
		0.553	−0.030	0.038	0.060	0.060	0.052	$\Delta \rho_{L-P}$
			0.004	0.141	0.119	0.166	−0.013	$\Delta \rho_{L-M}$
				0.688	−0.017	0.067	−0.239	$\Delta \lambda_{L-P}$
					0.007	0.121	−0.296	$\Delta \lambda_{L-M}$
						0.976	0.835	ΔC_a
							0.698	ΔC_b

($r \sim 0.5$; Table 5.2). The correlation of stock changes with wood density differences is small (between $r = -0.01$ and 0.19) and the correlation of stock changes with longevity differences absent. It is interesting to note that the height difference between late-successionals and pioneers has a higher influence on both ΔC_a and ΔC_b ($r = 0.53$ and 0.51, respectively) than the difference between late- and mid-successionals ($r = 0.42$ and 0.35, respectively). Longevity differences seem to

matter only for the changes in woody detritus where an increase is longevity was negatively correlated with ΔC_d.

5.7 Discussion

5.7.1 Limitations of Our Approach

Our modelling approach was deliberately simple, and the results are therefore easy to interpret. However, this simplicity is associated with a number of limitations: (1) we considered only two carbon pools – aboveground biomass and woody detritus – and therefore cannot make direct inferences on net ecosystem carbon balance. (2) Because the model considers only carbon, it ignores potential changes in productivity due to shifts in nutrient availability (Pastor and Post 1986; Chap. 9 by Wardle, this volume). (3) Edaphic and climatic effects were not considered when parameterising the model. Thus, the version of the model presented here ignores, for example, intraspecific variation in plant traits due to edaphic or climatic influences. (4) Finally, we prescribed the sequence of species replacement in each forest type based on empirical descriptions. While this is a valid approach for determining the consequences of species turnover, our model obviously cannot be used to study the mechanisms causing the turnover.

The simplicity of our approach arose, in part, from our desire to systematically evaluate the 'shifting traits' mechanism across a large geographic area. Thus, the model was centred around a few parameters (h_{max}, ρ, λ) that were available for most North American tree species and that we suspected a priori to strongly affect carbon dynamics. This simple design allowed us to parameterise the model for the major forest cover types ($n = 106$ successions) and tree species ($n = 182$) of an entire continent. Despite its simplicity, our model explained 63% of the variation in an independent dataset of old-growth forest biomass (see Table 14.3 in Chap. 14 by Lichstein et al., this volume). This suggests that our model captures key features of forest dynamics leading to biomass differences among forest types. Nevertheless, we urge caution in over-interpreting our results for individual successions.

5.7.2 Comparison with Independent Data

In the following, we confront our model results with independent data and ask (1) how well we do in predicting the general pattern and magnitude of carbon stock changes with successions – especially during the early old-growth stage –; and (2) to what extent the data provide support for the 'shifting traits hypothesis'. The data come from three different sources: forest biomass and woody detritus chronosequences (reviewed below), inventories (see Chap. 14 by Lichstein et al., this volume), and an evaluation of a new forest carbon cycle database (see Chap. 15

by Schulze et al., this volume). A more comprehensive synthesis of old-growth carbon dynamics including stock changes inferred from inventories, soil carbon dynamics, and estimates of net ecosystem exchange of CO_2 is provided in the synthesis chapter (Chap. 21 by Wirth).

5.7.2.1 Magnitude of Old-Growth Carbon Stock Changes – Long-Term Chronosequences and Inventories

To our knowledge, there are only 16 aboveground biomass chronosequences for temperate or boreal forests that extend beyond a stand age of 200 years (Fig. 5.8, Table 5.3). Pooling all forest types, the mean (median) biomass changes along these chronosequences during the first four successional stages (pioneer: 0–100 years; transition: 101–200 years; early old-growth: 201–400 years; and late old-growth: 401–600 years) are 91 (75), 32 (20), 19 (12), and 9 (4) g C m^{-2} year^{-1}. For the first three stages, this is in good agreement with our model results, where the mean (median) biomass changes were 94 (82), 44 (35), and 8 (5) g C m^{-2} year^{-1} (Fig. 5.9). However, for the later stages, our model predicts lower mean biomass changes than observations would suggest. This is particularly true for the late old-growth stage, where the model suggests equilibrium (-0.2 g C m^{-2} year^{-1}) but the data still suggest an increase (see above). The difference between the model and the chronosequences during the early old-growth phase is partly due to the fact that the chronosequences extend to an average age of only 316 years. The modelled biomass change between 201 and 300 years was 12 (8) g C m^{-2} year^{-1}, which is closer to the chronosequence estimate. Another important similarity between the model and chronosequences is the predominance of constant or increasing biomass. Except for the Lake Duparquet chronosequence (Paré and Bergeron 1995), no biomass declines were observed in the data.

Of the chronosequences calculated from the US Forest Inventory and Analysis database (FIA; see Chap. 14 by Lichstein et al., this volume) only those from the western US exceeded a time span of 200 years. The FIA data suggest somewhat lower biomass changes during the pioneer and transition stages, but higher rates during the early old-growth stage. However, the high values during the latter are due mostly to the temperate rain forests in the Pacific Northwest.

In addition to the chronosequences summarised above, data on carbon stocks and fluxes in broad stand-age classes were recently compiled for meta-analyses by Pregitzer and Euskirchen (2004) and Schulze et al. (Chap. 15, this volume – based on the database of Luyssaert et al. 2007). In these two studies, the fraction of boreal and temperate forest stands older than 200 years was 9% and 11%, and the fraction of stands older than 400 years only 3% and 2%, respectively. Although the database compiled by Pregitzer and Euskirchen (2004) contains limited biomass data for stands older than 200 years, these are not included in their analysis. Hence, this study is not considered further here. Schulze et al. (Chap. 15, this volume) give an overall mean biomass accumulation rate of 30 g C m^{-2} year^{-1} between stand
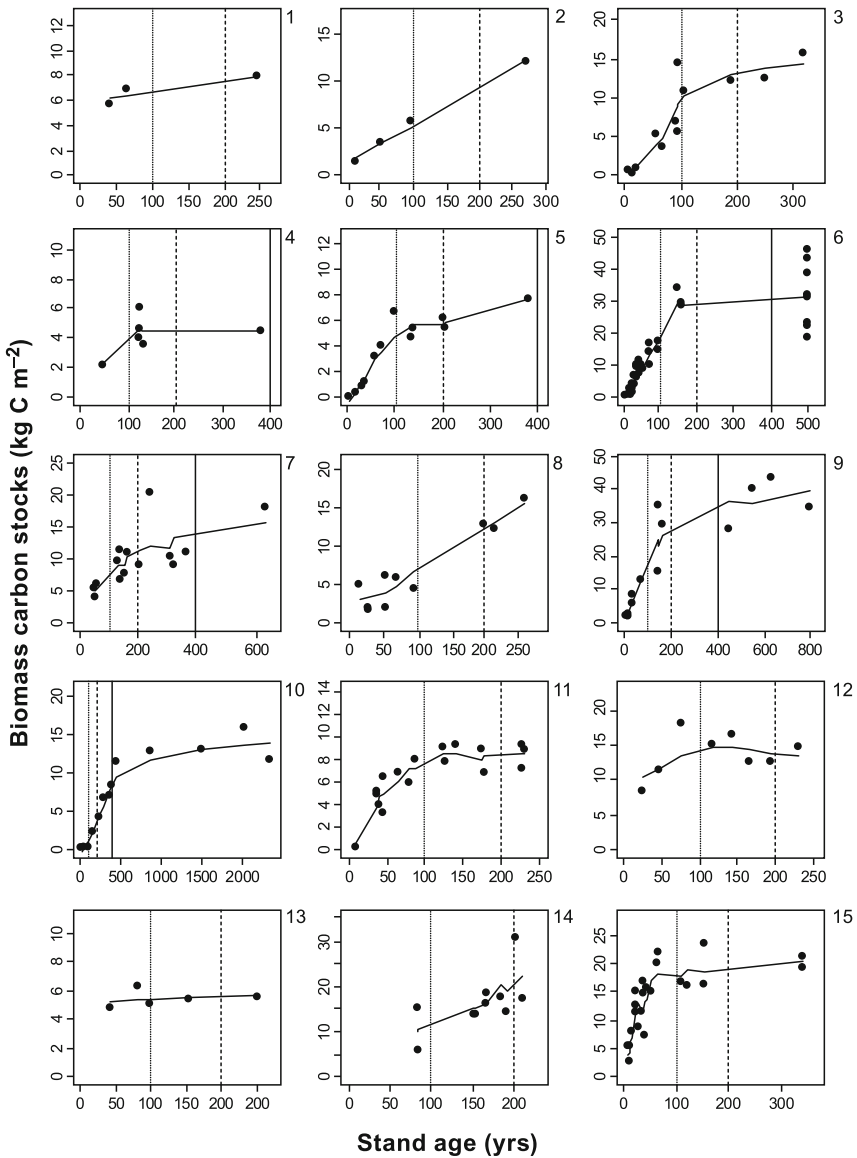
Fig. 5.8: Temperate and boreal chronosequences of aboveground biomass carbon extending to stand ages beyond 200 years. The data (*black dots*) were taken from publications (see legend to Fig. 5.10), and where necessary were digitised from figures. The *vertical lines* delineate the successional stages 'pioneer,' 'transition', and 'early old-growth.' The intersections between the *vertical lines* and the *fitted curves* were used to calculate the changes in biomass during each successional stage. The curves were fit with Friedman's super smoother (subsmu-function in R – with parameters *span* = 0.2 and *bass* = 10). The numbers *1–15* indicate the sequences described in Table 5.3

Table 5.3 Temperate and boreal chronosequences of aboveground biomass carbon extending beyond a stand age of 200 years. Labels refer to the panel numbers in Fig. 5.8 (except sequence 16) and to the references listed below the table. For 'Type' descriptions, see Sect. 5.6. Species dominating during early and late stages of the succession are listed in the *Pioneer* and *Late* columns, respectively; species abbreviations are given below the table. *P* Pioneer, *T* transition, *EOG* early old-growth $C_{b,x}$ estimated biomass (kg C m^{-2}) at stand age x (years); ΔC_b estimated biomass change (g C m^{-2} year^{-1}) in the pioneer (0–100 years), transition (101–200 years), and early old-growth stage (201–400 years)

Label[a]	Name	Type	Duration (years)	Pioneer[b]	Late[b,d]	$C_{b,100}$	$C_{b,200}$	$C_{b,400*}$	ΔC_b-P	ΔC_b-T	ΔC_b-EOG
1	Fraser Exp. Forest	c_fc_i	245	Pincon	Pincon	6.4	7.4	8	64	10	13
2	Zotino Pine		270	Pinsyl	Pinsyl	5	9	12.5	50	40	50
3	Metolia		316	Pinpon	Pinpon	10	13	14.3	100	30	11
4	Yakutia		380	Largme	Largme	4	4.5	4.5	40	5	0
5	Zotino lichen Pine		383	Pinsyl	Pinsyl	4.5	6	7.5	45	15	8
6	Wind River Range		500	Psemen	Psemen, Tsuhet	20	29	31	200	90	10
7	SW Montana		640	Pinalb, Pincon, Piceng[c], Abilas[c]	Pinalb, Pincon, Piceng[c], Abilas[c]	8	11	14	80	30	15
8	Cascade Mountains	c_fc_j	260	Pinmon, Pincon	Tsumen	7	12	16	70	50	67
9	Andrews		795			16	27	34	160	110	35
10	Michigan Sand Dune		2,348	Pinstr, Pinres[c]	Pinres, Pinstr, Tsucan	2	4	8.5	20	20	23
11	Zotino dark taiga	hc	230	Betsp, Poptre	Abisib, Picobo, Pinsib	7.5	8.1	8.2	75	6	3
12	Lake Duparquet		230	Popbal, Poptre, Betpap	Thuocc, Abibal, Poptre[c]	14	13.5	13.4	140	-5	-3

13	Bonanza Creek		250	5.5	5.7	5.9	55	2	4	Picgla	Betpap, Poptre
14	Adirondack Mountains	mix	410	8.0	9.6	14.6	80	16	25	Betall, Faggra, Picru, Tsucan	Betall, Faggra, Picru, Tsucan
15	Chesapeake Bay	$h_i h_j$	340	17	18	20.5	170	10	18	Faggra, Carsp., Quesp.	Lirtul, Quesp.
16	Fontainebleau	$h_i h_i$	211	10.5	20	20	105	95	-	Fagsyl	Fagsyl
Mean							91 ± 52	32 ± 36	19 ± 19		
Median							75	20	12		

[a]References: *1* Ryan and Waring (1992); *2* Wirth et al. (2002); *3* Law et al. (2003); *4* Schulze et al. (1995); *5* Wirth et al. (2002b); *6* Janisch and Harmon (2002); *7* Forcella and Weaver (1977); *8* Boone et al. (1988); *9* Beverly Law, personal communication; *10* Lichter (1998); *11* C. Wirth, unpublished data; *12* Paré and Bergeron (1995); *13, 16* various sources compiled in the Luyssaert et al. (2007) database; *15* Brown and Parker (1994); *16* Keeton et al. (2007)

[b]Species abbreviations: Abilas *Abies lasiocarpa*, Abisib *Abies sibirica*, Betsp *Betula* sp., Betall *Betula alleghaniensis*, Carsp *Carya* sp., Faggra *Fagus grandifolia*, Largme *Larix gmlinii*, Lirtul *Liriodendron tulipiferum*, Piceng *Picea engelmannii*, Picgla *Picea glauca*, Picobo *Picea obovata*, Picrub *Picea rubra*, Pinalb *Pinus albicaulis*, Pincon *Pinus contorta*, Pinmon *Pinus monticola*, Pinpon *Pinus ponderosa*, Pinres *Pinus resinosa*, Pinsib *Pinus sibirica*, Pinstr *Pinus strobus*, Pinsyl *Pinus sylvestris*, Popbal *Populus balsamifera*, Poptre *Populus tremula*, Poptro *Populus tremuloides*, Psemen *Pseudotsuga menziesii*, Quesp *Quercus* sp., Tsucan *Tsuga canadensis*, Tsuhet *Tsuga heterophylla*, Tsumen *Tsuga mertensiana*.

[c]Species are admixed (i.e. non-dominant).

[d]Data for the late old-growth stage (LOG: 401–600 years) were available only for four sequences: ΔC_b for the LOG stage are available for sequences 6, 7, 9, and 10 and are 5.1, 8.5, 15.0, and 10.0 g C m^{-2} year^{-1}, respectively, with a mean of 9.6 ± 4.1 g C m^{-2} year^{-1}
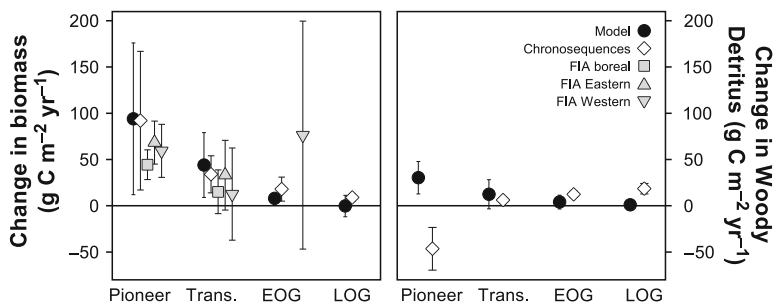
Fig. 5.9 Comparison of modelled and measured changes of aboveground biomass (*left panel*) and coarse woody detritus (*right panel*) in g C m^{-2} year^{-1} within the four successional stages 'pioneer,' *Trans.* 'transition', *EOG* 'early old-growth', and *LOG* 'late old-growth'. *Error bars* standard deviation. The sample unit is a forest sequence. FIA Unites States Forest Inventory and Analysis database (see Chap. 14 by Lichstein et al., this volume)

ages 100 and 300 years, which is in good agreement with the estimates presented above.

In addition, we evaluated the woody detritus chronosequences compiled in Harmon (Table 8.2). As noted by Harmon (Chap. 8), the woody detritus stocks followed either a "reverse J-" or "U-" shaped curve. Mean (median) stock changes during the four successional stages were −46 (−23), 6 (2), 12 (3), and 19 (6) g C m^{-2} year^{-1}, respectively. Thus, in contrast to biomass (see above), carbon accumulation rates for woody detritus increased with age. Unlike the woody detritus chronosequences (where young stands may be initiated with a woody detritus 'legacy'), our model considers only de-novo woody detritus (i.e. stands are initiated with zero woody detritus). This explains the large discrepancy between the model prediction and the observation during the pioneer stage (Fig. 5.9). During the succeeding stages all fluxes are positive. The model suggests decreasing accumulation rates 12 (6), 3 (1), and 1 (0.2) g C m^{-2} year^{-1} for the transition, early, and late old-growth stages, respectively, while the observations suggest the opposite (Fig. 5.9 – white diamonds).

These comparisons show that the predictions from our model are roughly in agreement with the few observations we have of biomass accumulation rates in old-growth forests. However, the modelled carbon accumulation in woody detritus is substantially lower than the observed rates, most likely because the latter are based on data from chronosequences from boreal or high-elevation sites with slowly decomposing coniferous woody detritus. For the early old-growth stage, both the data and the model suggest a significant carbon accumulation in the biomass and woody detritus, but the measured rates exceed the modelled rates by factor of 3 (31 versus 11 g C m^{-2} year^{-1}) and the discrepancy is even larger for the late old-growth stage (0.8 vs 28 g C m^{-2} year^{-1}). We believe that part of the discrepancy is due to the fact that we did not attempt a comparison at the level of FCT (see above). Compared with the spectrum of forest types that we model, in the chronosequence data forest types on marginal sites (boreal, high-elevation, dry) are

over-represented. Trees in such forests tend to grow and decompose more slowly, thus accumulation of carbon is shifted to later stages of stand development compared with forests on more fertile sites. Also, we might have missed an additional mechanism in our model that causes a late-successional carbon accumulation in the biomass and wood detritus.

5.7.2.2   Evidence for the 'Shifting Traits Hypothesis'

Our model predicts that successional species turnover involving a shift in key traits, particularly h_{max}, may induce a gain or loss in biomass and woody detritus carbon even late in succession. Given that conifers tend to grow taller than hardwoods, carbon gain is expected if hardwoods are replaced by conifers, and a loss is expected if the reverse happens (Fig. 5.4). However, there are also pronounced differences in stature within the two phylogenetic groups. The available observations for testing the 'shifting traits hypothesis' are the 15 true chronosequences in Fig. 5.8 (of which only 10 are from North America) and the six mesic seres extracted from the US inventory data (see Fig. 14.3 in Chap. 14 by Lichstein et al., this volume). For the reasons given in Sect. 5.7.1, we do not attempt a quantitative site-by-site validation of successional trajectories, but rather look at qualitative features.

   For the US inventories (Fig. 14.3, op cit.), our model would predict – based on a shift in h_{max} values – a biomass decline for five successions: the Piedmont transition from *Liriodendron* (h_{max} = 61 m, λ = 250 years) to *Quercus/Carya* ($h_{max} \sim$ 30/33 m), the New England transition from *Pinus strobus/Quercus rubra* (h_{max} = 43/30 m) to *Quercus/Carya/Acer rubrum* (h_{max} = 30/33/28 m), the Cascade Mountains transition from coastal *Pseudotsuga menziesii* (h_{max} = 73 m) to *Tsuga heterophylla* (h_{max} = 52 m), the Rocky Mountains transition from *Pseudotsuga menziesii* ($h_{max} \sim$ 50 m) to *Picea engelmannii/Abies lasiocarpa* (h_{max} = 44/35 m), and the sub-boreal upper Midwest transition from *Pinus resinosa/Pinus strobus* (h_{max} = 32/43 m) to *Abies balsamea/Picea glauca* (h_{max} = 23/55 m). For four out of these five transitions the inventory data indeed suggest declines, which are, however, small in all but the Cascade Mountains series. No decline occurred in the Rocky Mountain series, most likely because of limited growth rates of *Pseudotsuga* at higher elevation (see legend to Fig. 14.3; Chap. 14 by Lichstein et al., this volume). There are also a number of transitions for which our model would correctly predict a biomass increase, which we do not list individually here.

   Only four of the long-term chronosequences in Fig. 5.8 involve pronounced species turnover (panels 8, 11, 12, and 13). The late-successional biomass decline in the Lake Duparquet sequence in panel 12 (Paré and Bergeron et al. 1995) can be explained by a shift in species composition from early-successional hardwoods (h_{max} = 23–27 m) to shorter, late-successional conifers (h_{max} = 22–23 m). The relatively constant biomass along the Bonanza Creek sequence in panel 13 is unexpected from the h_{max} values extracted from the literature for the late-successional *Picea glauca* (55 m) compared to the pioneers *Populus tremuloides*

and *Betula papyrifera* (∼25 m). However, h_{max} of *Picea glauca* in the Bonanza Creek LTER does not exceed 30 m (Viereck et al. 1983). This example also illustrates the limitation of our simplistic approach, which ignores site differences in h_{max} and other parameters. The strong increase in biomass in the Cascade Mountains sequence in panel 8 (Boone et al. 1988) from the early-successional pines, mostly *Pinus contorta* (h_{max} = 34 m), to *Tsuga heterophylla* (h_{max} = 52 m) is expected from the increase in h_{max}. In the Zotino dark Taiga sequence in panel 11 (C. Wirth, unpublished data), the pioneer phase at around 80 years dominated by *Betula alba* (h_{max} = 30 m) has a biomass that is 2 kg C m^{-2} lower than in the late-successional stage dominated by *Picea obovata* and *Abies sibirica* (h_{max} = 40 m for both species) (Nikolov and Helmisaari 1992). Taken together, these examples illustrate the validity of the 'shifting traits hypothesis': knowing the shift in a single trait, h_{max}, we can confidently predict the direction of change in biomass. The chronosequences in Fig. 5.10 do not allow us to validate our model predictions with respect to woody detritus pools. However, the effect of a change in the decomposition rate with a successional change from hardwoods to conifers is corroborated by the scenario shown in Fig. 8.7c in Chap. 8 by Harmon (this volume), where a change from conifers (slow decay) to hardwoods (fast decay) increased carbon accumulation; the opposite change induced a loss after 200 years.

5.7.3   Why so Few Declines?

While there are successions with a notable decline in biomass, the model results, as well as the chronosequence and inventory data presented in this chapter and in the analysis by Lichstein et al. (Chap. 14), clearly show that declines are the exception rather than the rule.

Citing a lack of appropriate field data to assess successional patterns in forest biomass, Bormann and Likens (1979) used the gap-model JABOWA to predict that New England hardwood forest biomass should peak at around 200 years and then decline towards an asymptote, which is eventually reached after around 350 years (i.e. negative ΔC_b during the early old-growth phase). This led them to postulate the 'stand-breakup hypothesis', which provides an elegant argument for late-successional biomass declines and which they believed to have a 'wide applicability' in terrestrial ecosystems. Why then is empirical evidence supporting this hypothesis so scarce?

The stand-breakup hypothesis requires a certain degree of synchrony of canopy tree mortality. In the JABOWA model (and many others), there is a hidden synchronisation due to the onset of stress-related mortality when the annual radial increments fall below a threshold, as must occur as the trees approach their maximum diameter (Bugmann 2001). As a consequence, model runs often exhibit damped oscillations of biomass. In our model, some degree of synchronisation among patches occurs as
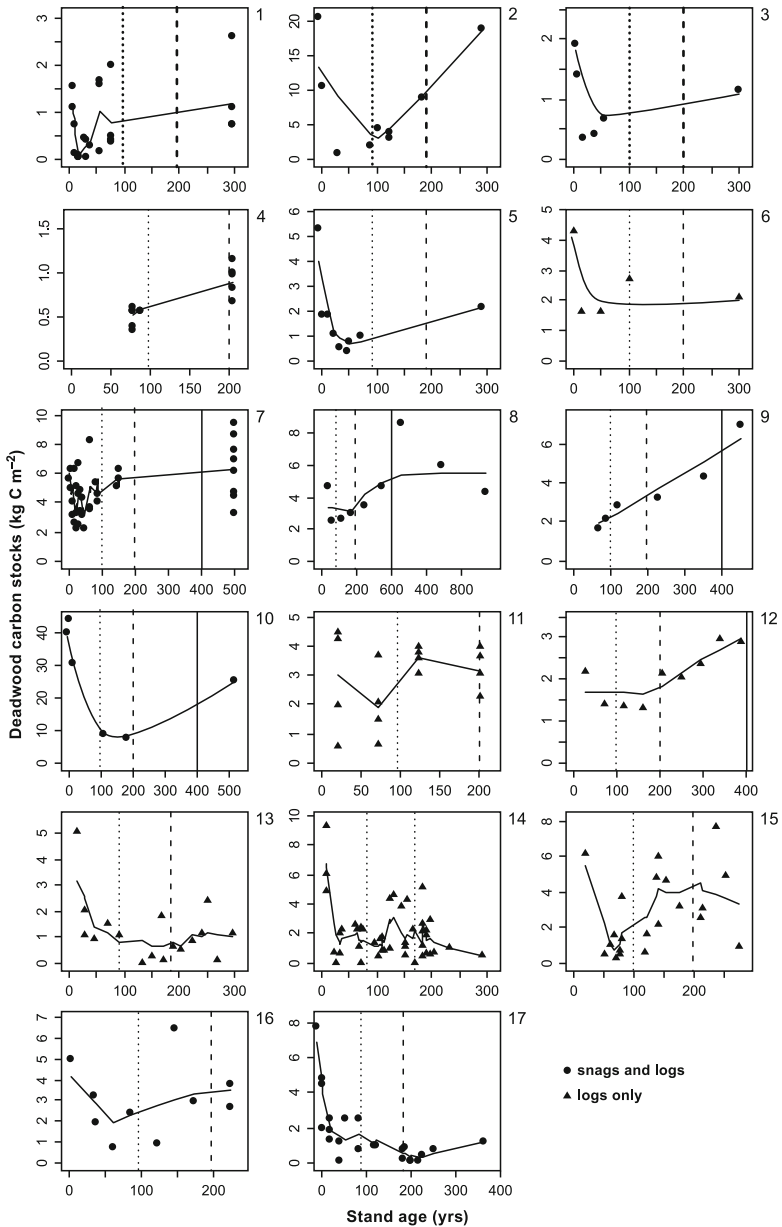
Fig. 5.10 Chronosequences of woody detritus extending to stand ages beyond 200 years. The data were taken from publications listed in Harmon (Chap. 8, Table 8.2, and see below) and where necessary were digitised from figures. Data are the sum of logs and snags (*circles*) or logs only (*triangles*). The chronosequences are arranged in the following order: *1* tropical forests, *2–6* temperate broadleaved, *7–11* temperate needle-leaved, *12–17* boreal needle-leaved. Curves were fit as in Fig. 5.8, except for two sequences with a low number of stands (*6* and *10*); in these cases,

the whole-patch mortality rate increases simultaneously across patches (Eqs. 5.5, 5.6). The degree of synchronisation is regulated by the parameters δ_1 and δ_2 in Eq. 5.6. Making them higher and more similar to each other increases the degree of synchrony. In the results presented here, we used values of δ_1 and δ_2 that create only a gently synchrony that is not sufficient to induce a pronounced 'stand breakup' behavior and subsequent oscillations. Simulations with other values of δ_1 and δ_2 have shown that the 'shifting traits' mechanism is still apparent in the biomass trajectories even under extreme synchrony, but the smooth transitions between successional stages become separated by low biomass valleys. Like JABOWA and other gap models, our model is not able to test the stand-break up hypothesis *per se*, because the degree of synchrony is prescribed. Nevertheless, the chronosequences examined in this chapter (Fig. 5.8) and in Chap. 14 suggest that late-successional biomass declines due to stand breakup are rare in temperate and tropical forests.

Several factors may reduce synchrony of mortality in natural forests, thus explaining the scarcity of observed late-successional declines. The pioneer cohort may consist of multiple species that differ in their longevities, so that canopy 'break up' would occur over an extended period of time. Alternatively, the pioneer cohort may consist of long-lived pioneers that start to die early on from repeated, small-scale, stochastic disturbances, rather than in a single wave of intrinsically triggered mortality. This happens, for example, in forests characterised by recurring surface fires, where some trees are killed by fire well ahead of their life expectancy, while the surviving trees – released from competition and fertilised by thermal mineralisation – may live even longer than usual (Wirth et al. 2002a).

Peet's (1981) extension of the stand-breakup hypothesis recognises the importance of the timing of sub-canopy regeneration. If canopy mortality leaves bare gaps (because understorey regeneration is suppressed by the pioneer cohort), then recovery of biomass in these gaps will be delayed until the new recruits attain substantial size. Under continuous regeneration, however, advanced recruits would form a sub-canopy layer with the potential to quickly fill gaps as they are formed. In this case, we would not expect a pronounced biomass decline, because the stand-level mean is not 'pulled down' by young patches with low biomass. Continuous regeneration is probably widespread, because most pioneer species – including long-lived pioneers (e.g. species of the genera *Pinus, Larix, Betula, Populus, Fraxinus* and some *Quercus* spp.) – have high canopy transparencies, allowing mid- and late-successional species to form dense sub-canopies beneath them

Fig. 5.10 (Continued) the smoothing algorithm failed and curves were drawn by hand. The *vertical lines* delineate the successional stages 'pioneer,' 'transition,' and 'early old-growth.' The intersections between the *vertical lines* and the *fitted curves* were used to calculate the changes in woody detritus during each successional stage. The numbers refer to sequences taken from the following sources: *1* Saldarriaga et al. (1998); *2* Carmona et al. (2001); *3* Roskowski (1980); *4* Shifley et al. (1997); *5* Tritton (1980) (cited in Gore and Patterson 1986); *6* Gore and Patterson (1986); *7* Janisch and Harmon (2002); *8* Spies et al. (1988) (Cascade sequence); *9* Spies et al. (1988) (Coastal sequence); *10* Agee and Huff (1987); *11* Brown and See (1981); *12* Clark et al. (1998); *13-15* Harper et al. (2005) (*13* organic, *14* clay, *15* sand); *16* Siberia dark Taiga near Zotino - C. Wirth, unpublished; *17* Wirth et al. (2002b)

(Oliver and Larson 1996). In extreme cases, the understorey regeneration eventually outgrows the still-living pioneers (Schulze et al. 2005), leaving no gap whatsoever.

The 'shifting trait hypothesis' suggests yet another mechanism that could prevent a long-term biomass decline due to 'stand breakup'. A large number of successional pathways exist in which relatively short-statured and short-lived pioneers are replaced by taller and longer-lived late-successional species. With some notable exceptions (see Sect. 5.7.2.2), this is typically the case for conifer-conifer and hardwood-conifer successions. In the few cases where observations suggest a late-successional biomass decline, a shift in traits towards shorter-lived, smaller species may be the underlying driver of the decline rather than 'stand breakup' (e.g. Paré and Bergeron 1995; see Fig. 14.3, lowest panel, in Lichstein et al. Chap. 14, this volume).

5.8 Conclusions

Both data and current theories are insufficient to provide a comprehensive picture of old-growth forest carbon dynamics. Beyond a stand age of 200 years, data on forest carbon dynamics are extremely limited. Odum's 'equilibrium hypothesis' and the 'stand-breakup hypothesis' by Bormann and Likens (1979) have been the dominant theories predicting either carbon constancy or late-successional declines in carbon stocks as forests age. The latter was largely in line with one prevailing view in forestry management, according to which old stands 'break up' and become 'overmature' and 'senescent'.

The modelling exercise presented in this chapter served three purposes: (1) to integrate available tree trait information and succession descriptions in order to shed new light on late successional carbon trajectories; (2) to provide a systematic account of an alternative theory of forest carbon trajectories, termed the 'shifting traits hypothesis'; and (3) to characterise and understand the spectrum of carbon fluxes for different phases of stand-development of North American forests. Our main findings are:

- Traits relevant for the build up of biomass and woody detritus carbon stocks (maximum tree height, longevity, and wood density) differ more between phylogenetic groups (conifers vs hardwoods) than between species in different shade-tolerance classes (i.e. successional guilds) within phylogenetic groups. Conifers become taller and are longer-lived than hardwoods. Within conifers, maximum height increased significantly, and wood density decreased significantly, with increasing shade-tolerance.
- Modelled equilibrium biomass increased strongly with increasing maximum height and, to a lesser degree, with increasing longevity. Modelled equilibrium woody detritus also increased with increasing maximum height but decreased with increasing longevity. As a consequence of the opposing effects of longevity on biomass and woody detritus, aboveground carbon stocks were sensitive primarily to maximum height.

- We parameterised the model for 106 North American forest successions, spanning all major forest types on the continent. The model predicts that for most of these successions, 201- to 400-year-old stands (early old-growth) are either carbon-neutral or still accumulating carbon. Few successions exhibited a pronounced late-successional decline. These results are consistent with independent data from inventories and long-term chronosequences. For the late old-growth stage (401–600 years) our model predicts equilibrium behaviour for most successions, when in fact the data suggest continued accumulation of carbon.
- Successions progressing from early- to late-successional conifers, and from early-successional hardwoods to late-successional conifers, tended to accumulate carbon during the early old-growth phase (201–400 years). In the latter case, accumulation was enhanced by the fact that woody detritus of conifers decomposes more slowly than that of hardwoods. In contrast, successions progressing from early-successional conifers to late-successional hardwoods tended to lose carbon during the early old-growth stage.
- In trying to understand why late successional declines in aboveground carbon stocks are so rare (both in our model predictions and empirical data), we explored a range of explanations. The 'shifting trait hypothesis', where trait combinations change along succession predominantly from short/short-lived to tall/long-lived species, is only one of them. A lack of synchronous canopy mortality and a buffering effect of understorey regeneration may additionally operate to prevent late-successional declines.

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Chapter 6
Functional Relationships Between Old-Growth Forest Canopies, Understorey Light and Vegetation Dynamics

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6.1 Introduction

Old-growth forests are characterised by the presence of old trees (>200 years of age), considerable amounts of large pieces of dead wood and a complex horizontal and vertical structure (see Chap. 2 by Wirth et al., this volume). These three elements create a unique understorey environment, including light, that differs somewhat from earlier successional or second-growth (i.e. forests that have regrown following harvesting) forests. Identifying factors that influence variation in light availability within forested ecosystems represents an important component in our understanding of the complex determinants of understorey vegetation dynamics. Based on an extensive review of the literature on old-growth forests in boreal, temperate and tropical biomes, this chapter discusses (1) the distinct structural and compositional features that are likely to influence the understorey light environment in old-growth forests, (2) the particular understorey light conditions found under such forests, and (3) the unique understorey vegetation assemblage that can develop in old-growth forests. We focus, as much as possible, on shared trends among all three biomes, but we also discuss some of the fundamental differences that differentiate them. Comparisons with second-growth forests are also often made to highlight the uniqueness of old-growth forests.

6.2 Structural and Compositional Features of Old-Growth

Old-growth forests possess distinct structural and compositional features that influence understorey light environment and vegetation growth and dynamics (Chap. 2 by Wirth et al., this volume). Since such forests are generally found where small-scale disturbances predominate, their disturbance regime tends to be characterised by gap dynamics [see Chaps. 2 (Wirth et al.) 10 (Bauhus), 13 (Grace and Meir), and 19 (Frank et al.), this volume]. Old-growth forests generally have

canopies that are heterogeneous horizontally due to the presence of gaps, and highly structured vertically due to variable tree heights and multiple layers of vegetation.

Trees in old-growth forests often have longer longevity but are not necessarily all shade-tolerant, late-successional species. For instance, *Pinus strobus*, a mid-shade-tolerant species of eastern North America, can live as long (380 years) as any of the associated shade-tolerant species, e.g. *Acer saccharum* (400 years) or *Fagus grandifolia* (300 years). Similarly, *Pseudotsuga menziesii*, a rather shade-intolerant conifer on the west coast of North America, normally lives longer than the associated shade-tolerant *Tsuga heterophylla*.

Contrary to popular belief, old-growth forests are not necessarily composed of "giant trees". Indeed, some of the largest trees in the world are early-successional species such as *Pseudotsuga menziesii* on the west coast of North America and *Eucalyptus regnans* in Australia. However, old-growth forests generally have older and larger trees than managed forests simply due to the length of time they have had to grow and develop since the last catastrophic disturbance.

Also, old-growth forests do not necessarily contain more tree and other plant species than earlier successional or second-growth forests. In fact, mid-successional forests tend to be more species rich because they often contain both early- and later-successional species (Connell 1978). Over time, mid-successional forest having low disturbance will tend to have a more uniform environment, which allows the coexistence of some fairly specialised plant species (Hubbell et al. 1999). How it is that some low disturbance old-growth tropical forests can contain several hundred tree, shrubs, vine, and epiphytic species in relatively small areas still remains somewhat of a mystery. This question has recently triggered an intense debate about the veracity of the niche theory and a new theory, the neutral theory (Bell 2000; Hubbell 2001), has been proposed. In brief, the neutral theory states that the high species diversity found in some ecosystems is not due primarily to a high number of niches or highly specialised species, but rather to a stochastic processes of extinction, immigration and speciation (Hubbell 2001). Many papers have argued for or against the new theory (Volkov et al. 2003; Chase 2005), but Gravel et al. (2006) suggested an elegant explanation where both theories (niche and neutral) can be reconciled. They suggest that niche theory better explains the distribution of species when species richness, niche overlap and dispersal capabilities of species are low, whereas the reverse is true for the neutral theory.

Because old-growth forests favour shade-tolerant or late-successional tree species that can become established and develop in the understorey, they tend to have a more uneven or complex structure. This structural complexity is neither well understood nor studied. Traditionally, foresters have simplified old-growth forest structure as uneven aged, with a regular inverse J shape age or diameter class distribution. In reality, this is not always the case and old-growth forests exhibit a tremendous variability of structures and compositions.

The vertical distribution of foliage in the understorey has been shown to differ between second-growth and old-growth forests, in boreal (Aubin et al. 2000), northern temperate deciduous (Angers et al. 2005), and tropical (Montgomery and Chazdon 2001) forests. Old-growth forests tend to have less vegetation near

the forest floor and a more continuous distribution of foliage vertically than young forests (Brown and Parker 1994; Montgomery and Chazdon 2001). In a comparison of old-growth northern hardwood forests with forests logged 10–30 years before (through selection cuts and diameter-limit cuts), Angers et al. (2005) observed the presence of a dense and uniform sub-canopy foliage layer in forests that have been partially logged. They suggested that this layer resulted from the recruitment of pre-established shade-tolerant regeneration following simultaneous creation of numerous canopy openings during partial harvesting. Similar development of trees or shrubs after human disturbance has been observed worldwide (Royo and Carson 2006).

Due to the presence of large trees, with large crowns, single tree gaps tend to be large in old-growth forests (Dahir and Lorimer 1996), while smaller trees with slender crowns that die in second-growth forests (often because they become overtopped) create smaller gaps or sometimes only sub-canopy gaps below the canopy layer (Connell et al. 1997). The creation of large gaps can be enhanced in tropical forests where vines attaching tree crowns together cause simultaneous tree falls (Strong 1977). Also, due to sparser understorey vegetation in closed canopy parts of old-growth forests, canopy openings that extend to the forest floor are more likely to occur than in second-growth forests (Montgomery and Chazdon 2001). Canopy gaps may be filled rapidly by already established vegetation, and if that vegetation comprises mainly shade-tolerant trees, the gap will fill rapidly vertically. However, if the gap is occupied mainly by low-stature plant species such as low shrubs or ferns, the gap may not fill quickly vertically, providing an opportunity for more shade-intolerant species to become established. Therefore, in terms of pre-established vegetation at the moment of gap formation, the initial conditions are very important to the future dynamic of that gap (Poulson and Platt 1996; Beaudet et al. 2004; Royo and Carson 2006).

Gaps in temperate deciduous forests can also be filled relatively quickly by crown expansion of surrounding trees (Runkle and Yetter 1987; Frelich and Martin 1988; Young and Hubbell 1991; Brisson 2001). An average lateral growth of 18 cm per year has been reported for temperate deciduous trees (Runkle and Yetter 1987). Lateral filling is however very limited in conifer forests (Umeki 1995; Stoll and Schmid 1998), which would explain why some old-growth conifer forests tend to remain open longer following gap formation (see Fig. 6.1).

6.3   Understorey Light Environments and Dynamics

Old-growth forests present a complex, changing, and heterogeneous light environment. Understorey light availability varies depending on the type of vegetation, size and orientation of gaps, penumbral effects, leaf movement, cloud distribution and movement, atmospheric aerosols, topography, height of the canopy, seasonal trends in plant phenology and seasonal and diurnal movement of the sun (Baldocchi and Collineau 1994; Gendron et al. 2001). It is generally recognised that ground-level mean light availability is not sufficient to capture the complexity of forest light
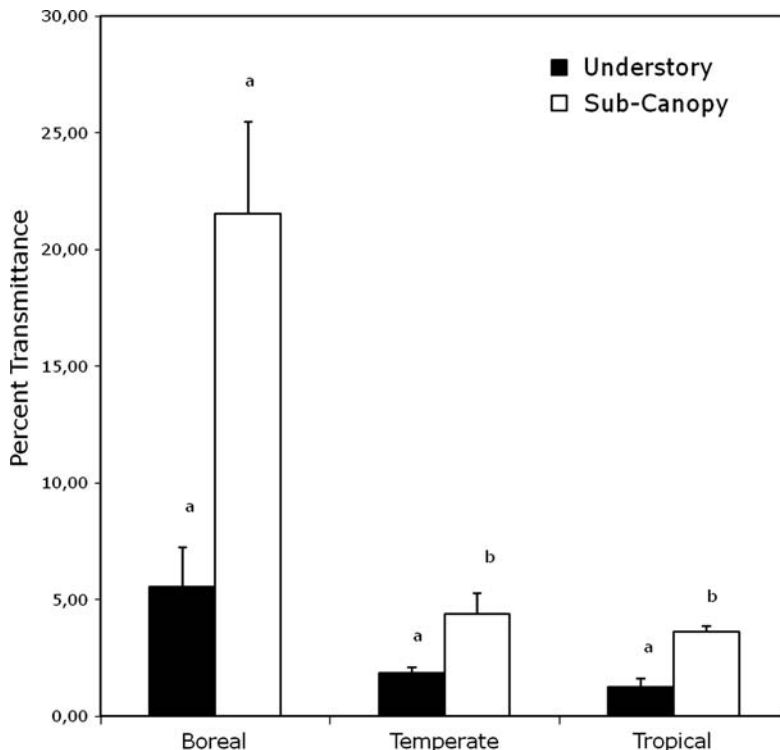
Fig. 6.1 Comparison of percent light transmittance near the forest floor and above the understorey vegetation among boreal, temperate and tropical biomes (mean data for the calculation listed in Table 6.1). Means at the forest floor and above the understorey vegetation among biomes were compared with Tukey t-tests. Although the mean percent light transmittance was much higher at the forest floor in the boreal biome compared to the other two biomes, the value was not significantly different (at $P < 0.05$). However, the value above the understorey vegetation in the boreal biome was significantly higher ($P < 0.05$) compared to the other two biomes

environments (Nicotra et al. 1999; Moorcroft et al. 2001; Beaudet et al. 2007). Other aspects of the light environment (variance, frequency distribution, spatial autocorrelation, shape of vertical profile, etc.) need to be taken into account, and often better differentiate forest types (e.g. old-growth vs second-growth forests).

Forest canopies not only attenuate the quantity, but also modify the quality of light that reaches the understorey. In terms of light quality, they attenuate more the photosynthetically active radiation, between 400 and 700 nm, than the far-red between 700 and 800 nm, which causes the red (655–665 nm) to far-red (725–735 nm) ratio to decrease under forest canopies. Changes in this ratio have been shown to affect many growth and morphological variables, especially in shade-tolerant plants (Lieffers et al. 1999; Ballaré 1999). However, light quality is known to fluctuate in the same manner as light quantity (Lieffers et al. 1999).

Compared to second-growth forests, understorey light availability in old-growth forests tends to vary much more, both horizontally and vertically, than at any other

particular point in the natural succession of a forest (Nicotra et al. 1999; Bartemucci et al. 2006) or compared to managed forests (Beaudet and Messier 2002). Although absolute mean light levels at the forest floor and above the main understorey vegetation layer tend to increase from tropical to boreal forests (Table 6.1, Fig. 6.1), overall they generally range from less than 5% in closed forests to a maximum of 65% full sunlight in large recent gaps in boreal forests. Spatially, the frequency distribution of understorey light levels is often markedly right-skewed, with most microsites having low light conditions, and a few microsites with higher light levels (Fig. 6.2). In the darkest areas of old-growth forests, the extremely low light conditions limit both the survival and growth of the understorey vegetation, even of the most shade-tolerant species. In understorey microsites, where the canopy transmits more than approximately 5–10% of full sunlight, the vegetation tends to be highly structured vertically (Bartemucci et al. 2006). In larger gaps, light levels as high as 65% above the main understorey vegetation (e.g. >5 m) tend to be associated with very low light levels (<1%) near the forest floor due to a strong light attenuation by the vegetation layer, which tends to develop after gap formation (Beaudet et al. 2004). This vertical and horizontal heterogeneity in light levels is also extremely dynamic (Aubin et al. 2000). For instance, following a canopy disturbance caused by an ice storm that increased light near the forest floor from 1% to 20%, it took as little as 3 years for the light level to recover to pre-gap conditions (Beaudet et al. 2007). In fact, light levels often tend to become, at least momentarily, even lower than before the opening of the main canopy, due to development of a dense understorey layer (Beaudet et al. 2004, 2007). Furthermore, constant understorey vegetation growth and dieback, tree mortality and large branch breakages continuously create a fluctuating light environment. Smith et al. (1992) found little year-to-year correlation in light environment in a mature lowland moist tropical forest of Panama, indicating the need for frequent assessment of the light environment for long-term studies of plant responses. Beaudet et al. (2007) also found little correlation in a mature temperate forest before and after a severe ice-storm, but good correlation thereafter. Becker and Smith (1990) found a very weak positive spatial autocorrelation (2.5 m) in a mature tropical forest of Panama in a typical year, but autocorrelation up to 22.5 m in a very dry year where leaf fall was severe.

While average light availability reaching the forest floor might not differ greatly between old-growth and second-growth forests, the understorey vertical profile is often quite different. For instance, results reported by Montgomery and Chazdon (2001) indicate a stronger light attenuation between 9 m and 1 m in second-growth compared to in an old-growth tropical forest (suggesting the presence of a denser understorey vegetation layer in second-growth). Similar results were found in temperate forests between managed and mature unmanaged forests (Beaudet et al. 2004). Such a sub-canopy sapling layer is expected to homogenise light conditions near the forest floor in managed compared to old-growth forests (where gaps are not all created simultaneously, hence greater heterogeneity) (Angers et al. 2005). Accordingly, spatial autocorrelation between light measurements indicates the presence of larger patches with higher light in old-growth than in second-growth tropical forests (Nicotra et al. 1999).

Tropical forest

Temperate forest

Boreal forest
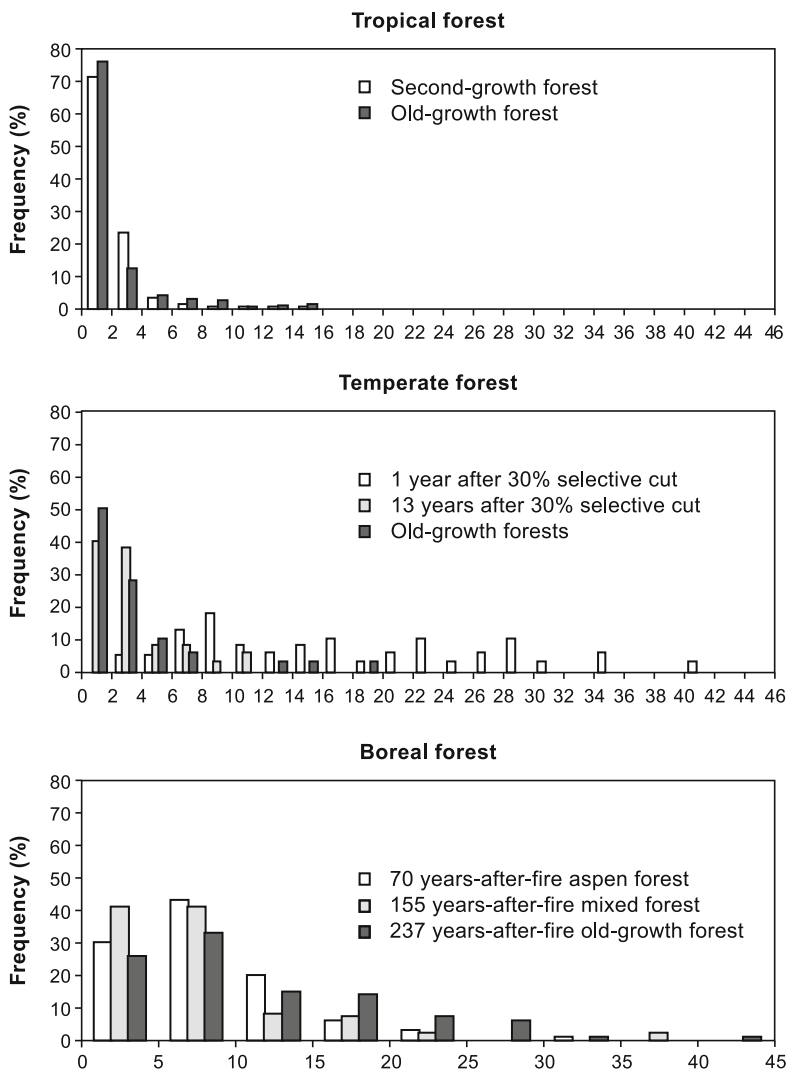
Fig. 6.2 Frequency distribution of light levels (%PPFD) at 1 m above the forest floor of tropical (open bar: second growth, solid bar: old growth) (redrawn from Nicotra et al. 1999), temperate (open bar: 1 yr after a 30% selection cut, grey bar: 13yrs after a 30% selection cut, and solid bar: old-growth *Acer saccharum* dominated forest in Québec, Canada) (selection cut data from Beaudet et al. 2004; old-growth data from Beaudet et al. 2007) and boreal forests (open bar: aspen stands, grey bar: mixed stands, solid bar old forests) (redrawn from Bartemucci et al. 2006). Light availability in old-growth forests increases from tropical to the boreal forests. In all three figures, we can see that the frequency distribution of light is similar, except for one-year after a 30% selective cut. However, in all three biomes, we tend to find microsites with relatively high %PPFD (> 10%) only in older or old-growth forests.

Table 6.1 Comparison of light in various mature or old-growth forests of the boreal, temperate and tropical forests

Forest composition or location	Mean percent transmission (range)		Reference
	At forest floor	Above understorey vegetation	
Boreal or conifer-dominated			
Cedar-dominated, Quebec	4.5 (0–15)	27 (10–65)	Bartemucci et al. 2006
Black spruce, Alberta	9.6		Ross et al. 1986
Cedar-hemlock, Coastal British Columbia	(0.6–0.8)	(1.2–23.4)	Messier et al. 1989
Old-growth mixed conifer, Washington		12.7	North et al. 2004
Cool western hemlock/Douglas-fir California		29.6	North et al. 2004
H.J. Andrews, Oregon		14.65	Van Pelt and Franklin 2000
Wind River, Washington		12.67	Van Pelt and Franklin 2000
Goat Marsh, Washington		8.73	Van Pelt and Franklin 2000
Giant Forest, California		19.17	Van Pelt and Franklin 2000
Bull Creek, California		9.58	Van Pelt and Franklin 2000
Douglas fir, Oregon	0.6 (0.1–1.7)		Canham et al. 1990
Temperate deciduous			
Sugar maple, Quebec	3.8		Messier and Bellefleur 1988
Sugar maple –Yellow birch – American beech, Quebec	2.3	7.7	Beaudet et al. 2004
Sugar maple- Beech, Quebec	2.8 (1.1–6.1)	4.3 (1.0–19.2)	Beaudet et al. 1999
Sugar maple- Beech, Quebec[a]	1.9 (0.4–5.3)	3.7 (0.7–12.9)	Beaudet et al. 2007
Broad-leaved, Mumai, Japan		2.5	Kato and Komiyama 2002
Beech- Sugar maple, Ohio	1.3 (0.3–3.8)		Canham et al. 1990
Magnolia-beech, eastern United States	1.3 (0.4–2.5)		Canham et al. 1990
Sugar maple, Michigan		3.6	Scheller and Mladenoff 2002
Tropical			
La Selva, Costa Rica	1.5 (1.0–2.0)		Chazdon and Fetcher 1984
La Selva, Costa Rica		3.0	Montgomery and Chazdon 2001
La Selva, Costa Rica		3.8[b] and 4.6[c]	Montgomery 2004

(*continued*)

Table 6.1 (Continued)

Forest composition or location	Mean percent transmission (range)		Reference
	At forest floor	Above understorey vegetation	
Barro Colorado Island, Panama		3.9[b] and 4.0[c]	Montgomery 2004
Cocha Cashu, Peru		4.4[b] and 4.9[c]	Montgomery 2004
Kilometer 41, Brazil		4.0[b] and 4.2[c]	Montgomery 2004
Nouragues, French Guiana		3.1[b] and 3.4[c]	Montgomery 2004
La Selva, Costa Rica		1.5 (0–22.4)	Nicotra et al. 1999
Chilamate, Costa Rica		1.5 (0–7)	Nicotra et al. 1999
El Roble, Costa Rica		1.5 (0–17)	Nicotra et al. 1999
Costa Rica	(1–1.5)		Oberbauer et al. 1988
Ivory Coast	0.5		Alexandre 1982
La Selva, Costa Rica	2.3 (0.3–11.9)	4.1 (0.3–28.6)	Clark et al. 1996
La Selva , Costa Rica	0.5 (0–0.9)		Canham et al. 1990
Queensland, Australia	0.5 (0.4–1.1)		Björkmann and Ludlow 1972
Oahu, Hawaii	2.4 (1.5–3.8)		Pearcy 1983

[a]Same site as in Beaudet et al. 1999, but measurements taken 7 years after an ice storm affected the canopy
[b]Taken at 0.65 m
[c]Taken at 1.75 m

Finally, understorey light at any particular point varies also temporally within a year due to various phenological events. In most of the tropics, alternating wet and dry seasons cause various patterns of leaf fall, and different tree species have different timing and extent of leaf fall, thus creating more variability. In temperate deciduous forests, the seasonal variations in light are related to temperature variation that makes deciduous trees shed their leaves in the autumn and grow them back in the spring. However, there exists a 2–4 week difference among species in terms of timing of leaf production in the spring and leaf abscission in the autumn, and such differences can be used by some understorey plants that flush early or keep their leaves late in the season to gain some additional days of photosynthetic production. As such, understorey plants can survive in extremely variable light environments through acclimatisation of the form and function of foliage and crown, or the timing of sprouting from rhizome and roots to capture the better lit microsites that are constantly created. Although all of these characteristics can be found to some extent in earlier successional stages, they tend to be more acute in old-growth forests. Like the spatial distribution of light, frequency distributions of light in old-growth forests are generally right-skewed and the understorey is exposed to low light most of the time and only occasionally to high light events (Oberbauer et al. 1988). Note that, despite being rare, these high light events or 'sunflecks' can be crucial for plant survival in the shade (Chazdon 1988).

An important difference between tropical, temperate and boreal forests is that in the former the sun passes near the sky zenith most of the year, while at higher latitudes the sun tends to be at angles below the zenith for extended periods of time. Above 23.5° of latitude (north and south of the tropics of Cancer and Capricorn, respectively) the sun never reaches the sky zenith (Campbell and Norman 1998). As a result, light in the tropics tends to be more vertically distributed and have a higher flux in the middle of the day than at higher latitudes. This vertical distribution reduces the surface area of shadows projected to the forest floor and can contribute to the development of a more complex vertical forest structure (but cf. Chap. 17 by Grace and Meir, this volume).

The major differences in and around gap light regimes among close mature forests are largely a function of canopy height, gap size, latitude and sky conditions (Canham et al. 1990; Fig. 6.3). A study by Gendron et al. (2001) has demonstrated the very complex variability in light conditions throughout the growing season and among various types of microsites in secondary deciduous forests. Some forests, such as 25-year-old Norway spruce, may have a greater net photosynthetic gain under overcast days compared to sunny days, due in part to the higher penetration of diffuse light within the canopy (Urban et al. 2007). The incredible complexity in both spatial and temporal variability in the understorey light environment calls for a re-assessment of the "gap" versus "non-gap" characterisations of the understorey environment in most forests, particularly old-growth forests (Lieberman et al. 1989; Beaudet et al. 2007).

Simple measures of forest structure such as estimated aboveground biomass and leaf area index (LAI) are not correlated with average light transmittance (Brown and Parker 1994). Information about the vertical arrangement of the canopy
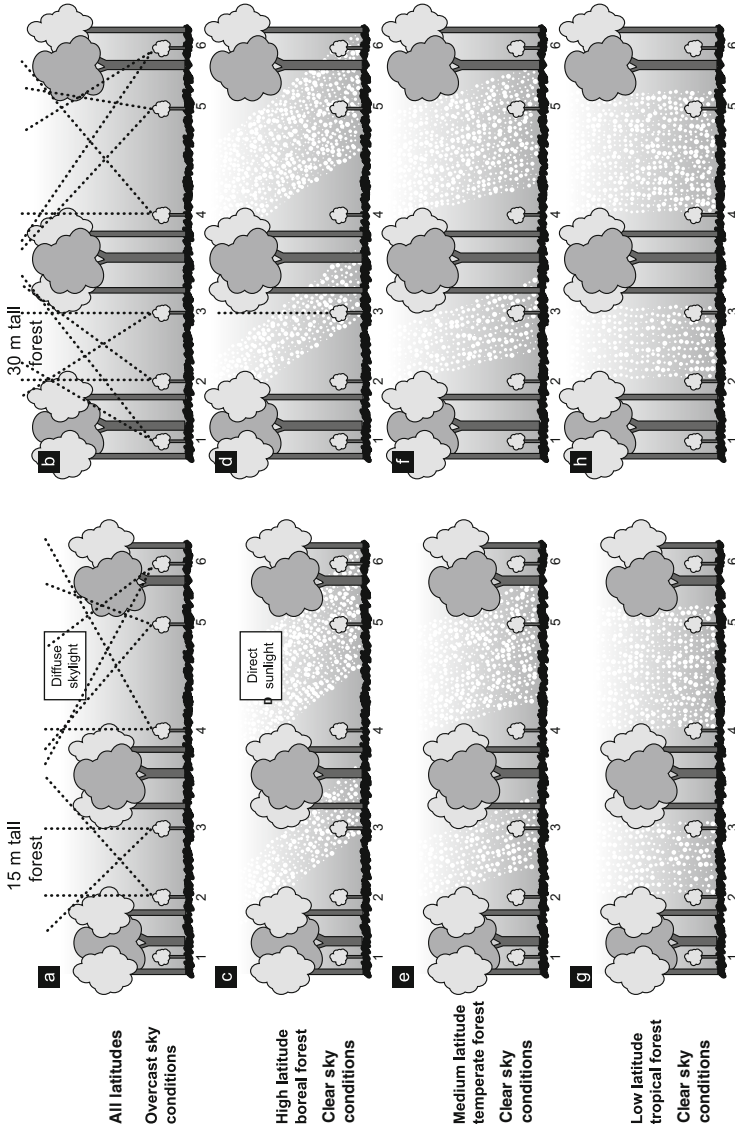
Fig. 6.3 Effects of latitude, tree height, gap size, location within gaps, and sky conditions on the distribution of direct and diffuse light reaching the forest understorey. The numbers *1* to *6* represent the six broad microsites found in forest understorey: *1* forest shade, *2* small shade gap, *3* small sunfleck gap, *4* large shade gap, *5* large sunfleck gap, *6* forest edge opening. The amount of direct (*'shafts of sunlight'*) and diffuse (*striated background*) light that each of those six microsites receive depends on the location in and around gaps, the size of the gap, the sky conditions, the mean height of the forest and the site latitude. For example, microsites *2* and *4*, situated on the southern side of a small (< 10 m) and large (> 30 m) gap respectively, will receive direct light only in very low latitude forests. Microsites *3* and *5*, situated on the northern side of the same small and large gaps respectively, will receive direct light only in medium- and low-latitude forests. In high latitude forest, depending on the tree height and latitude, the same microsites may not receive any direct light

(e.g. variation in leaf area density) provides better predictions of light transmission (Brown and Parker 1994). Although the spatial and temporal variability in understorey light dynamic is hard to predict, there have been many recent attempts at modelling it in various forest types (the different approaches are reviewed in Lieffers et al. 1999). Most models report a good correlation between simulated and measured light values at any point above the understorey vegetation (Beaudet et al. 2002; Piboule et al. 2005). These models incorporate some allometric and geometric measures of trees, some values of tree species canopy transmittance, and positioning of each individual tree. Sensitivity analyses showed that the crown radius of individual trees has a large impact on predicted light transmission at the stand-level (Beaudet et al. 2002; Rüger et al. 2007). Light below the main overstorey canopy is related to tree density, basal area, length of the canopy, and transmittance value of the canopy. In contrast, light near the forest floor is influenced through complex interactions among canopy, subcanopy, and understorey vegetation (Montgomery and Chazdon 2001; Beaudet and Messier 2002; Beaudet et al. 2004; Montgomery 2004; Bartemucci et al. 2006). Aubin et al. (2000) suggested different light extinction coefficients that take into account understorey vegetation characteristics and accurately estimate understorey light transmission.

6.4 Consequences for Understorey Vegetation Composition and Dynamics

Little is still known about the understorey vegetation characteristics of old-growth forests. As stated by McCarthy (2003), most definitions of old-growth forests are based essentially on tree species composition, forest structure and disturbance characteristics. Studies on understorey vegetation were essentially descriptive before 1980, and were mainly for the purposes of classification. Matlack (1994a) pointed out the need for further research to fill "our monstrous ignorance about the understorey dynamics of forest communities". Numerous gaps in our knowledge of understorey vegetation communities still exist. For instance, long term or geographically broad studies are missing. This lack of basic knowledge impedes the development of a sound understanding of the understorey functional and structural characteristics of old-growth forests.

The many attempts at relating understorey vegetation diversity and dynamics to light conditions have failed, probably due to the highly dynamic nature of the light environment and to the importance of other factors such as soil properties, micro-topography, presence of dead wood, and time since last disturbance. In effect, two recent studies have found that the spatial patterning of understorey species groups under early-successional and old-growth forests is influenced mainly by factors other than light, including disturbance history, chance and neighbourhood effects such as clonal reproduction (Frelich et al. 2003; Bartemucci et al. 2006). Furthermore, since increases in light conditions might not be followed by an increase in soil resource availability (see Chap. 10 by Bauhus, this volume),

understorey plants need to be able to establish and develop in a belowground environment where belowground competition levels are high.

Although the overall alpha diversity (i.e. number of species) of old-growth forests is generally not greater than in forests of other successional stages, old-growth forests are still characterised by fairly unique plant species or assemblages (Table 6.2). Some of the uniqueness of "old-growth" species assemblages can be related to three characteristics: (1) the fact that those forests have been there for long periods of time, allowing particular plants to establish and prosper; (2) the special understorey light conditions created by the small-scale disturbance regime; and (3) the presence of a very heterogeneous micro-topography of mounds and pits created by the uprooting of large trees (Beatty 2003). This spatial microsite heterogeneity provides a wide range of environmental conditions and may "serve to segregate species that might otherwise out-compete one another" (Beatty 2003). Many species are associated with windthrow mounds or bases of large trees (Rogers 1982), while others need nurse logs for their establishment (Scheller and Mladenoff 2002).

Many studies have shown that the understorey of old-growth forests is dynamic and not in a steady-state (e.g. Brewer 1980; Davison and Forman 1982). These long-term changes in understorey herbaceous communities might also be attributable to disturbances that happened centuries ago. Brewer (1980) was still observing changes in the understorey caused by a major disturbance that occurred 150 years ago. Oren et al. (2001) suggested that herb diversity should be highest in young stands, lowest in mature stands, and increase again in old growth stands.

6.4.1   Traits of the Understorey Vegetation

To be successful in old-growth forests, understorey plant species need to be adapted to survive for prolonged periods with a low availability of resources. In old-growth forests, the amount of time a tree spends in the shade could last up to several hundreds of years because of the small and irregular disturbance characteristic of such forests. In fact, Parent et al. (2006) revealed the very special strategy of *Abies balsamea*,which stays small by bending and thus can survive for almost 100 years in very deep shade. In the following section, we present a general list of traits that can favour plant survival in the shade. We have separated them into traits related to plant form and function, and those related to resource allocation.

6.5   Acclimatisation of Plant Form and Function to Low Light Availability

The low light conditions that characterise the understorey of old forests induce physiological adjustments (i.e. acclimatisation) in the photosynthetic apparatus of leaves that are generally geared towards maximising light capture (benefits) while decreasing maintenance and construction expenditure (costs). Leaves in the

Table 6.2 Literature review of biological traits associated positively (+) or negatively (−) with old growth forests and second growth forests for temperate, boreal and tropical biomes

	Boreal		Temperate		Tropical	
	Old growth forest	Second growth forest	Old growth forest	Second growth forest	Old growth forest	Second growth forest
Vegetative traits						
Status		+ Exotic[3a]	+ Native[1,2]	+ Exotic[1]		+ Exotic[4,(5)]
Raunkiaer life forms		+ Therophyte[9]	+ Geophyte[1,6] + Hemicryptophytes[6] + Chamaephyte[7] − Therophyte[7]	+ Therophyte[1,8]		
Life cycle, longevity and growth		+ Annual[9]	+ Perennial[1,2,10] + Slow growth[7,21]	+ Annual[1,8] − Long juvenile period[11] − Slow growth[11]	+ Slow growth[17]	+ Fast growth[17]
Growth form	+ Bryophyte[3,13] + Lichen[3,13] + Shrub[13]	+ Tall broad leaved shrub[14,15] + Grasses[3] − Bryophyte[16]	+ With large storage below ground organs[10,22]	+ Woody species[1,(12)] − Shallow rooted[11]		+ Shrub[15] + Woody climbers[17] − Epiphytes[18]
Pollination/flowering phenology			Phenology: + Early and short flowering time[1,7]	Phenology: + Summer of fall flowering species[(7),8]	+ Dioecious[19]	+ Hermaphroditic[19] Vector: + Insect[19] + Self-compatibility[20] − Mammal[19]
Regenerative traits						
Seed size			+ Large[24,25]	+ Small[1,(7)]	+ Large[17,20]	+ Small[17,20,23]
Seed production			+ Low[6]	− Low[11]	Few seeded fleshy fruit[20]	+ Many-seeded dehiscent fruit[20]
Dispersal mode		+ Wind[9] + Animal ingestion[9]	+ Ant or gravity[17,24,25,26] + Limited[6,22]	+ Wind[1,25] + Animal ingestion[1,25]	+ Animal[19]	+ Explosive[19] + Wind[4,17,28] − Animal[19]

(continued)

Seed longevity + Short[7]+ Seed bank[(7),(12),29] – Seed bank[17]
+ Recalcitrant
seed[(17)] + Seed bank[17] **Resource uptake** Light requirement+ Shade tolerant[31] + Shade
tolerant[1,6,21,22,**30**]+ Shade intolerant and mid-shade tolerant species[1,22,**30**]+ Shade tolerant[17]+ Shade
intolerant[17] Nutrient requirement+ Ericaceous[3,32] + Nitrogen or phosphate demanding [26] Water requirement + Xeric[3]   Specialised microhabitat requirements+
Saprophyte[16]– Saprophyte[16,33]
– Pyrophilic[3,16]
– Specialised
microhabitat[16]+ Saprophyte[1]– Saprophyte[1] Mycorrhizal affinity + Always having association[7]+ Only sometimes having association[(7)] [a]References (*in parenthesis*
studies on second growth forests originating from agriculture, *bold* studies on undisturbed forests for several centuries but not old growth. For tropical forest, except from
Opler et al. 1980, the studies are on woody species only): *1* Aubin et al. 2007, *2* Bossuyt et al. 1999, *3* Hart and Chen 2006, *4* Finnegan and Delgado 2000, *5* Roth 1999, *6*
Hermy et al. 1999, *7* Graae and Sunde 2000, *8* Moore and Vankat 1986, *9* Halpern 1989, *10* Rogers 1982, *11* Meier et al. 1995, *12* Bellemare et al. 2002, *13* Clark et al.
2003, *14* Aubin et al. 2005, *15* Royo and Carson 2006, *16* Haeussler et al. 2002, *17* Whitmore 1990, *18* Gentry and Dodson 1987, *19* Chazdon et al. 2003, *20* Opler et al.
1980, *21* Scheller and Mladenoff 2002, *22* Olivero and Hix 1998, *23* Khurana et al. 2006, *24* Froborg and Eriksson 1997, *25* McLachlan and Bazely 2001, *26* Wulf 1997,
27 Matlack 1994b, *28* Janzen 1988, *29* Gilliam and Roberts 2003, *30* Collins et al. 1985, *31* De Grandpré and Bergeron 1997, *32* Nilsson and Wardle 2005, *33* Moola and
Vasseur 2004

understorey have low photosynthetic capacity (A_{max}) and low dark respiration (R_d), and invest more in light-harvesting complexes and less in soluble enzymes like ribulose-1,5-biphosphate carboxylase/oxygenase (RUBISCO) than leaves in the sun (Boardman 1977; Björkman 1981; Evans 1989). Also, leaves exposed to low light tend to have thin or no palisade mesophylls and lower leaf mass per area than leaves found in high light environments. Some species also have special adaptations to efficiently use sun flecks – light flecks can represent up to 50% of daily energy (Chazdon 1988) – such as keeping stomata open under low light, rapid induction times, and post-illumination carbon fixation (Chazdon and Pearcy 1991). Plants growing in the understorey can sustain a smaller number of leaves above the light compensation point and have a lower LAI than plants growing in a sunlit environment (Monsi and Saeki 1953). Leaf display in the shade is also oriented towards maximising light capture and minimising self-shading. On the other hand, given the variability of the light environment, an important adaptation for many understorey plants is to be able to adjust their form and function to take full advantage of an increase in light availability (Messier et al. 1999). This acclimatisation capacity is particularly important for tree species that will eventually reach the sunlit canopy (cf. Sect. 4.5.3, Chap. 4 by Kutsch et al., this volume). Acclimatisation to high light availability is frequently associated with higher leaf A_{max} and R_d, a decrease in the ratio of light harvesting complexes to soluble enzymes (Boardman 1977; Björkman 1981; Evans 1989; Meir et al. 2002) and large palisade mesophylls in leaves (Chazdon and Kaufmann 1993; Oguchi et al. 2003). Plants growing under high light also have a more vertical growth, steeper leaf angles, and higher LAI than plants in the shade. However, despite the acclimatisation potential of many plants to different light environments, surviving in the understorey of forests for extended period of time requires more than acclimatisation of the form and function of the photosynthetic apparatus to low light conditions. In fact, physiological acclimatisation to low light appears to be generally similar for shade-tolerant and shade-intolerant species (Kitajima 1994; Walters and Reich 1999; Henry and Aarssen 2001; Chap. 17 by Grace and Meir, this volume).

6.6 Resource Allocation and Shade Tolerance

Resource allocation is a critical determinant of plant survival in the shaded understorey. Given the slow rate of growth in the shade, a plant's survival appears to be dependent largely on its capacity to avoid or recover from damage. Causes of damage that can greatly affect understorey plant survival include leaf, branch and tree falls, trampling by large vertebrates, herbivory, pathogens and snowfall. For instance, mechanical damage is a major cause of mortality of seedlings, saplings and understorey herbs in tropical forests (Clark and Clark 1989), and up to 77% of understorey seedlings of woody species can suffer some type of mechanical damage in as little as 1 year (Alvarez-Claré 2005). Allocations to materials that increase tolerance to physical damage help explain species differences in shade tolerance.

For instance, higher tissue density of trees is associated with an increase in shade tolerance of seedlings (Augspurger 1984; Kitajima 1994; van Gelder et al. 2006; Alvarez-Claré and Kitajima 2007). The probability of survival of seedlings of tropical trees is related to a higher modulus of elasticity (a measure of stiffness), higher toughness and higher density of leaves and stems (Alvarez-Claré and Kitajima 2007). In addition, tissue density is positively correlated to cellulose and lignin content per unit volume in tree stems, which could increase protection from pathogens (Alvarez-Claré and Kitajima 2007). Understorey leaves of shade-tolerant evergreen species can live for many years and should also tolerate or avoid being damaged (Walters and Reich 1999). Long-lived leaves are characterised by their high mass per unit area (LMA) (Wright et al. 2004) and LMA is positively correlated to increased leaf toughness and resistance to physical damage in the understorey (Alvarez-Claré and Kitajima 2007). In addition, understorey long-lived leaves may allocate resources to carbon-based defences (such as tannins) because this types of defence is associated with low maintenance respiration (Coley et al. 1985). Thus, allocation to biomechanical strength and tissue defences are important traits that determine tolerance to shade in old growth forests.

Another trait common to the understorey vegetation is the capacity to store reserves that can be used to increase the rate of recovery after damage or maintain physiological functions during unfavourable periods (Kobe 1997; Canham et al. 1999; Walters and Reich 1999; Poorter and Kitajima 2007; Myers and Kitajima 2007). This is particularly important for temperate and boreal understorey plants, which not only have to endure physical damage, but are also exposed to long winters that are unfavourable for photosynthesis (Gaucher et al. 2004). Shade-tolerant species also tend to allocate more biomass to roots than shade-intolerant species (Kitajima 1994; Messier et al. 1999), probably because of strong competition for soil resources in the understorey.

Due to the limited rate of carbohydrate synthesis in the shade, there are clear life-history trade-offs that result from adaptation to understorey conditions. For instance, leaf area ratio (LAR, the ratio of leaf surface area to plant biomass) of shade-tolerant species is significantly lower than the LAR of shade-intolerant species (Walters and Reich 1999). The high LAR of shade-intolerant species is usually associated with a high growth potential but also with higher costs of maintenance and construction. Thus, maintaining a high LAR can be beneficial if light availability increases, but detrimental under the low light conditions typical of the understorey of old-growth forests (Walters and Reich 1999). Differences in LAR help explain why shade-tolerant species have low relative growth rates and shade-intolerant species have high relative growth rates, and why these differences are maintained under different light regimes (Kitajima 1994; Kobe et al. 1995). Yet, under low light conditions (0–4%), relative growth rate is similar between shade-tolerant and shade-intolerant species, and shade-intolerant species do not benefit from their high LAR (Walters and Reich 1999). Instead of maximising light capture for growth, shade-tolerant species invest their limited carbohydrate pool in traits that increase survival in the shade and that come at the expense of slower biomass accumulation (Kitajima 1994; Messier et al. 1999; Walters and Reich 1999). Thus,

shade tolerance is usually associated with species that grow slowly even when light conditions are favourable. It is interesting to note that some trade-offs may change with plant size. Clark and Clark (1992) found that initial differences in growth rate among species changed later or when trees became larger. This supports the findings of Messier et al. (1999) and Messier and Nikinmaa (2000) that light requirement tends to vary with tree size.

6.6.1 Comparison among Biomes and Forest Types

In an effort to characterise the main differences and similarities in composition, form and function of understorey vegetation in different forest types around the world, we have listed and compared the main biological traits associated positively or negatively with old-growth forests vs second-growth forests among temperate, boreal and tropical biomes (Table 6.2).

In the boreal biome, vegetation diversity is globally low (291 vascular species for boreal north America; Hart and Chen 2006) due to the extreme climate and recent formation. Most boreal forest species possess a broad ecological amplitude (Bartemucci et al. 2006; Hart and Chen 2006). A majority of these species persist through succession via clonal reproduction. Boreal forests are characterised by natural large scale disturbances caused by recurrent fire and insect epidemics [Chaps. 2 (Wirth et al.) and 13 (Bergeron et al.), this volume]. Thus, its understorey vegetation possesses a transient nature (Hart and Chen 2006), fluctuating from a high cover of pioneer species after fire to a sparse cover of late-successional species with time (De Grandpré and Bergeron 1997; Clark et al. 2003). The diversity in vascular plants generally decreases from early- to late-successional forests (De Grandpré and Bergeron 1997; Chipman and Johnson 2002; Haeussler et al. 2002; Hart and Chen 2006). This decline is related to a long-term decrease in light, soil nutrients and pH (Hart and Chen 2006). On the contrary, bryophyte communities tend to increase in cover and richness in old-growth boreal forests (De Grandpré et al. 1993; Clark et al. 2003; Hart and Chen 2006). Under the closed canopy of old-growth forests, the understorey is generally sparse and dominated by shade-tolerant, vegetatively propagated and low-nutrient-requiring species (Hart and Chen 2006), such as low-lying evergreen (De Grandpré et al. 1993; Bartemucci et al. 2006), ericaceous species (Nilsson and Wardle 2005; Hart and Chen 2006), or bryophytes and lichen (Clark et al. 2003; Nilsson and Wardle 2005; Hart and Chen 2006). In southern boreal forest, some tall broad-leaved shrubs persist through all stages of succession (e.g. *Acer pensylvanicum*; (Hibbs 1979; Hibbs and Fischer 1979), *Corylus cornuta*; (Kurmis and Sucoff 1989) and *Acer spicatum*; (Aubin et al. 2005).

In the temperate deciduous biome, species diversity is intermediate between that of the boreal and tropical biomes. In temperate forests, the timing of seasonal canopy closure allows for the existence of specialised understorey herbs that take advantage of these fluctuating light conditions. These herbs may be grouped in three different life-history strategies according to their light requirement (Collins

et al. 1985). First, the sun herbs comprise the spring ephemerals and species associated with open environment (Collins et al. 1985). The spring ephemerals perform their reproduction and growth cycle in the spring before canopy closure. These species possess particular life history traits such as a slow vegetative growth, no seed bank, a long juvenile period, and no long-distance seed dispersal vector (Bierzychudek 1982). These early-flowering species have more than 50% full sunlight availability in the spring. However, a short blooming period in a season where the weather may often interrupt insect activity reduces their access to pollinators. This is compensated by a characteristic set of floral biological traits that favour pollination (e.g. autogamy and pollination by a variety of visitor types; Motten 1986). Many spring ephemerals occupy very specific types of microhabitats and have a very slow recovery after disturbance (Meier et al. 1995). Therefore, they are recognised as sensitive to human disturbance (Meier et al. 1995) and are generally associated with old-growth forests (Aubin et al. 2007). For species associated with open environments, large gaps represents the preferred habitat for establishment and growth. The size of the gap will determine their persistence (Collins et al. 1985). Some of these shade-intolerant species are widely dispersed, while others possess a seed bank. Second, the light-flexible herbs are adapted to experience both high light environments under leafless canopy and dense shade under fully developed canopy (Collins et al. 1985). Light-flexible shrubs are spatially dispersed over sun and shade patches. They have a flexible morphology, adopting a multilayer morphology in a gap and a prostrate morphology in the shade (Collins et al. 1985). Some light-flexible species will reproduce vegetatively in the shade but predominantly with seeds in gaps (e.g. *Aster acuminatus*; (Collins et al. 1985)). Third, shade herbs will mature and senesce beneath a closed canopy (Collins et al. 1985), being physiologically and morphologically adapted to low light intensities. Following an opening of the canopy, many of these species will exhibit signs of light inhibition (Collins et al. 1985; Neufeld and Young 2003). Such species are generally small and grow close to the ground with a horizontal leaf arrangement and little vertical stratification (Collins et al. 1985).

The tropical biome is home to tremendous plant diversity. Two-thirds of the flowering plants in the world occur in the tropics (i.e. 170,000 species; (Whitmore 1990)). As identification to species level of the entire flora is a difficult task in the highly diversified tropical forest, studies on this biome have generally focused on woody species and have neglected other understorey species. However, in some neotropical rainforests, understorey species represent up to 50% of the total richness of the vascular plant flora (Gentry and Dodson 1987). For instance, epiphytes may represent up to 35% of the total species richness in wet tropical rainforests (Gentry and Dodson 1987). Species richness is reflected in the broad range of life history strategies of its understorey flora, which is likely to vary with life stage (Svenning 2000). Richness is also reflected in the wide range of specialisation, such as plant–pollinator interactions (Bawa 1990) and nutrient uptake strategies such as tank plants, nests and trichomes (Whitmore 1990).

Low light availability (Svenning 2000) and the presence of a diverse and plant-specific community of insects and pathogens (Augspurger 1984) are generally

recognised as limiting expansion of understorey plants, resulting in a complex niche differentiation. Light tolerance is expressed vertically and horizontally: shade-tolerant species inhabit the forest floor in really low light environments (around 1%: Table 6.1.), while light-demanding species are found either up in trees, e.g. epiphytes and climbers, or in gaps. In the shady environment of the understorey of old-growth tropical lowland evergreen rainforest, ground vegetation is generally sparse. Understorey vegetation is composed mainly of tree saplings, while forest floor herbs are patchy. Plant life history strategies are closely related to their position relative to the canopy.

6.7   Conclusions

There exist some similarities in understorey conditions among old-growth forests around the world. Overall, old-growth forests tend to have a complex vertical and horizontal structure that favours a relatively heterogeneous light environment. Because of the low disturbance rate, opaque forest canopies and longevity of the dominant tree species of such forests, understorey light tends to be extremely low near the forest floor. As such, "old-growth" understorey plant species, although varied in form, share many morphological, allocational and physiological attributes. This is especially true for tree species that need to get established and grow for decades in deep shade, i.e. they must be able to reduce their growth when light is insufficient and grow in height when light is increased transiently. Such successful understorey tree species normally have the following attributes:

1. They can become established in deep shade (often with less than 1% full sunlight).
2. They grow slowly in shade and have a low mortality rate, but can still acclimatise to an increase in light availability caused by small sub-canopy or overstory canopy disturbance.
3. They allocate a large proportion of carbon to storage, defence and biomechanical strength.
4. They can tolerate several episodes of suppression and release.
5. They can cope with strong below-ground competition for water and nutrients by overstory tree species.
6. They have the capacity to spread their crown horizontally to capture diffuse light in the shade.
7. They have a low photosynthetic light compensation point and may have adaptations that allow them to use sunflecks efficiently.

Although old-growth forests have often been characterised as gap-phase forests, there is no such thing as a clear gap and non-gap environment (Lierberman et al. 1989). Rather, the small disturbances and longevity of the dominant tree species create a very heterogeneous, complex and unpredictable understorey environment, which acts as a selective filter for unique species adaptations.

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Chapter 7
Biosphere–Atmosphere Exchange of Old-Growth Forests: Processes and Pattern

Alexander Knohl, Ernst-Detlef Schulze, and Christian Wirth

7.1 Introduction

Forests are important agents of the global climate system in that they absorb and reflect solar radiation, photosynthesise and respire carbon dioxide and transpire water vapour to the atmosphere (Jones 1992). Through these functions, forests act as substantial sinks for carbon dioxide from the atmosphere (Wofsy et al. 1993; Janssens et al. 2003) and sources of water vapour to the global climate system (Shukla and Mintz 1982). Since old-growth forests differ in age, structure and composition from younger or managed forests (see Chap. 2 by Wirth et al., this volume) the question arises whether these characteristics also result in differences in the biosphere–atmosphere exchange of carbon, water, and energy of old-growth forests.

This chapter reviews studies using two contrasting experimental approaches: the eddy covariance technique, and paired catchment studies. The eddy covariance technique is a micrometeorological standard method to directly quantify the exchange of trace gasses between forest ecosystems and the atmosphere by measuring up- and down-drafts of air parcels above the forest (Baldocchi 2003). Fluxes of scalars such as carbon dioxide, water vapour as well as sensible heat can be inferred from the covariance between scalar and vertical wind speed (Aubinet et al. 2000). The advantages of this approach are that no disturbances or harvests are needed to assess fluxes and that the eddy flux tower typically integrates over a flux source area of approximately 1 km^2. This approach, however, assumes that the underlying surface, i.e. the forest, is horizontally homogeneous, which is typically the case over managed, even-aged forests. Old-growth forests, however, are often characterised by a dense and structured canopy including canopy gaps and a diverse range of tree heights (see Chap. 2 by Wirth et al., this volume; Parker et al. 2004). Additionally, in many parts of the world, old-growth forests occur mainly in complex – often sloped – terrain of mountain ranges, which are less favourable or accessible for anthropogenic land use [see Chaps. 15 (Schulze et al.) and 19 (Frank et al.), this volume]. This raises the question of how these characteristics of old-growth forests affect the direct measurement of biosphere–atmosphere exchange of

carbon, water, and energy. With the second approach, i.e. paired catchment studies, only water exchange is quantified. This is done by comparing the streamflow of two catchments that are similar with respect to soil, topography and climate but differ in land use or vegetation cover (Andréassian 2004). The method is suited to the study of differences in evapotranspiration and water yield between contrasting land-use types, forest developmental stages, and management strategies. Topographic complexity *per se* does not pose a problem. However, this comes at the expense of a lower temporal resolution and the need for multi-year calibration periods.

In this chapter, we summarise results from studies in old-growth forests across the globe in order to (1) describe structural characteristics of old-growth forests relevant for biosphere–atmosphere exchange (Sect. 7.2); (2) show how these characteristics influence net ecosystem carbon fluxes (Sect. 7.3); (3) investigate the interplay between canopy structure, water, and energy fluxes (Sect. 7.4); and (4) study the absorption of radiation, particularly of diffuse radiation in old-growth forests (Sect. 7.5).

7.2 Characteristics of Old-Growth Forests Relevant for Biosphere–Atmosphere Exchange

When forest ecosystems advance in age they typically undergo changes in their structural properties (see Chap. 2 by Wirth et al., this volume). Old and large trees are more at risk to external forces such as disturbance by wind or by rotting of the heartwood due to fungal attack (Dhôte 2005; Pontailler et al. 1997). As a consequence, individual trees, or parts of trees, sporadically die resulting in small scale canopy gaps (Spies et al. 1990). These gaps then supply light to lower parts of the canopy that were previously in shade. With this light supply, individuals previously limited by light are able to enhance their growth and finally close the canopy gap. In old-growth forests gaps are typically very dynamic, leading to ongoing changes in canopy structure, light environment, and hence species composition (see Chap. 6 by Messier et al., this volume). The spatial extent of canopy gaps and speed of canopy closure is likely to depend on species, site conditions and disturbance intensity, and varies greatly among biomes. For old-growth forests in the Pacific Northwest of the United States canopy gaps were reported to remain open for decades (Spies et al. 1990). Even in cases where canopy gaps in old-growth deciduous forests caused by, e.g., storms were closed within a few years, the light quantity and quality reaching understorey vegetation may remain dynamic for decades or even longer (see Chap. 6 by Messier et al., this volume). As a consequence of these gap-phase dynamics, old-growth forests typically form a canopy consisting of diverse age classes and also varying heights of individual trees and canopy parts. Older and tall trees may act as shelter for younger trees. The 450-year-old Douglas fir/Western hemlock forest at the Wind River Canopy Crane Research Facility (WRCCRF) consists of

an extremely complex outer canopy surface due to high and narrow crowns and numerous larger and smaller gaps (Parker et al. 2004). As a result, the surface area of the canopy reaches more than 12 times that of the ground area. The outer shape of the canopy strongly influences the permeability to solar radiation and the coupling of environmental conditions such as air temperature and humidity with the atmosphere. Since the top canopy consists of narrow crowns, a large part of leaf area is distributed to lower parts of the canopy, hence allowing solar radiation to penetrate deeply into the canopy resulting in a high efficiency in trapping light and hence low surface reflectance (Weiss 2000).

Along with processes leading to canopy gaps, coarse woody detritus, either standing or lying on the ground, accumulates and may account for a substantial fraction of the carbon pool within in an ecosystem. The amount and decay rates of coarse woody debris vary among biomes and environmental conditions (see Chap. 8 by Harmon et al., this volume.). At the WRCCRF forest about 25% of aboveground biomass is dead, resulting in large carbon pools contributing to heterotrophic respiration (Harmon et al. 2004). Also, old-growth forests often contain large aboveground biomass stocks (see Chap. 15 by Schulze, this volume) for temperate and boreal biomes. Pregitzer and Euskirchen (2004) show a consistent increase in biomass carbon pools with age for boreal, temperate and tropical ecosystems. Similarly, soil carbon pools are also often large due to carbon accumulation during stand development since the last disturbance (Harmon et al. 2004; Pregitzer and Euskirchen 2004).

All these structural features typical of old-growth forests are expected to influence biosphere–atmosphere exchange of such forests. In this chapter we will focus on structural features of old-growth, i.e. the fact that old-growth forests tend to be uneven-aged, horizontally and vertically structured forests, which at high age show gap dynamics and contain large amounts of woody detritus. In general, we concentrate on forests located in the temperate zone, but also include some examples from the boreal and tropical zones.

7.3   Exchange of Carbon Dioxide

Old-growth forests are often considered to be insignificant as carbon sinks since it is assumed that they are in a state of dynamic equilibrium (Odum 1969; Salati and Vose 1984) where assimilation is balanced by respiration as a forest stand reaches an old stage of development (Jarvis 1989; Melillo et al. 1996). This hypothesis is based on studies showing a decline with stand age in net primary productivity at stand level (Yoder et al. 1994; Gower et al. 1996; Ryan et al. 1997) and in photosynthesis at tree level (Hubbard et al. 1999; and see Chap. 4 by Kutsch et al., this volume) and the general idea that ecosystem respiration increases with stand age (Odum 1969). Potential mechanisms such as increasing respiration costs and nutrient or hydraulic limitation are critically discussed by Kutsch et al. (Chap. 4, this volume) and Ryan et al. (2004). Recent studies find carbon uptake rates in old-growth

forests indicating a small-to-moderate carbon sink (Phillips et al. 1998; Carey et al. 2001), sometimes even comparable to younger forests in the same region (Anthoni et al. 2004). Data for coniferous forests show that, even when old, some forests can retain their capacity to absorb carbon from the atmosphere, as shown for a 450-year old Douglas fir/Western hemlock site in Washington (Paw et al. 2004), a 250-yearold ponderosa pine site in Oregon (Law et al. 2001), a 300-year old *Nothofagus* site in New Zealand (Hollinger et al. 1994), and 200- to 250-year old boreal forests (Roser et al. 2002). This is supported by results from studies in mixed and deciduous forests that remained significant carbon sinks even when at high age, such as a 250-year old uneven-aged mixed beech forest in Germany (Knohl et al. 2003), a 200-year old mixed forest in China (Guan et al. 2006; Zhang et al. 2006), and a 350-year old uneven-aged mixed forest in the United States (Desai et al. 2005).

In this book, Kutsch et al. (Chap. 4) and Schulze et al. (Chap. 15; and see Luyssaert et al. 2008) argue that structure not age determines the capacity of forest ecosystems to absorb carbon from the atmosphere, and hence old forests may remain carbon sinks even at high age. The argumentation is based on a global dataset of net primary productivity, biomass, stand density and net ecosystem exchange measurements (Luyssaert et al. 2007) showing that a decline in productivity is more strongly related to leaf area index than to stand age, and that it only occurs when stand density drops below 330 trees ha^{-1} in temperate forest and 690 trees ha^{-1} in boreal forest, independent of tree age. This finding is supported by recent grafting studies showing that leaf level decline in photosynthesis is also related not to age, but to tree structure (Mencuccini et al. 2007; Vanderklein et al. 2007). Moreover, we also find that even 211-year old *Pinus sylvestris* trees have the ability to maintain high growth rates, as seen by an increase in radial growth by factor of five immediately after thinning. This indicates that these trees have been limited not by an age-related effect but by competition for resources (Fig. 7.1). Once resources became more abundant again due to exclusion of competitors, even old trees increase their growth. Individuals with previously high growth rates responded more strongly to thinning than individuals with smaller growth rates. These findings are supported by a study in the temperate zone. Tall 140-year old Norway spruce trees in southern Germany showed an increase of about 50% in annual stem volume increment after stand thinning via harvest (Mund et al. 2002).

A global compilation of net ecosystem exchange data from eddy covariance (Luyssaert et al. 2007) reveals that there are several old-growth forests (older than 200 years) that are net carbon sinks (Fig. 7.2). It is important to note that the global coverage of eddy covariance flux measurements is strongly biased towards younger and managed forests. Only very few flux towers are located in old-growth forests.

Additionally, some of these old-growth forests are ecosystems where factors other than just age play an important role. A chronosequence of boreal forests in Canada shows – following classical theory – a decrease in net ecosystem productivity with age, with the oldest forests (aged around 160 years) being close to carbon neutral (Amiro et al. 2006). However, a more detailed study from the same
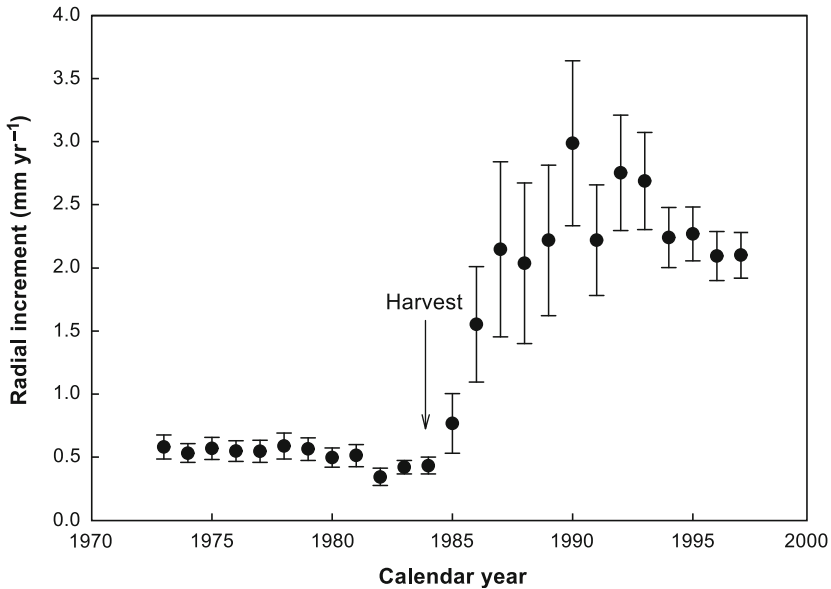
Fig. 7.1 Radial stem increment of 211-year-old *Pinus sylvestris* trees (*n* = 9) in Central Siberia. The stand was thinned via harvest in 1983 resulting in a strong increase in radial growth. *Error bars* Standard error

old-growth forest reveals that the low net ecosystem productivity at this site is determined mainly by a combination of low stand density and large heterotrophic respiration due to peat decomposition depending on changes in water table depth (Dunn et al. 2007). Midday carbon uptake rates of this old-growth forest, however, are not lower than at other – much younger – ecosystems (Goulden et al. 2006). Similarly, a recent study of eddy covariance measurements across five chronosequences in Europe showed a strong age-related pattern of net ecosystem exchange, where young forests are carbon sources, intermediate forests carbon sinks and the only older forests in this study was close to carbon neutral (Magnani et al. 2007). However, when looking more closely at the oldest forest in that study, a boreal coniferous forest in Sweden, it seems likely that factors other than just age are important such as horizontal advection of CO_2 (A. Lindroth, personal communication).

There has been a recent controversial discussion over whether the eddy covariance technique can be used to accurately measure the exchange of carbon between forest and atmosphere in terrain typical of old-growth forests, i.e. mountainous regions or tall and dense canopies (Kutsch et al. 2008). Advection, i.e. a non-turbulent transport of scalars such as CO_2, has been observed at several sites across the globe, often in dense forests, even at sites with only a minor slope (Staebler and Fitzjarrald 2004; Aubinet et al. 2003, 2005; Feigenwinter et al. 2008; Kutsch et al. 2008). Measuring advection directly is technically challenging since it requires
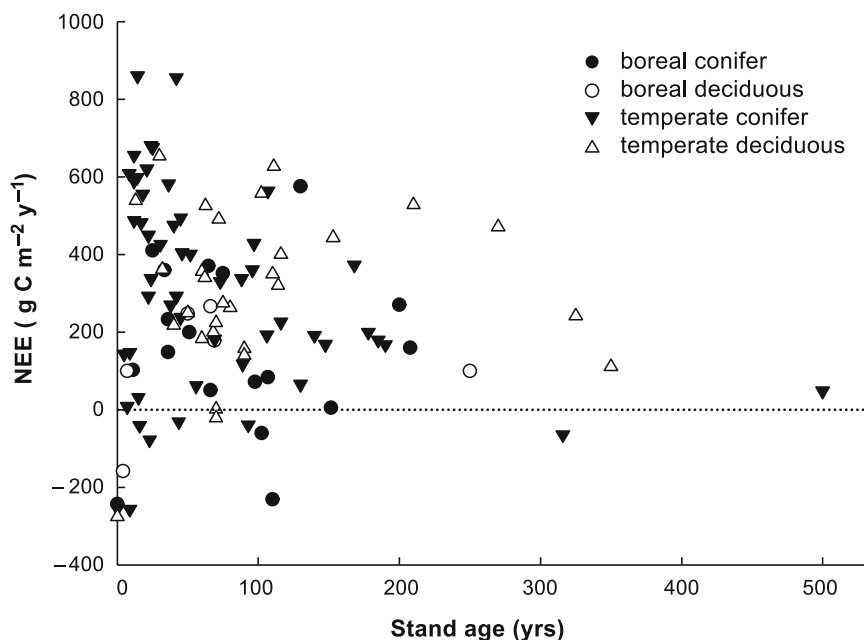
Fig. 7.2 Net ecosystem exchange (*NEE*) vs stand age for coniferous and deciduous forests in temperate and boreal biomes. NEE is derived from eddy covariance measurements and compiled in a global database (Luyssaert et al. 2007). *Positive values* carbon sink, *negative values* carbon source

additional tower measurements on a horizontal gradient and hence has so far only been done at a few selected sites. Advection often occurs at night during conditions of low turbulent mixing and hence results in a loss of CO_2 from the ecosystem not measured by the eddy covariance system. Most studies, however, correct empirically for non-turbulent conditions using the so-called u*-correction, where all flux data with a friction velocity (u*) value below a certain threshold are replaced by an empirical model (Goulden et al. 1996). Recent studies, however, question the validity of this correction (Kutsch et al. 2008). Furthermore, in tall and dense forests, such as tropical forests, the choice of u* threshold may lead to very divergent annual sums of net carbon exchange. Miller et al. (2004) show that a u*-correction turns the closed tropical forest at the FLONA Tapajós km 83 tower site (Brazil) from a large sink of approximately 400 g C m^{-2} $year^{-1}$ into a carbon source of 50–100 g C m^{-2} $year^{-1}$ (cf. Chap. 17 by Grace and Meir, this volume). Since old-growth forests are often characterised by tall and dense canopies with heterogeneity in their horizontal and vertical structure, and since they are often located – at least in Central Europe – in less accessible, often mountainous, terrain, there is a risk that advection may play a significant role in the carbon exchange of such forests. Therefore, annual sums of net ecosystem exchange in old-growth forests may carry an uncertainty or even biases larger

than the 30% typically given for eddy covariance measurements (Baldocchi 2003; Loescher et al. 2006).

More interesting than just the question of whether old-growth forest are carbon sinks or not, is the understanding of the processes controlling carbon dynamics in old-growth forests. Net ecosystem exchange is the balance of assimilation and respiration. Since both are expected to be high in old-growth forest due to high biomass and large carbon pools (Pregitzer and Euskirchen 2004), small changes in the control of assimilation and respiration may shift the balance between them, leading to day-to-day and year-to-year variability. Guan et al. (2006) showed for a 200-year-old temperate mixed forest in north-eastern China that assimilation and ecosystem respiration are both close to 10 g C m^{-2} day^{-1} during the summer. Depending on cloud cover, overcast and sunny conditions, this ecosystem switches between being a sink or source on a day to day basis. A similar sensitivity to environmental conditions is observed on an annual time scale for the oldest forest being studied with the eddy covariance technique, the 450-year-old coniferous forest at the Wind River Canopy Crane Research Facility (WRCCRF). This forest switches between being a carbon sink or a carbon source depending on the timing of key transitions periods during the course of the year (Falk 2005, 2008). Net carbon uptake occurs mainly during the wet and cool period in spring, while the ecosystem releases carbon during the dry and hot summer. The timing of the transition from wet and cool to dry and hot determines the annual carbon balance (Falk et al. 2005, 2008).

In summary, we need to extend the simplified picture concerning net carbon exchange of forests along ecosystem development where old-growth forests are considered to be carbon neutral (Odum 1969; Salati and Vose 1984; Jarvis 1989; Melillo et al. 1996). More than forest age, forest structure seems to determine the capacity of forest ecosystems to absorb carbon from the atmosphere (Fig. 7.3). Young forests typically carry the legacy of a previous disturbance. They may act as carbon sources over years to decades depending on how fast decomposable carbon such as coarse woody detritus and exposed soil carbon is respired, and how rapidly new active biomass develops (see also Chap. 8 by Harmon, this volume). Common disturbances include harvest (Giasson et al. 2006), fire (Amiro 2001), wind-throw (Knohl et al. 2002), and insects (Schulze et al. 1999). The initial respiration component will depend on how much carbon remains at the site after disturbance. Including the effect of disturbances in the assessment of carbon uptake by forests is essential since disturbances typically lead to a rapid release of large amounts of carbon that have been accumulated over a long period of time (Körner 2003). Once net assimilation of active biomass exceeds respiration from plants, coarse woody debris, and soil, forests act as carbon sinks. The duration of this period is expected to depend on site conditions, species, and disturbance history. When stand density falls below a critical threshold at which canopy closure is not fully sustained (see Chap. 15 by Schulze et al., this volume), when photosynthesis declines due to structural changes in tree morphology (Martinez-Vilalta et al. 2007; Vanderklein et al. 2007; and Chap. 4 by Kutsch et al., this volume), and when the amount of respiring carbon increases compared to photosynthetic active biomass, then forest
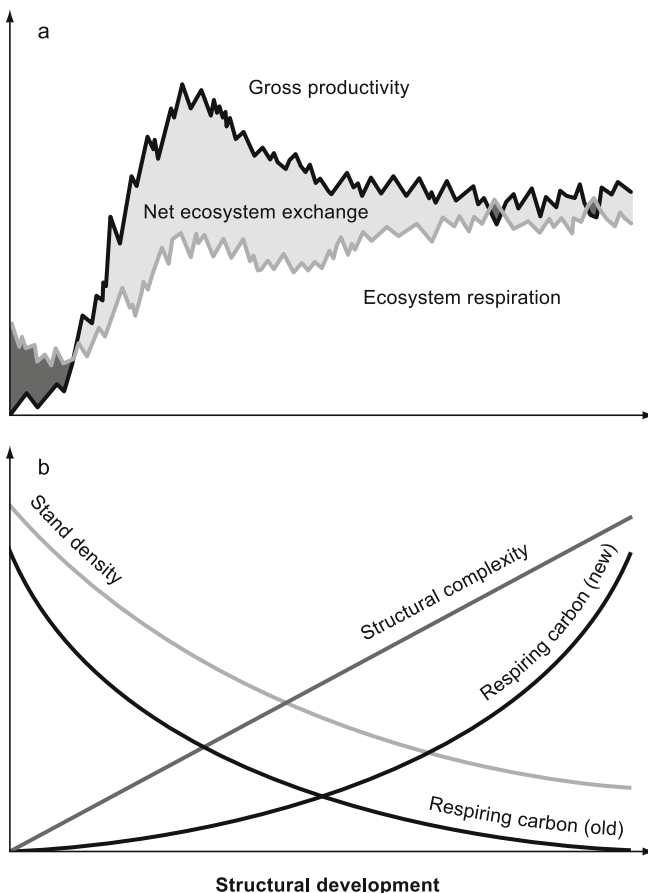
Fig. 7.3 Changes in carbon dynamics and stand properties with structural development of forest ecosystem

ecosystems may become close to carbon neutral. Depending on the amount of carbon accumulated as coarse woody debris on the forest floor or as soil organic matter in the soil (see Chap. 11. Gleixner et al., this volume) and lost as dissolved organic carbon old-growth forests may, however, never reach carbon balance, and continue to accumulate carbon at a low rate. This stage needs to be seen as highly dynamic. Small climatic variations may switch the ecosystem from being a carbon sink to a carbon source and vice versa (Falk et al. 2005, 2008). Similarly, small-scale disturbances and regeneration lead to changes in growth rates of individual trees, both remaining tall trees and young rejuvenating trees. Even though there is a correlation between structural development and stand age, we expect that this varies strongly from biome to biome and from site to site depending on site quality, soil properties, climate, nitrogen deposition and competition.

7.4 Exchange of Water and Energy

Water and energy exchange in forest ecosystems is strongly controlled by surface reflectance, the partitioning of available energy into latent and sensible heat, and stomatal conductance controlling transpiration (Jones 1992). At many sites across the globe, it has been observed that old and taller trees exhibit a lower stomata conductance and hence show lower transpiration rates (Ryan and Yoder 1997). Potential mechanisms are that older and taller trees are hydraulically limited due to increased resistance along the extended hydraulic path length and due to higher gravitational potential opposing the upward transport of water in tall trees (see Sect. 4.3, in Chap. 4 by Kutsch et al., this volume). As a result, stomata of old and tall trees may show a stronger response to high vapour pressure deficit than of younger trees, resulting in lower transpiration rates (Hubbard et al. 1999). The available data, however, do not all support the hydraulic limitation hypothesis (see also Sect. 4.3.3 in Chap. 4 by Kutsch et al., this volume). In a 450-year-old Douglas fir stand (60 m tree height) in the Pacific Northwest (United States) leaf level stomatal conductance did not differ in stands of 20 years (15 m tree height) and 40 years (32 m tree height) of age during summer time measurements even though carbon isotope measurements suggested that the older trees were hydraulically limited during spring (McDowell et al. 2002). Similarly, ponderosa pines stands in Oregon show smaller canopy conductance for old (250 years) than for younger (25 years and 90 years) stands as long as water is not limited. During summer, however, when soil dries out, the younger stands show a strong decline in transpiration while the old stand maintains high transpiration rates due to access to ground water (Irvine et al. 2004). At the ecosystem scale, however, evapotranspiration was controlled by available energy and hence both old and young stands had almost identical evapotranspiration flux rates. Old-growth forests may even have higher evapotranspiration, i.e. latent heat fluxes, than younger forests due to an albedo (surface reflectance) effect. At a series of Douglas fir stands in the Pacific Northwest evapotranspiration was highest at the 450-year-old stand (Chen et al. 2004). Surface net radiation measurements revealed that these high fluxes were driven by high surface net radiation, i.e. the difference between incoming and outgoing long and short wave radiation. The increase in net radiation was caused by lower surface reflectance (albedo) at the old stand compared to the younger stands. This decline in albedo, however, is not necessarily related to stand age, but to surface roughness, here called surface rugosity, and describing canopy complexity (Ogunjemiyo et al. 2005). Remote sensing data showed a linear decline in albedo with surface rugosity in the vicinity of the WRCCRF site (Ogunjemiyo et al. 2005). Young stands absorbed about 79% of incoming radiation, while older stands absorbed 89%, an increase of about 12.7% in available energy resulting in a net radiation larger than 650 W m^{-2} for the old-growth stand (Ogunjemiyo et al. 2005). In order to maintain a physiologically acceptable leaf temperature, the old-growth stands need to increase transpiration, resulting in high water fluxes. As with the exchange of carbon dioxide, structure, i.e. tree height, canopy rugosity and root depth, rather

than age *per se*, controls the exchange of water and energy between old-growth forests and the atmosphere as measured by eddy covariance.

Paired catchment studies provide a longer-term and larger-scale picture of water exchange in response to forest structure. In these studies, precipitation and runoff is monitored in two catchments (control and treatment) which have to be broadly similar with respect to soil, topography, climate and (initially) vegetation cover (Andréassian 2004; Brown et al. 2005). The target variable is usually the streamflow or, if expressed as a fraction of precipitation, the water yield. Watershed evapotranspiration can also be estimated as the difference between precipitation and streamflow, assuming that the storage change term is small (Brown et al. 2005). After a multi-year calibration period, the 'treatment catchment' is subject to an experimental manipulation, e.g. complete or partial deforestation or just thinning. To control for climate variability, the treatment effect is then estimated as the difference between two regression lines relating the target variable of the control and treatment catchment before and after the manipulation, respectively. Existing catchment studies tend to focus on rather drastic land-use changes such as the conversion from forest to non-forest vegetation. The need for a common calibration period precludes the comparison of vegetation attributes that require a long time to develop, such as structural or compositional changes with stand age. Thus, catchment chronosequence studies do not exist and the only way of studying the effect of stand age is to follow experimental manipulations over time with the longest observation periods being in the order of 50 years. In the following discussion, we will focus on two key results emerging from existing meta-analyses of catchment studies with respect to the effect of (1) deforestation; and (2) differences in forest structure and composition.

Deforestation of primary forests and, here especially, old-growth forests is a global phenomenon [see Chaps 18 (Achard et al.) and 19 (Frank et al.), this volume] and thus of particular relevance for the topic of our book. For the temperate zone, existing reviews found unequivocally that the short-term response to deforestation – despite considerable variability – is an increase in water yield (Hibbert 1967; Bosch and Hewlett 1982; Sahin and Hall 1996). This increase was proportional to the fractional reduction in forest cover and to the mean annual rainfall. This general response was explained by the circumstance that forests exhibit higher rates of evapotranspiration than grasslands, which usually replace forests after deforestation (Zhang et al. 2001). The magnitude of the deforestation response differed between forest types (see below). In the subtropics the effect of deforestation on streamflow during the dry season depended on how deforestation changes the infiltration opportunities (Bruijnzeel 1988). If infiltration is reduced, quick surface runoff during the wet season will lead to a reduced water yield during the dry season. If infiltration remains constant, deforestation leads to an increase in water yield – as was the case for temperate forests. One consequence of increased water yield is an increased propensity for floods to occur. In his review of paired catchment studies, Andréassian (2004) concluded that deforestation indeed increased the frequency of flood peaks by about 40% (range –18% to 200%)

and the volume of floods by about 20% (range –5% to 104%). However, the large ranges illustrate that there is considerable variability.

The question arises whether gradual changes in cover and species composition as they usually occur when a forest approaches the old-growth stage lead to detectable changes in catchment hydrology. Studies of old-growth forest structure indicate that the gap area is usually in the order of 10–30% (e.g. Messier et al. 2007). Several reviews of paired catchment studies concluded that cover reductions less than 20% cannot be detected 'hydrometrically' (Bosch and Hewlett 1982; Stednick 1996). However, a more recent Turkish study reported a significant increase in streamflow after an 11% reduction of forest cover following a light thinning in a hardwood forest (Serengil et al. 2007). It is likely that such subtle treatments are simply understudied and that structural changes associated with gap creation may indeed have an effect on the water balance. However, to what extent the cover reduction is counterbalanced by an increase in surface rugosity associated with gap opening (see above) remains unclear and warrants further study. There is evidence that changes in species composition influence water yield in a predictable fashion. Hornbeck et al. (1997) followed the changes in streamflow in three watersheds of the Hubbard Brook experimental forest after logging over a period of 30 years. Streamflow generally decreased with regrowth, but the watersheds with a high proportion of typical pioneer species with higher stomatal conductance (e.g. *Betula* sp. and *Prunus* sp.) returned faster to lower pre-fire streamflow levels. Swank and Douglas (1974) reported a significant reduction in water yield after deciduous forest had been converted to pine stands. This was ascribed to higher evapotranspiration in the pines stands as a consequence of higher leaf area, higher rain fall interception and a longer season. This is in agreement with results from the above-cited meta-analyses, according to which the relative deforestation response was strongest in conifer forests (20–25 mm per 10% cover reduction), followed by deciduous forests (17–19 mm, with no additional effect of mean annual rainfall) and eucalypt forests (6 mm; Sahin and Hall 1996). In summary, these findings suggest that structural and compositional changes, such as an increase in gap area and changes from deciduous to coniferous species (or vice versa), as they occur during the transition to the old-growth stage, have the potential to affect evapotranspiration rates. While canopy opening associated with gap formation would increase water yield, compositional changes may alter streamflow in both directions. The balance of these effects is unknown. Furthermore, direct evidence is lacking and difficult to obtain with paired catchment studies.

7.5 Effect of Diffuse Light

Several studies have shown that canopy photosynthesis is enhanced under conditions with a high proportion of diffuse light compared to conditions with the same global radiation but with a lower proportion of diffuse light (Young and Smith 1983; Hollinger et al. 1994; Baldocchi et al. 1997; Gu et al. 2003; Niyogi et al.
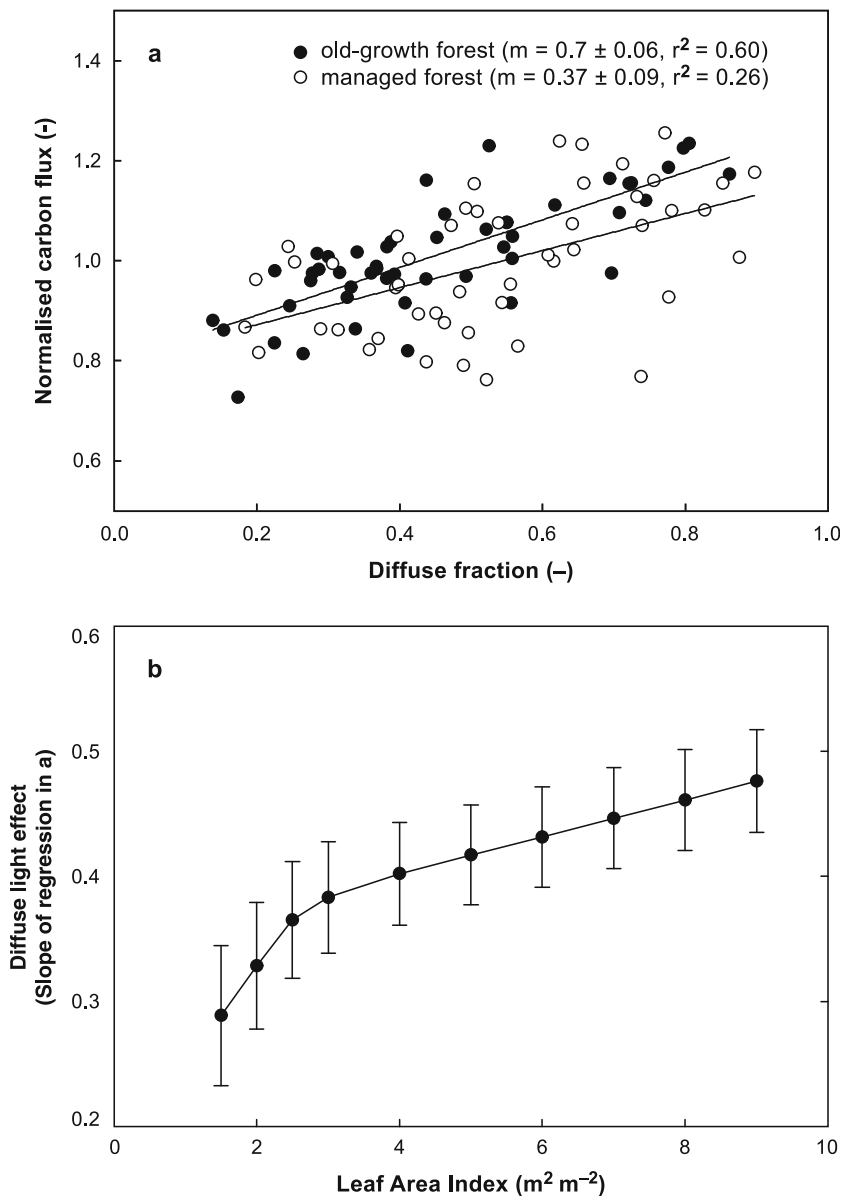
Fig. 7.4 (**a**) Influence of diffuse light on carbon fluxes (gross primary productivity normalised by photosynthetic active radiation, vapour pressure deficit and air temperature) from eddy covariance measurements at two flux sites showing the diffuse light effect. (**b**) Influence of leaf area index on the diffuse light effect (slope of regression in **a**) as modelled with the multi-layer canopy model CANVEG (after Knohl and Baldocchi 2008)

2004). Roderick et al. (2001) argue that under clear sky conditions, few leaves – only those at the top – receive a large amount of direct light, which, however, cannot be used efficiently due to light saturation, while shaded leaves receive only little light. Under conditions with an increased proportion of diffuse light, more light penetrates deeper into the canopy since diffuse light is omni-directional and thus reaches leaves that are typically shaded under clear sky conditions. Shade leaves operate mostly on the linear part of the light response curve and hence respond sensitively to small increases in available light. As a result more leaves within the canopy receive light resulting in – even if the individual amount is smaller – a higher sum total of photosynthesis when integrated over all leaves. Since old-growth forests are characterised by tall, often multi-layered, canopies one might think that the photosynthesis-enhancing effect of diffuse light would be more pronounced in old-growth forests than in younger forests with a less complex canopy. Combing eddy covariance flux data and ecosystem modelling, Knohl and Baldocchi (2008) tested two hypothesis: (1) canopy structure influences the photo-synthesis-enhancing effect of diffuse light, and (2) the photosynthesis-enhancing effect of diffuse light increases with increasing leaf area. To answer hypothesis (1), Knohl and Baldocchi (2008) compared the effect of diffuse fraction (diffuse short wave incoming radiation divided by total short wave incoming radiation) on gross carbon flux (derived from eddy covariance measurements and normalised by photosynthetic active radiation, vapour pressure deficit and air temperature), at two beech forest sites in Germany. Both sites are located within 25 km of each other, have a similar leaf area index (approximately 6 m^2 m^{-2}), exhibit similar carbon fluxes (Anthoni et al. 2004), but differ in their canopy structure. The old-growth forest at the Hainich site consists of a multi-layer canopy with frequent canopy gaps, while the managed forest at Leinefelde is even-aged, resulting in a well-defined canopy layer (Anthoni et al. 2004). The slope of the normalised carbon flux versus the diffuse fraction reflects the influence of diffuse light on ecosystem carbon uptake. Comparing both sites, the old-growth forest shows only a slightly higher – and not significantly different – response, indicating that canopy structure in itself may not have an impact on the diffuse light effect (Fig. 7.4a).

The diffuse light effect, however, increases with increasing leaf area index (Fig. 7.4b). Canopies with high leaf area index contain a larger area of leaves shaded from direct sunlight and hence benefit from an increase in diffuse light. If we assume that forests increase their leaf area index with age (see Chap. 15 by Schulze et al., this volume), our model results suggest that old-growth forests benefit more from diffuse light than younger forests with smaller leaf area index.

7.6 Conclusions

Old-growth forests differ from younger forests not only in age, but also in structure. These structural changes alter the exchange of carbon, water and energy between forest and atmosphere in manifold ways. Adapted from Chen et al. (2004), Fig. 7.5

Albedo H LE NEE   Albedo H LE NEE   Albedo H LE NEE

Pioneer   Transition   Old-growth
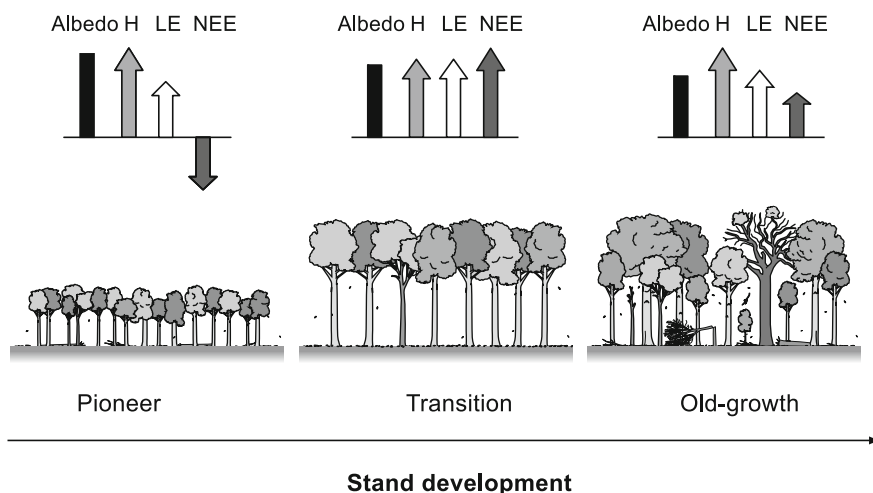
Stand development

Fig. 7.5 Changes in biosphere–atmosphere exchange in relation to stand development. *H* Sensible heat exchange, *LE* latent heat exchange, *NEE* net ecosystem exchange

summarises these processes. Albedo decreases with stand development if surface rugosity increases (Sect. 7.4). Sensible heat fluxes are expected to be high at young age, when latent heat flux is low due to low transpiration; low at intermediate age, when latent heat fluxes are high; and high at high age, when a low albedo increases net radiation and hence available energy. Hydraulic limitations of transpiration in old stands may partially be offset by the increase in net radiation. Contrary to the albedo effect identified with eddy covariance, paired catchment studies indirectly suggest that a more open canopy structure in old-growth forests may lead to a decrease in evapotranspiration. However, the degree of canopy opening required to produce this effect is probably in the order of over 20%, i.e. quite large. Furthermore, old-growth forests may continue to accumulate carbon and hence act as carbon sinks. Currently, old-growth forests do not have to be reported in national carbon-budgets under the United Nations Framework Convention on Climate Change. Protecting old-growth forests and accounting for their climate change mitigation function would help maintain their potential capacity as carbon sinks as well conserve their large carbon pools.

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Chapter 8
Woody Detritus Mass and its Contribution to Carbon Dynamics of Old-Growth Forests: the Temporal Context

Mark E. Harmon

8.1   Introduction

Woody detritus is an important component of forested ecosystems. It can reduce erosion and affects soil development, stores nutrients and water, provides a major source of energy and nutrients, and serves as a seedbed for plants and as a major habitat for decomposers and heterotrophs (Ausmus 1977; Harmon et al. 1986; Franklin et al. 1987; Kirby and Drake 1993; Samuelsson et al. 1994; McMinn and Crossley 1996; McCombe and Lindenmayer 1999). Woody detritus also plays an important role in controlling carbon dynamics of forests during succession. Along with live woody parts of trees, dead wood or woody detritus is a large pool undergoing a relatively large change in stores during succession (Davis et al. 2003). In contrast, carbon in the mineral soils represents a large store, but generally changes slowly [see Chaps. 11 (Gleixner et al.) and 12 (Reichstein et al.), this volume]. Moreover, the organic layer lying above the mineral soil can change very rapidly, but generally represents a small proportion of total forest carbon stores.

Woody detritus takes many forms. Fine woody detritus (FWD), with the exception of roots, is typically less than 7.6–10 cm in diameter, the former being based on lag-times of fire fuels. For woody roots the size break is usually 2 mm, which is based on conventions on the maximum size of live fine roots. Coarse woody detritus (CWD) exceeds these diameters (usually >7.6 cm), but also typically must exceed a length of 1 m. Woody detritus is present in the form of roots, stumps, branches (including attached dead branches), standing dead (i.e. snags), and downed material. Very few inventories measure all these forms and size classes, standing and downed "dead" material being the most commonly measured.

This chapter reviews what is known about how aboveground woody detritus mass changes over forest succession. To understand the quantity and quality of woody detritus in old-growth forests it is also necessary to understand the preceding stages of succession. Moreover, to understand how succession starts it is necessary to understand the amount of woody detritus present at the time of disturbance. This review starts with the processes that underlie these changes, considers how these processes control amounts of woody detritus in old-growth forests and then

combines these processes to examine the expected theoretical trends during succession. Observed changes, largely through the use of chronosequences (substitution of space for time) are compared to model predictions of mass and net changes in stores. Finally, I conclude with suggested improvements to reduce uncertainties concerning trends in woody detritus mass during succession and the role it plays in forest carbon dynamics.

8.2   Underlying Processes

8.2.1   Disturbance

Disturbances, events that significantly restructure the forest, are a logical point to start an analysis of secondary succession. What exactly constitutes a disturbance is scale dependent (Pickett and White 1985). In the context of this chapter, disturbances are events that significantly restructure forests at the level of stands. Although "partial" disturbances such as thinning, low intensity fires, and insect attacks clearly fall under disturbances at some scales, the majority of observational and theoretical studies on woody detritus have considered only "catastrophic" or "stand-replacing" disturbances – ones that kill the majority of trees. This chapter therefore emphasizes the latter type of disturbance. Gap dynamics, a smaller scale form of tree-level disturbance important in old-growth forests, is treated below under mortality.

Stand-replacing disturbances restructure forests in two ways and both control the nature of the legacy of material left, which influences much of the succession that follows. First, by killing trees, disturbances create woody detritus. Second, disturbances can remove woody detritus (e.g. fires and timber harvest). The maximum input of woody detritus occurs when none of the formerly live material is removed (e.g. windthrow or insect-kill). Disturbances related to pathogens such as fungi, may also have very high levels of woody detritus input, although some losses may occur during the process of trees dying, especially if the pathogen decomposes wood. The minimum woody detritus input occurs for intensive timber harvest, with the removal of stems, branches, and roots. However, it would be more typical for harvest systems to leave branches, roots, and unmerchantable parts of the stems, which probably amounts to at least one-third of the live tree biomass (Harmon et al. 1996). Fires remove far less live wood, but this highly variable process is likely to change from ecosystem to ecosystem, and fire to fire. Except in extremely severe fires, it is unlikely that much of the large diameter live wood burns.

Some disturbances also remove woody detritus present at the time of the disturbance. In the case of timber harvest, merchantable woody detritus is often removed in salvage operations. Fire is the disturbance most likely to remove woody detritus, but little is known about the amounts involved. Consumption of woody detritus increases as moisture and piece diameter decrease, and as the degree of decay increases (Brown et al. 1985; Rienhardt et al. 1991). In most situations the consumption of large woody detritus is linked to consumption of the forest floor because woody detritus alone does not generally provide a continuous enough fuel bed to support a

fire on its own. The burning forest floor interacts with large wood detritus providing the energy feedback required to maintain dead wood consumption (Harmon 2001). This is important because it means that, without deep forest floor layers, large pieces of woody detritus may not be completely consumed.

In regions where there is a significant difference in the decomposition rates of standing versus downed wood, the type of disturbance can influence the longevity of the legacy woody detritus (i.e. that left by the disturbance). For example, if standing wood decomposes slower than downed wood (which would be typical of drier climates), then fires, insects, and pathogen-related disturbances might create a lag or slower initial phase in the decomposition of the legacy wood. Disturbances that create downed wood, such as timber harvest and windthrow, might lead to a more rapid loss of legacy wood. Conversely, if standing wood decomposes faster than downed wood (typical of wet, cool climates) then disturbances that create standing dead wood would have an initial rapid loss of legacy wood followed by a slower phase as trees fall to the ground. Disturbances that create substantial amounts of downed woody detritus in this situation might have legacy wood disappear at a slower rate than those creating snags.

The nature of disturbances also determines the decomposition rates of legacy wood in more direct ways. The presence of a wood-decomposing pathogen might impact future decomposition rates by short-circuiting decomposer colonization; hence disturbance of an old-growth forest with high incidence of heart-rot may lead to faster decomposition than disturbance of a younger forest with few incidences of heart-rots. Attacks by insects such as bark beetles may also speed the colonization process, although only by a few years given that trees dying from all causes are rapidly attacked by these insects (Kirby and Drake 1993). Fire is likely to slow decomposition, but this may only be true for wood that is in the intermediate stages of decomposition (Harmon 2001). Fire charred trees are typically attractive to wood-boring insects, and many species specialize in finding fire-killed trees. Wood fully colonized by decomposers is also likely to be little affected by charring, although decreasing albedo is likely to heat the wood and lead to faster biological activity. Charring is most likely to slow decomposition in woody pieces that have the decayed portions fully removed by fire, thus eliminating the normal colonization sequence.

The size of material input by disturbance is dependent on the age of the forest being disturbed. The largest size pieces should result from old-growth forests being disturbed. Repeated harvests of forests at short intervals would likely result in the smallest material being input by disturbance, because of the removal of larger diameter stems and the smaller size of the trees.

8.2.2 Forest Re-Establishment

The ultimate source of new or de novo woody detritus following disturbance is the forest that follows. While it is beyond the scope of this chapter to review all aspects of this process, perhaps most important is the rate the new forest re-establishes. In cases where a seedling bank is present or species can sprout, forest re-establishment

can be quite rapid. If seeds must disperse and germinate, and seeding survival is low, then re-establishment could be extremely slow. Tree planting can speed the recolonization over natural rates, although not all plantings are successful. Regardless of the average rate of forest re-establishment, there can be a considerable range between the slowest and fastest rates observed in a landscape (Yang et al. 2005).

There are several important aspects of re-establishment regarding woody detritus. The faster the re-establishment rate, the faster leaf area can be redeveloped and the faster net primary production (NPP) can return to predisturbance levels. This means biomass recovers more quickly and, as some of the new trees die, the losses from legacy wood can be replaced faster. Re-establishment also influences the species of trees present, and if the decomposition rates of species differ, then this can also influence woody detritus mass during succession. The species present during the succession can also influence the rate of NPP and mortality, both of which can influence woody detritus mass (cf. Chap. 5 by Wirth and Lichstein, this volume). The temporal pattern of NPP during succession can strongly influence the amount of de novo woody detritus present. As forests re-establish, NPP generally increases and eventually levels out. There is, however, considerable evidence that there is a decline in NPP as forests continue to age (Ryan et al. 1997). The mechanism responsible for this decline and its extent is not well understood [see Chaps. 4 (Kutsch) and 7 (Knohl), this volume, for a critical appraisal of NPP decline]. However, if present, this pattern of declining NPP once a certain age is reached is likely to introduce non-linear patterns to woody detritus mass during succession and may mean that woody detritus in the old-growth is lower than the mid-succession phase.

8.2.3 Mortality

Mortality is the process that creates woody detritus. It occurs by natural or by human-related causes. It can occur as single tree parts (e.g. branch pruning), as single individuals, or as entire stands (i.e. as landscape units). In this chapter I have used disturbances to account for mortality processes that kill an entire stand. At the level of individual trees and parts, I refer to this process as "regular" mortality, recognizing there is a continuous gradient of mortality from tree parts to trees to stands. Gap formation, the process of mortality for single or small groups of trees, is an important form of mortality creating many aspects of old-growth structure including the small-scale spatial variability of woody detritus.

Mortality has been difficult to study because it is highly variable in time and space (Franklin et al. 1987). To understand this process, one needs to observe a population frequently over time to determine rates and causes, although some stand reconstruction methods can give rough approximations of long-term rates (McCune et al. 1988). In models of mortality there is a tendency to only consider self-thinning, but trees are often killed by causes unrelated to density-dependent

mechanisms, such as wind, ice damage, insects, pathogens, and outright accidents [e.g. the second highest cause of death in Pacific Northwest forests in the United States is being crushed by another tree or snag (Franklin et al. 1987)]. Considered over the life of a stand, the inputs of woody detritus from self-thinning, gap dynamics, stand level disturbances, and other density-independent causes are probably quite similar in amounts – they just occur at different stand ages (Harmon et al. 1986).

Despite the difficulty in studying and understanding this process, it is clear that average mortality rates in older forests vary significantly from ecosystem to ecosystem. At the continental scale, the tendency is for mortality to increase with productivity, although the cause of this relationship is not clear. Tropical forests have the highest mean mortality rate-constants (0.0167 year^{-1}) followed by deciduous (0.012 year^{-1}) and then evergreen forests (0.01 year^{-1}) (Harmon et al. 2001). There is also a change in the proportion of mass dying over succession. In forestry circles, mortality rates are commonly thought to be highest in older forests, but in natural stands proportional mortality rates (i.e. expressed as a proportion of live mass dying) actually tend to be highest during the self-thinning stage of succession. For example, in the Pacific Northwest region, proportional tree mortality rates in old-growth forests appear to be one-third to one-half those of the self-thinning stage (Franklin et al. 1987). Mortality may appear to be lower in younger stands from a forest management perspective because much of the mortality is "captured" by thinning and salvage, whereas in old-growth forests much of the mortality is not utilized. While thinned and salvaged trees are utilized, these trees have still died in terms of ecosystem function.

The absolute amount of input to woody detritus via regular mortality generally increases during succession (Fig. 8.1), although the pattern of increase depends on the biomass present and the proportion dying in each phase of succession. The simplest case would be if the proportion of trees dying remains constant. Here, the input from mortality should mirror that of biomass, increasing and then stabilizing as biomass stabilizes. While it is likely that proportional mortality rates changes during succession, the complete development of stands has generally not been observed. Hypothetically, once trees establish after disturbance, proportional mortality should be low because tree-to-tree competition is low. As stands enter the self-thinning phase, the proportion of trees lost to mortality may increase as competition increases. This might lead to a temporary increase in absolute mortality inputs; however, the smallest trees are most likely to die in the self-thinning phase of stand development and this may offset the higher proportion of stems dying. Once trees reach their maximum crown diameter it is likely that density-independent mortality becomes more important, leading to a decrease in the proportional mortality rate as stands enter the old-growth phase. Mortality rates in the old-growth stage of succession are likely controlled by species longevity, the presence of pathogens and insects, and susceptibility to wind. Despite a decreased proportional mortality rate in the old-growth stage, high biomass in old-growth stands should lead to a high rate of absolute mortality inputs.
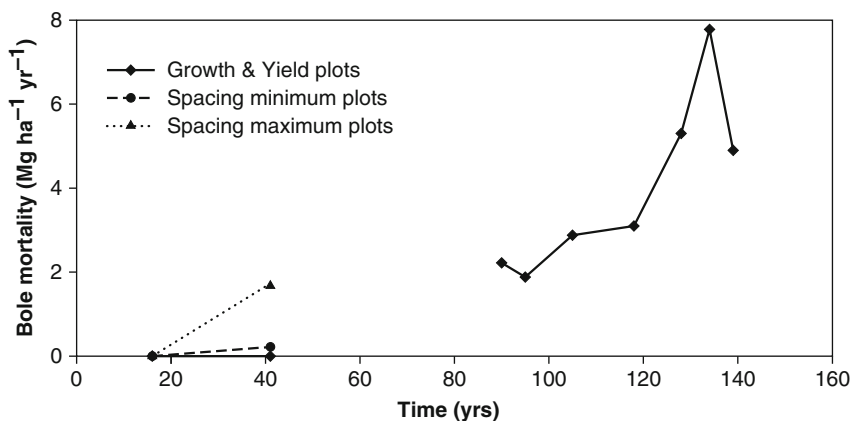
Fig. 8.1 Change in regular mortality input over succession for a *Picea-Tsuga* forest in coastal Oregon (after Harcombe et al. 1990)

Theoretically, as stands age, more and more NPP is allocated to replace biomass lost via mortality. This has been confirmed in relatively old forests in the Pacific Northwest where NPP is roughly equal to mortality losses (Harmon et al. 2004; Acker et al. 2002) and live tree biomass has remained relatively constant for decades (Franklin and DeBell 1988; cf. also Chap. 14 by Lichstein et al., this volume). It is not exactly known how a simultaneous decline in mortality and NPP in ageing stands effects biomass, but theoretically these parallel changes might lead to a stabilization of biomass around an asymptote. As mentioned above, if tree mortality cannot be replaced by new growth in very old forests, then it is possible for biomass and subsequently dead wood mass input to decline as forests age. However, this pattern of biomass decline seems to be of lower importance than previously thought [see Chaps 5 (Wirth and Lichstein) and 14 (Lichstein et al.), this volume].

8.2.4   Decomposition

Decomposition is the most important natural process controlling the loss of woody detritus. Many factors control its rate, ranging from the chemical and physical nature of the wood, to the environment at the micro- and macro-levels, and the decomposers involved (Harmon et al. 1986). There is a basic assumption that most wood decomposition involves respiration. While most likely true, fragmentation and leaching can lead to significant losses from pieces of woody detritus (Harmon et al. 1986; Spears et al. 2003). It should be borne in mind, however, that these two losses are not losses at the ecosystem level. This means that, at least theoretically,

current estimates of woody detritus decomposition rates are overestimating ecosystem losses. In practical terms, the size of this overestimation is likely small because fragmentation rates are often based on volume losses, and some volume losses are caused by respiration losses (Harmon et al. 2000), and leachates may decompose at high rates once they leave the wood and may not accumulate in the soil (Spears et al. 2003).

It is well known that different tree species produce woody detritus that decomposes at very different rates (Harmon et al. 1986). In some cases these differences can approach an order of magnitude even when the site conditions are identical (Harmon et al. 2005, 1995), but more typical might be a two-fold difference in the rate-constants describing decomposition. Differences in species are due largely to differences in heartwood decay resistance, with the heartwood of some species containing substances toxic to decomposers (Scheffer and Cowling 1966). Given that heartwood decay resistance is unlikely directly related to seral status (i.e. some pioneer species are decay resistant and some are not), it is possible for decay resistance to increase or decrease during succession (see Chap. 5 by Wirth and Lichstein, this volume).

Size also influences decomposition; however, there are many contradictory reports on its effect, which can be explained but only by understanding the interaction of size with species decay resistance and microclimate of the woody detritus. Under humid conditions in sites where excessive drying is not an issue, decomposition rate declines hyperbolically as piece diameter increases (Harmon et al. 1986; Mackensen et al. 2003), due in part to increases in the surface area to volume ratio as diameter increases (Fig. 8.2). However, it is also clear that the rate of decline is steeper for species that have decay resistant heartwood, because at small diameters all species lack heartwood, and the sapwood and bark of species
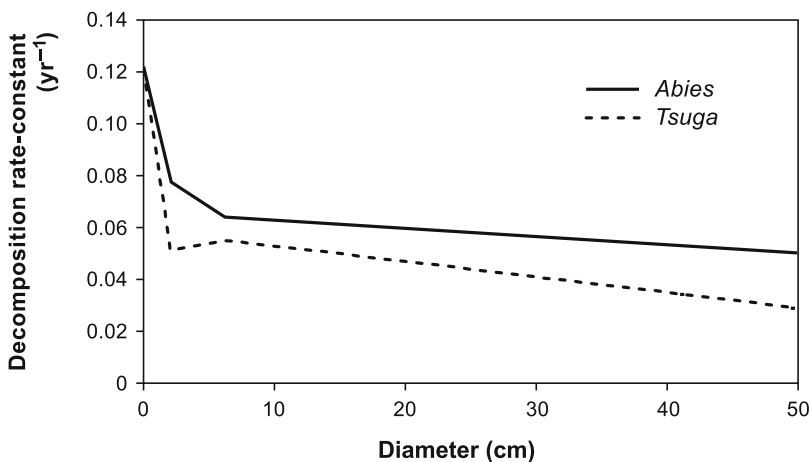
Fig. 8.2 Change in the decomposition rate-constant for woody detritus as a function of piece diameter (M.E. Harmon, unpublished data)

are usually quite similar in decay resistance. Therefore, for species with highly decay resistant heartwood, the larger the diameter, the more heartwood is present (Hillis 1977), and thus the overall decay resistance increases with diameter (Harmon et al. 1986). In climates or microclimates with excessive drying it is possible that smaller diameter wood decompose slower than larger diameter wood, because the smaller the diameter, the faster the drying rate. Given all these possibilities it is not surprising that one study contradicts another.

The effect of size on decomposition is potentially important because the size of woody detritus inputs changes over succession, with larger pieces being added as the forest ages. It is therefore likely that the largest pieces are added in the old-growth stage of succession due to density-independent mortality. In contrast, the smallest pieces are probably added during the self-thinning stage of succession as the smallest individuals are most likely to die.

As with any form of detritus, climate is an important control of decomposition rates. Examined globally, mean decomposition rates for coarse woody detritus decreases from tropical (0.176 year^{-1}) to deciduous (0.080 year^{-1}) to evergreen forests (0.032 year^{-1}) (Harmon et al. 2001). However, some of these differences are confounded with differences in species decay resistance. Plotting species with and without decay resistance against mean annual temperature indicates that the decomposition rate-constants of the former species increases as temperature increases, with a Q_{10} (i.e. the increase in rate-constant with a 10°C increase in temperature) in the range of 2.7–3.4 (Fig. 8.3; Yatskov et al. 2003). Interestingly, across the same range in mean annual temperature decay resistant species had a Q_{10}
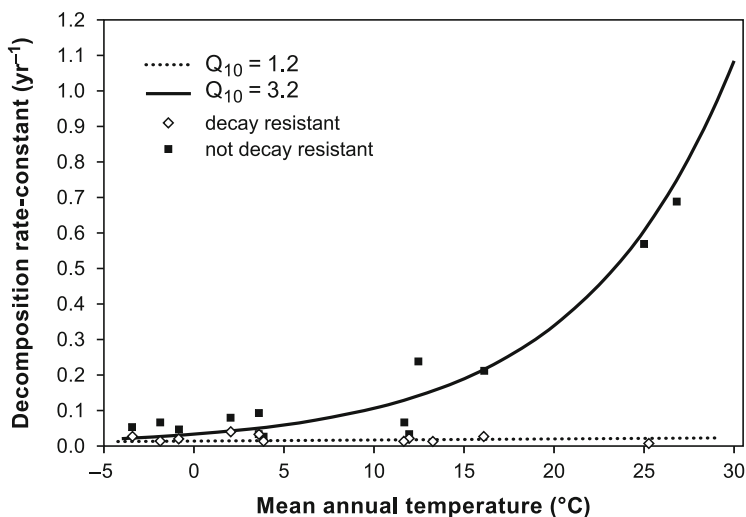
Fig. 8.3 Change in decomposition rate-constant (k) for coarse woody detritus in Russia as a function of mean annual temperature (after Yatskov et al. 2003). Q_{10} refers to the rate the decomposition-rate constant increases for a 10°C increase in temperature

of 1.2, indicating there was little increase in the decomposition rate constant with temperature. While the most obvious climatic control at the global level appears to be temperature (Mackensen et al. 2003), moisture balance can be important at a local scale (Harmon et al 2005). While the response of decomposers to moisture in wood is relatively straightforward, predicting the moisture is not. Below the fiber saturation point (~30% moisture content, water : dry weight basis) decomposer activity is limited (Fig. 8.4; Griffin 1977). As moisture content increases above fiber saturation, decomposer activity increases and eventually approaches an asymptote. However, when moisture reaches the point where pore spaces fill with water, the diffusion of oxygen becomes limiting, and this leads to a decrease in decomposer activity.

The moisture balance of wood is obviously controlled by precipitation amounts, but also by temperature and solar radiation, as well as by the size and exposure of the material. These factors interact in complex ways that have yet to be examined adequately. For example, standing wood (e.g. snags) is generally drier than downed (e.g. logs) or buried wood, but how this influences decomposition depends on the macroclimate. In climates that have low precipitation or a high potential to evaporate water, the moisture balance of standing dead material is likely to be low enough that decomposition is slowed. In the same situation downed wood, due to its greater protection, is likely to be less limited by excessive drying. This means that in dry climates, disturbance and mortality types that create standing dead wood are likely to lead to slower initial decomposition than those that create downed wood. These relationships change when the climate has very high precipitation and/or a low potential to evaporate water. Here downed wood may retain too much water to
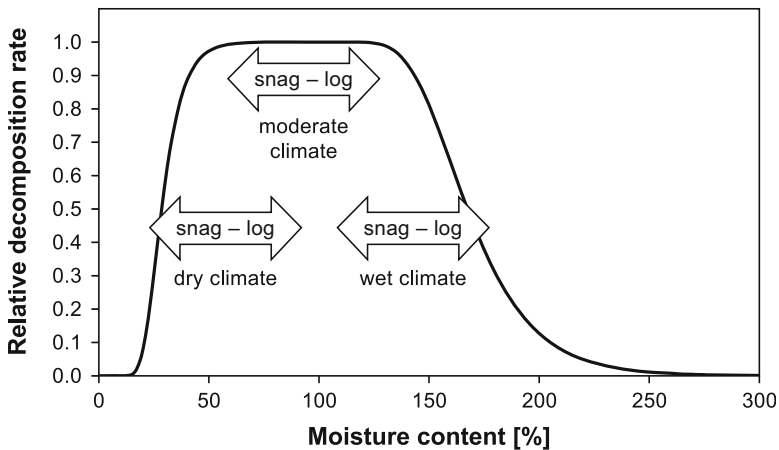
Fig. 8.4 Relationship between relative decomposition rate and moisture content (water to dry mass basis) for coarse woody detritus. Snags are always drier than logs due to their greater exposure to drying and lower interception of precipitation. The *arrows* indicate the range of conditions in three different climates (dry, moderate, wet)

support active decomposition and downed material will decompose slower than standing material. These relationships are also influenced by size, with larger diameter pieces retaining water longer than smaller diameter ones. Therefore, even in wet climates exposed smaller diameter pieces may be subject to excessive drying.

In addition to the position of the wood (i.e. standing versus downed), the age of the forest is likely to influence the moisture content of woody detritus. Increased exposure to solar radiation caused by disturbance should increase drying rates, leading to woody detritus in old-growth forests being moister than recently disturbed stands. However, as with position, the effect on decomposition is likely to depend on the macroclimate. In excessively wet climates, increased solar radiation is likely to speed decomposition, whereas in dry climates it is likely to retard decomposition. These effects may also depend on the rate of vegetation growth. Janisch et al. (2005) found little difference in log decomposition rates in harvested versus old-growth forests, a finding attributed to the rapid growth of vegetation that shaded the decomposing wood in recently harvested forests.

Perhaps the least understood control of decomposition rates is of the decomposer organisms; their effects are rarely considered in ecosystem models. The most general effect of organisms involves the lag introduced by their colonization of woody detritus (Harmon et al. 1986). Given the size of some of tree stems, it can take many years for decomposers to spread throughout (Kimmey and Furniss 1943; Buchanan and Englerth 1940). This leads to a lag in decomposition that could last decades. To some degree, these colonization effects are captured by decay resistance and moisture balance. For example, high decay resistance of heartwood leads to lower colonization rates in some species of dead trees, and thus to a lower decomposition rate. Likewise for waterlogged wood, the environment reduces the ability of decomposers to colonize and grow (Griffin 1977). When these factors are not an issue (i.e. in species with low decay resistance or environments were moisture is not limiting), the lag caused by colonization effects per se might last a decade or less (Harmon et al. 1986). The presence of macro-invertebrates, especially termites, can greatly change decomposition rates (Ausmus 1977). One of the reasons woody detritus in semitropical and tropical forests disappears quickly, at least for the species with minimal decay resistance, is the presence of termites (Harmon et al. 1995). The type of fungi present, and the degree to which stable material is formed, can also alter the decomposition rate. In particular, the presence of white-rot versus brown-rot fungi can determine whether lignin is degraded during the course of decomposition, with the former being able to degrade this substance and the latter not (Gilbertson 1980). This means that wood is not completely degraded by brown-rot fungi, and a substantial fraction of the initial mass (20–35%) may eventually be stored in the forest floor. In contrast, white-rot fungi decompose all wood constituents leaving little residue. The type of fungi present may also influence the decomposition rate; there is evidence that white-rots decompose wood faster than brown-rots (Harmon et al. 2005), although the generality of these observations needs to be further tested.

8.2.5   CWD Amounts in Old-Growth Forests

The amount of organic matter in woody detritus observed in old-growth forests spans several orders of magnitude, ranging from around 10 to 350 Mg ha^{-1} (Harmon et al. 1986, 2001; Harmon 2001). This range reflects differences in input rates versus decomposition rate-constants (Olson 1963). In general, as the NPP of old-growth forests increases, the live biomass, and the input of mortality increases. Thus, more productive old-growth forests can be expected to have more woody detritus than less productive ones. Those old-growth forests with lower decomposition rate-constants should have more woody detritus than those with higher ones; moreover, decreases in decomposition rate-constants can compensate to some degree for lower inputs rates via tree mortality. To eliminate productivity related differences, it is useful to compute the ratio of dead to live wood in old-growth forests (Harmon et al. 2001; Harmon 2001). These ratios average from 0.15 for tropical and deciduous forests to 0.25 for evergreen conifers, although values as low as 0.03 and as high as 0.65 have been observed (Harmon 2001). Aside from making an inventory of dead versus live wood stores, the dead to live wood ratio can be determined from the ratio of the mortality and decomposition rate-constants (Harmon 2001). Based on average mortality and decomposition rate-constants of forests, this ratio could range between 0.09 and 0.31, slightly wider than the means indicated by inventories. The dead to live wood ratio also indicates the potential for woody detritus to increase when a stand-level disturbance occurs. The range in mean ratios observed implies a four- to seven-fold increase depending on the forest.

8.3   Theoretical Trends

As discussed above, many processes control woody detritus mass over succession. Since these processes interact one can gain considerable insight by using a very simple model (Table 8.1) that tracks three carbon pools: (1) the live trees C_L, (2) the legacy woody detritus created and left by a disturbance C_{DL}, and (3) the de novo wood created from regular mortality of the live trees C_{DN}. In this model, the live tree mass is controlled by the balance of inputs via aboveground woody NPP (here simply termed NPP) and the output via regular mortality. It is assumed that disturbances kill all the trees in a stand. Legacy woody detritus mass is controlled by inputs from disturbance and the amount of previously dead material that is left by the disturbance. Losses from this pool are controlled by decomposition. De novo woody detritus mass is controlled by inputs from regular mortality (including those from gap formation) versus losses from decomposition. This model was programmed on a spreadsheet using an annual time step. The following simulations examine the effects of the various processes described in Sect. 8.2 on the pattern of woody detritus mass over time. In the first simulation, I assumed all the

Table 8.1 Equations and parameters used in the basic model simulations to examine temporal patterns of aboveground woody detritus following a stand replacing disturbance. The parameters are typical of a Pacific Northwestern forest

State variable	Equation
Net primary production	$NPP_t = NPP_{max}[1 - \exp(-r_{NPP}t)]^{L_{NPP}}$
Live carbon	$C_{L,t} = C_{L,t-1} + NPP_t - m \cdot C_{L,t-1}$
Legacy woody detritus	$C_{DL,t} = C_{DL,t-1} \cdot \exp(-k \cdot t)$
De novo woody detritus	$C_{DN,t} = C_{DN,t-1} + m \cdot C_{L,t} - k \cdot C_{DN,t-1}$
Parameters[a]	Value/units
Maximum NPP (NPP_{max})	3.5 Mg C ha^{-1} year^{-1}
Rate of NPP increase (r_{NPP})	0.1 year^{-1}
Lag parameter for NPP increase (L_{NPP})	2
Mortality rate-constant (m)	0.01 year^{-1}
Decomposition rate-constant (k)	0.02 year^{-1}

[a]Deviations in these parameters for specific simulation runs are discussed in the text

rate-constants controlling processes are time invariant and call this the basic model. In the following simulations I modified how these rate-constants changed over succession; the rational and values for the particular modifications are described under each simulation. Since I am most concerned about the relative patterns of change, I simulated a Pacific Northwest system to illustrate the general points using the parameter values listed in Table 8.1 It is therefore best to consider the time axis to be relative; the development of tropical forests would be faster and boreal forests slower. For a more realistic evaluation of specific ecosystems I refer the reader to Chap. 5 by Wirth and Lichstein (this volume).

The case in which all the process rate-constants remain unchanged reveals the fundamental system dynamic (Fig. 8.5). As expected, legacy (residual) wood decreases during succession and de novo increases. The shape of the total woody detritus curve is highly dependent on the amount of legacy wood removed. When none of the legacy woody detritus is removed, there is a reverse J-shaped curve with the amount of woody detritus in the middle stages of succession falling below that of the later stages (Fig. 8.6a). The depth of this mid-successional low point depends on the rate at which trees re-establish (Harmon et al. 1986); with slower rates of re-establishment having a lower dip than faster rates. While this type of curve is generally referred to as U-shaped in the literature, this is because many studies missed the initial period of very high mass. Regardless of name, the shape of the curve changes as the amount of legacy removed increases. When the amount of legacy wood equals that found in old-growth forests, the curve becomes more U-shaped, with the heights of the two arms more symmetrical than for the reverse J-shape. When all the legacy wood is removed the shape changes to a S-shape reflecting the sigmoid curve of the underlying live biomass. It should be noted that the shape of these curves is modified by the degree disturbance creates a distinct pulse of input. Simultaneous input creates the initial sharp peaks simulated here. However, Lang (1985) demonstrated that when the disturbance-related pulse is
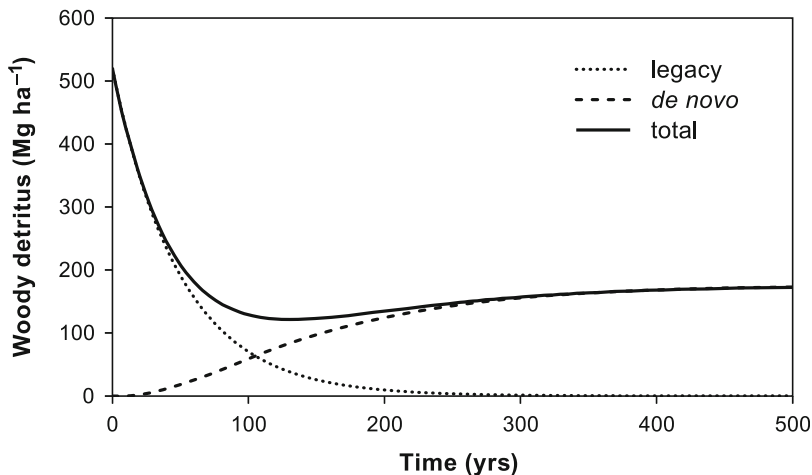
Fig. 8.5 The basic model of woody detritus mass during succession. Legacy mass is left by the disturbance and decreases as a negative exponential. De novo wood is continuously created by mortality in the new forest and also decomposes as a negative exponential function. Note that, in this example, dead wood in the old-growth stage >250 years is composed entirely of de novo wood

spread over time, the initial peak exhibits a broad shoulder and thus woody detritus mass can gradually increase as the disturbance progresses. Once the disturbance input ends, woody detritus mass decreases following the trend predicted by the basic model.

Based on classic ecosystems theory (e.g. Olson 1963) the average amount of woody detritus in old-growth forests will increase as decomposition rate-constants decrease and the mortality rate-constants increase (see Sect. 8.2.4). However, the shape of the successional curves is also dependent on the decomposition and mortality rates of the ecosystem in question. If all the legacy wood is left, then increasing the decomposition rate-constants causes the minimum to occur earlier and reach a lower value. As legacy wood is removed, the timing of the minimum is less subject to change than the value of the minimum; the latter decreases as the decomposition rate-constant increases. Changing the mortality rate-constant tends to have the opposite effects. When all the legacy wood remains, increasing the mortality rate-constant increases the minimum value and delays its timing. As legacy wood is removed, the effect of increasing the mortality rate-constant is to shorten the time required to reach the minimum, but does not seem to greatly influence the minimum mass.

The effect of delaying forest regeneration was explored by changing the timing of NPP recovery to 30 years. As long as some legacy wood is left by the disturbance, a delay in regeneration lowers the minimum mass curves (Fig. 8.6b). However, as the fraction of legacy wood left decreases, a regeneration lag also causes the minimum to occur later in succession. This is because the more important de novo wood becomes, the stronger the lag on regular mortality inputs becomes. The effect of
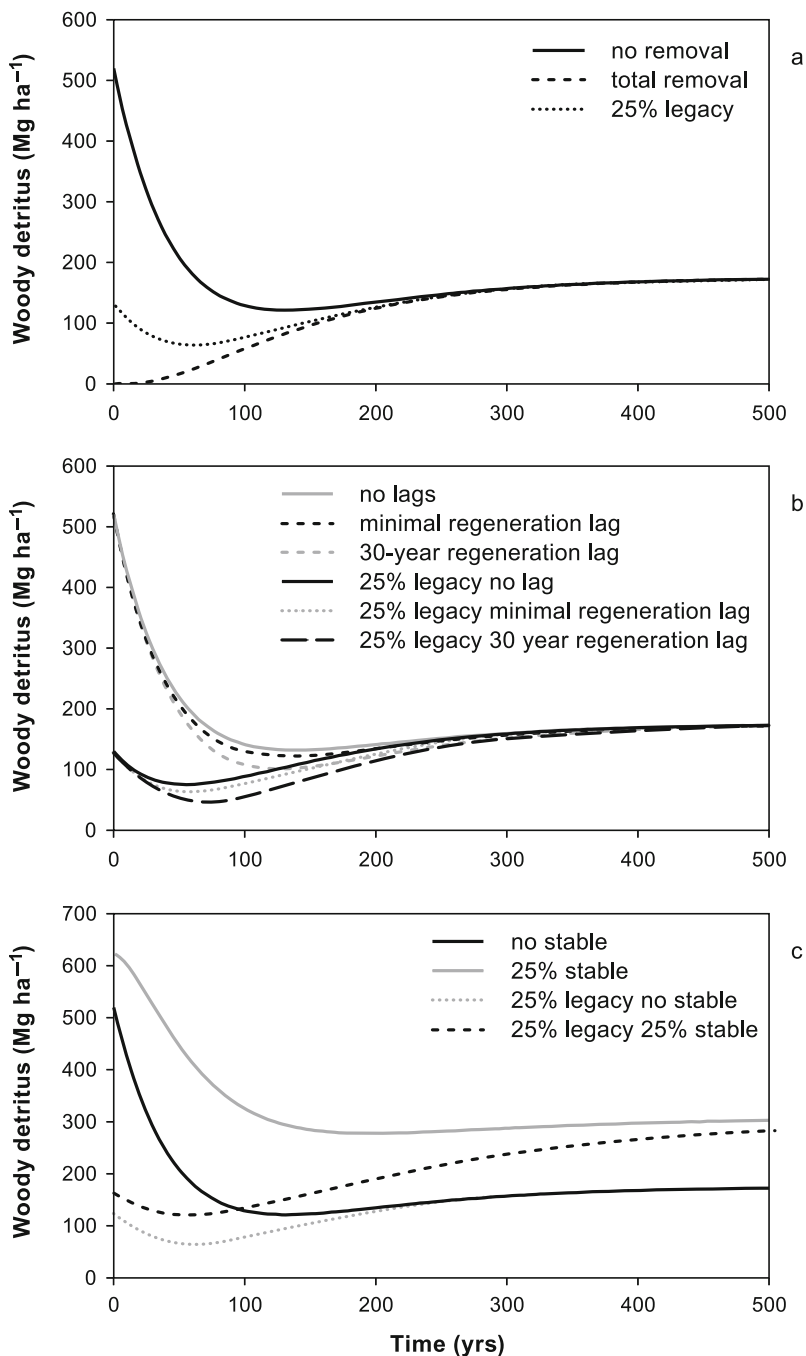
Fig. 8.6 **a** Predictions of the basic model with various proportions of remaining legacy wood. The shape of the mass curve changes from a reverse-J, to a U, and to an S-shape as more legacy wood is removed. **b** Effect of regeneration lags on the mass of woody detritus for the

regeneration lags is most noticeable when all the legacy wood is removed as it parallels the lagged curve for live biomass. This set of experiments indicates that depending on the amount of legacy wood and the length of the regeneration lag, old-growth woody stores may be the highest (no legacy wood) or lowest (abundant legacy wood and no regeneration lag) during succession.

If brown-rot fungi are the primary decomposers in a forest, then a stable material (i.e. lignin) may be left during decomposition. To simulate this situation I assumed an equivalent of 25% of the wood formed to be stable material, based in part on the fraction of lignin in the wood. I also assumed that this stable material decomposed at 0.005 year^{-1}, which is one-quarter the rate-constant assumed in the basic model. The inclusion of a stable fraction leads to more woody detritus during succession regardless of the amount of legacy woody (Fig. 8.6c). This indicates that old-growth forests dominated by brown-rot decomposers should have more woody detritus than those with only white-rots. This difference should increase as the fraction of stable material increases and the difference in decomposition rates between the stable and other wood increases. The presence of a stable fraction can change the successional curve shape. For example, in the case where legacy wood is reduced by 75%, the presence of a stable fraction leads to a very long period of woody detritus accumulation into the old-growth stage.

As stated in Sect. 8.2.1, the form of mortality and the climate may create lags in legacy wood decomposition. This would be typical of disturbances creating standing dead trees in a dry climate. To simulate this situation I assumed legacy woody detritus had a lag of 10 years before maximum rates of decomposition were reached. In an environment with high precipitation and/or low evaporation rates, the converse might happen with standing dead wood decomposing faster than downed wood. Specifically, in cases where disturbance created standing dead wood, the legacy wood might decompose slower as wood fell to the ground. To simulate this case I allowed standing wood to decompose at twice the rate of downed wood and had all standing wood fall to the ground between 10 and 20 years after disturbance. These simulations indicate that lags have a greater effect on the temporal pattern of woody detritus than an initial period of elevated decomposition rates (Fig. 8.7a). As would be expected, lags increase the amount of woody detritus during succession relative to when decomposition rate-constants are unchanging, causing the reverse J- and U-shapes to become shallower. If the decomposition lag is extended (in these simulations to 30 years), it is even possible for the lag to offset the expected dip in the curves. Thus it would appear that when there are long lags in decomposition of residual wood, that woody detritus mass is likely lowest in old-growth forests whenever there is little removal of legacy wood.

Fig. 8.6 (Continued) case where either all or 25% of the legacy remains. The *no lags* simulation represents the basic model. **c** Effect of including a stable phase of wood decomposition for the cases where either all or 25% of the legacy wood remains. The *no stable* cases represent the basic model
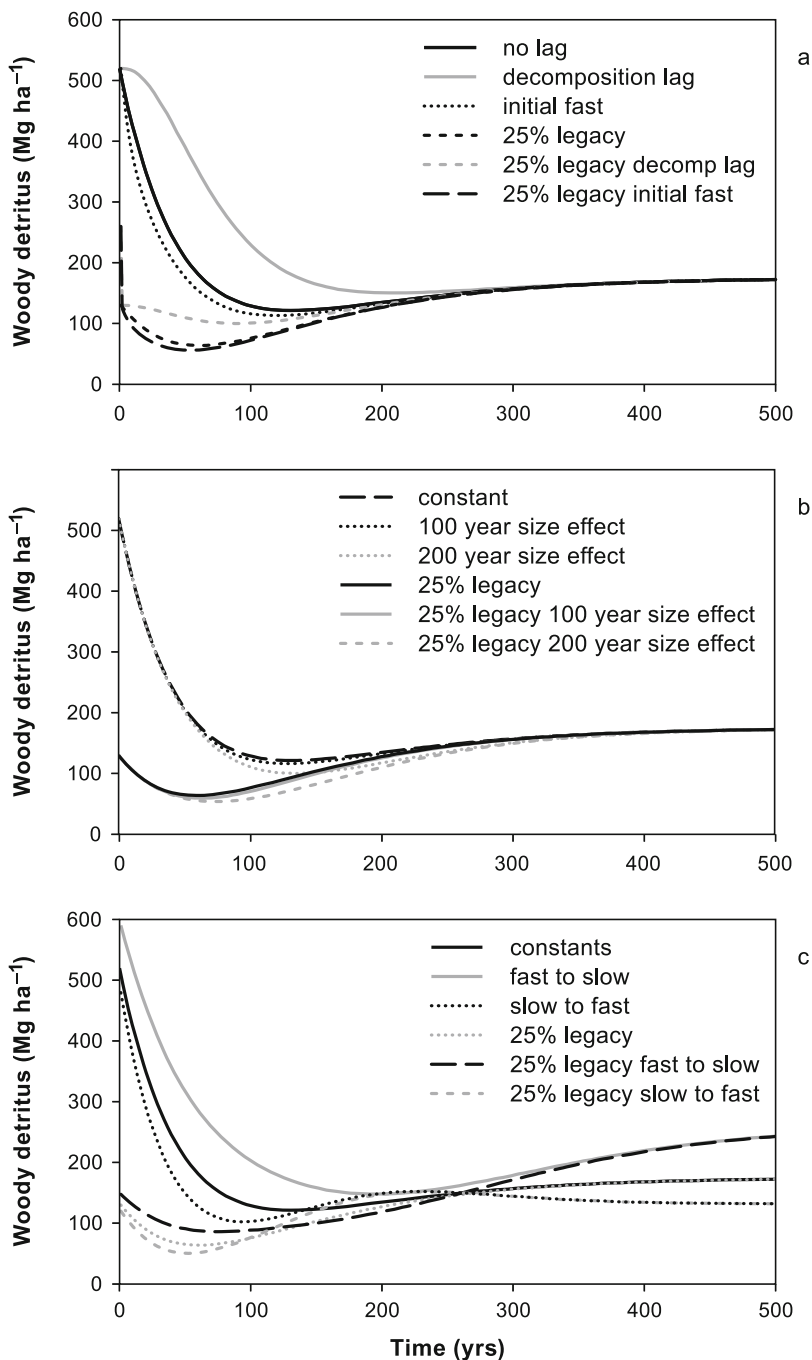
Fig. 8.7 **a** Effect of changing decomposition rates due to changes in position (i.e., snags becoming logs) for the case where either all or 25% of the legacy wood remains. The disturbance was assumed to create snags. In the decomposition lag case, snags were assumed to decompose slower

Decomposition rate-constants of the de novo woody detritus is likely to change over time, because as the forest grows the size of woody detritus also increases, leading to a decrease in decomposition rates assuming there is sufficient moisture. To simulate this I decreased the rate of decomposition of de novo woody detritus five-fold as forests aged, in one case up to 100, and in another case up to 200 years (Fig. 8.7b). Simulations indicate that the longer it takes for decomposition rates to decrease, the longer and deeper the decline in woody detritus during the middle stages of succession. This is because the higher decomposition rate-constant early in succession delays the rate at which de novo wood accumulates. If the decrease in decomposition rates associated with size increase takes 100 years or less, then the effect of decomposition-size dependence is relatively minor. If this decrease in decomposition rates takes 200 years, then the mass is around 20% lower at the minimum point and this minimum occurs around 20 years later. Increasing the difference in decomposition rate-constants between the smallest and largest wood ten-fold (or twice the initial experiment) does not change the timing of the minimum mass, although it does reduce the minimum mass amount. In the case of the 100- and 200-year transitions periods, the minimum is 10% and 30% lower, respectively than the basic parameterization. A ten-fold difference from the smallest to largest pieces of wood is probably at the upper limit of differences one could expect, and it is also likely that the majority of the changes in size would occur in less than 200 years. These simulations show that, while there is a size effect, it is small compared to other factors.

Another change during succession is caused by replacement of one tree species with another, particularly if the decomposition rate-constants of the species differ. In this set of simulations I assumed that species decomposition rate-constants differed from each other by a factor of two, and that half-way through the simulation the mixture of the species was 50:50. I examined two cases, one in which a decay-resistant species was replaced by a decay non-resistant species and vice versa. These simulations indicated that the potential effect of species replacement is quite complex, causing secondary periods of woody detritus loss (Fig. 8.7c). This complexity results from the fact the late-successional species dominates the legacy wood and the early-successional species dominates the early phases of the de novo wood. This causes the effects of the early- and late-successional species to offset each other somewhat early in succession; specifically, as the fraction of legacy wood left increases the late-successional species comprises more and more of woody detritus in the early phases of succession. The simulations indicate that the effect of the early-successional species is strongest in the middle phases of

Fig. 8.7 (Continued) than logs, simulating a dry climate. In the initial fast case, snags were assumed to decompose faster than logs, simulating a very wet climate. **b** Effect of size changes in decomposition rates assuming smaller diameter wood decomposes faster than large diameter wood for the case where either all or 25% of the legacy wood remains. The transition from small to large diameter wood takes either 100 or 200 years, representing different rates of growth. **c** Effect of changing species composition during succession on woody detritus mass for the cases where either all or 25% of the legacy wood remains. *Fast to slow* indicates a fast decomposing species ($k = 0.0265$ year^{-1}) is replaced by a slow one ($k = 0.0135$ year^{-1}) and vice versa

succession because de novo input approaches the maximum at this point. In the case where the late-successional species decomposes slowly, the legacy wood is greater than when the late-successional species decomposes quickly. This is because of differences in the old-growth store. When the pioneer species decomposes slowly, it is possible to have a peak in woody detritus mass in the middle of succession, and this peak becomes more evident as the fraction of legacy wood left increases and as the difference in species decomposition rates increase. These simulations indicate that when old-growth trees species have faster decomposition rate-constants than early-successional species, it is possible for woody detritus stores to decrease as stands enter the old-growth stage.

Declines in NPP as forests reach the later stages of succession were explored by decreasing NPP by 20 and 50% between an age of 150 and 300 years. As with species change, declining NPP can introduce complexity into the woody detritus temporal pattern (Fig. 8.8). The greater the decline in NPP, the lower the mass after the disturbance, regardless of the amount of legacy wood is left (this is because mortality inputs are lower in the old-growth phase). The decline in NPP also leads to a secondary decline in woody detritus that is proportional to the decline in NPP. These simulations indicate that either a reduction in NPP or an increase in decomposition rate-constants as forests age could lead to mid-successional forests having more woody detritus than old-growth forests.

Repeated disturbance was explored by changing the interval of disturbance from 500 years in the base case to 50 and 100 years. In one set of simulations all the legacy woody detritus was retained, and in another, representing intensive forestry, 75% of the legacy wood and 50% of the regular mortality was removed by harvest. These simulations indicate that the shorter the disturbance interval, the less woody
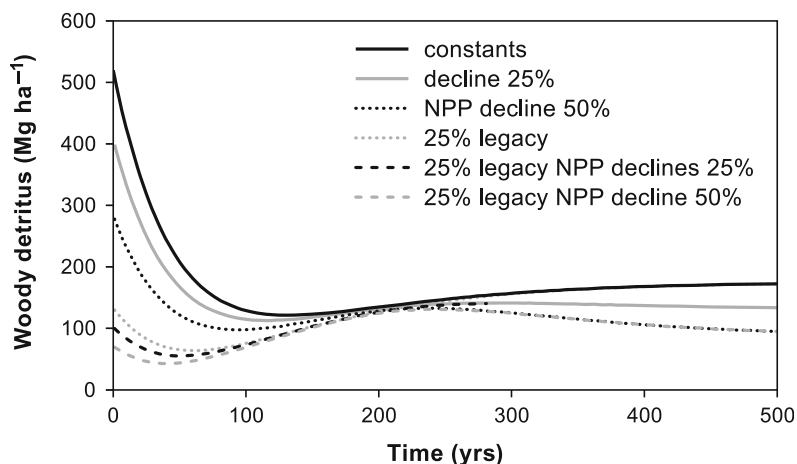
Fig. 8.8 Effect of a 25% and 50% decline in net primary production (NPP) during the latter phases of succession on woody detritus mass for the cases where either all or 25% of the legacy wood remains

detritus occurs during succession (Fig. 8.9a). This pattern is due to two factors. First, the shorter the interval, the smaller the forest is when it is disturbed and less is input as legacy wood. Second, the shorter the interval, the less likely that de novo wood will accumulate. When the interval of disturbance was reduced to 50 and 100 years, the average amount of woody detritus is 45 and 59% of the average of the 500 year interval, respectively. Harvest of legacy and de novo wood greatly reduces the amount of woody detritus, with the maximum never exceeding the amount occurring during the natural succession (Fig. 8.9b). Moreover, the average mass of woody detritus of intensively harvested forests is 10% and 17% of the 500 year natural cycle for 50 and 100 year harvest intervals, respectively. These simulations may indicate why old-growth forests are often considered to have the maximum store of woody detritus. However, the other simulations indicate that
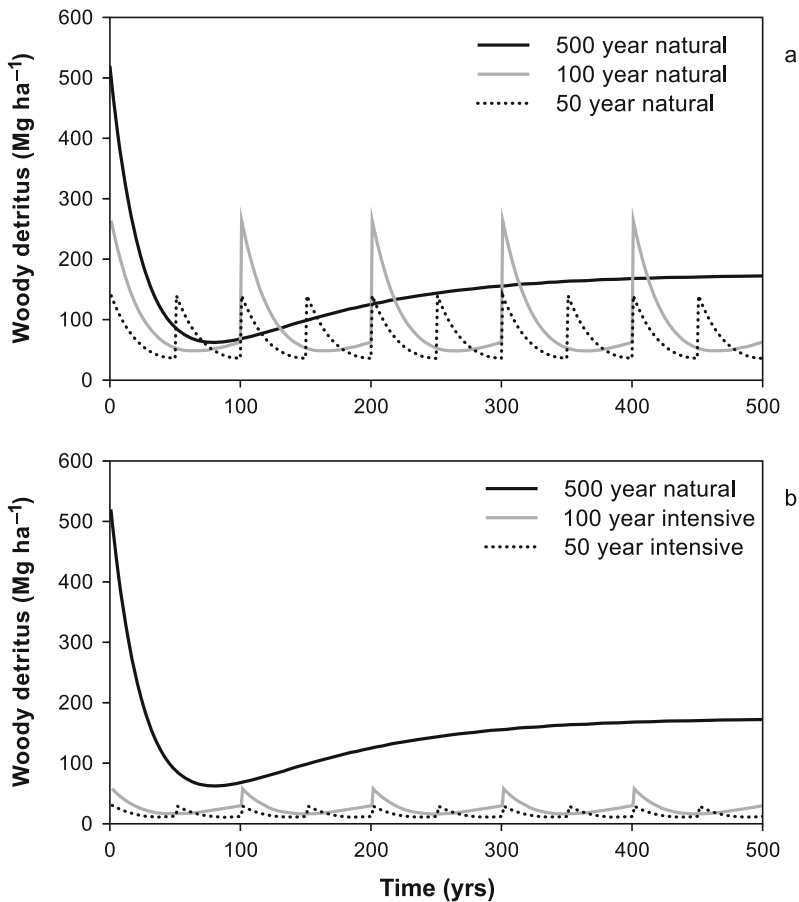
Fig. 8.9 Effect of repeated disturbance on woody detritus mass for (a) natural disturbance cycle that leaves all the legacy wood, and (b) an intensive harvest system that removes 75% of the legacy and 50% of the mortality of the post-disturbance forest

following natural disturbance this may not be the case, especially if considerable legacy wood is left by the disturbance. Other factors, such as the length of regeneration lags, differences in the decomposition rates of early and late seral trees, and the degree to which NPP decreases as stands age, may cause old-growth forests to have less than the maximum stores of woody detritus during succession.

8.4   Comparison of Theoretical and Observed Temporal Trends

8.4.1   Studies Matching the Classic Model

Both reverse J- and U-shape trends in woody detritus biomass, predicted by the so-called classic model, have been commonly observed in field studies using chronosequences (Table 8.2, and see Fig. 5.9 in Chap. 5 by Wirth and Lichstein, this volume). While the U-shaped curve is more commonly observed, this is often due to the fact that many studies do not sample directly after disturbance and consequently miss the initial peak in mass.

The Pacific Northwest is one of the best studied regions regarding woody detritus successional patterns. Agee and Huff (1987) sampled stands 1 to 515 years after catastrophic fires in moist Pacific Northwest conifer forests and found a distinct reverse J-shaped curve with initial aboveground woody detritus 7.5 times higher than the minimum amount of woody detritus that occurred in forests 110 years of age. Intermediate amounts of woody detritus, equivalent to one-third the initial pulse, were present in forests 515 years after disturbance. Spies et al. (1988) reported a U-shaped woody detritus mass curve in moist conifer forests of the Pacific Northwestern United States. Spies et al. (1988) estimated the initial mass of woody detritus would have been at least nine times larger than at 40 years of age, indicating a reverse-J shaped for fire disturbed stands. Accumulation of de novo wood in this system started 50 years after the disturbance, whereas most of the legacy wood had disappeared within 100 years, leaving the lowest mass in forests of 100–150 years of age. Similar patterns were observed by Janisch and Harmon (2002) in a chronosequence of harvested and fire-disturbed conifer forests in southwestern Washington State. For forests originating from harvest, a U-shaped curve of woody detritus mass was followed, with de novo wood beginning to accumulate noticeably after 70 years. This also roughly corresponded to the time of the minimum mass. By using live masses observed in old-growth forests and observed decomposition rates of legacy wood, the analysis of Janisch and Harmon (2002) indicated that a fire-disturbed forest would have followed the reverse-J shape.

Several eastern hardwood forests appear to follow the classic model prediction. Gore and Patterson (1986) examined the mass of downed woody detritus in cut and uncut northern hardwood forests in New England and found evidence for a reverse-J shaped curve with a minimum between ages of 20 and 60 years. Examining their regional

Table 8.2 Summary of findings from woody detritus chronosequence studies. Some of the individual chronosequences are also shown graphically in Wirth and Lichstein (Chap. 5, Fig. 5.10)

Biome	Main genera	Time period (years)	Stands (number)	Disturbance	Temporal pattern	Reference
Standing and downed woody detritus sampled						
Conifer	Abies	0–70	37	Fire-wave	Reverse-J[a]	Lambert et al. (1980)
Conifer	Abies, Picea	33–110	26	Harvest	U-shaped	Sturtevant et al. (1997)
Conifer	Picea	4–152	7	Fire	Reverse-J[a]	Manies et al. (2005)
Conifer	Picea	20–250	91	Fire	Reverse-J[b]	Harper et al. (2003, 2005)
Conifer	Pinus	2–383	16	Fire	Reverse-J	Wirth et al. (2002a, b)
Conifer	Pinus, Picea, Abies	11–426	71	Fire	Reverse-J	Clark et al. (1998)
Conifer	Pseudotsuga, Tsuga	1–515	6	Fire	Reverse-J	Agee and Huff (1987)
Conifer	Pseudotsuga-Tsuga	40–90	166	Fire	Reverse-J	Spies et al. (1988)
Conifer	Pseudotsuga-Tsuga	8–500	36	Harvest, fire[c]	U-shape	Janisch and Harmon (2002)
Deciduous	Acer, Fagus, Betula	10–>110	23	Harvest	Reserve-J	Gore and Patterson (1986)
Deciduous	Acer, Fagus, Betula	1–110	6	Harvest	U-shape	Roskoski (1980)
Deciduous	Nothofagus	2–191	9	Mixed	Mixed	Carmona et al. (2002)
Deciduous	Quercus, Carya, Acer	70–110	10	Harvest	U-shaped	Shifley et al. (1997)
Tropical	Mixed	9–>200	23	Slash and burn	U-shaped	Saldarriaga et al (1988)
Downed woody detritus sampled						
Conifer	Mixed[d]	0–360	4,840	Fire	Mixed	Brown and See (1981)
Conifer	Picea	1–30	3	Wind	Reverse-J	Knohl et al. (2002)
Conifer	Pinus	0–79	5	Harvest, fire[e]	U-shape	Howard et al. (2004)
Deciduous	Nothofagus	10–>150	12	Wind	Reverse-J	Davis et al. (2003)
Deciduous	Quercus, Carya, Acer	1–100	3	Harvest	Reverse-J	Idol et al. (2001)

[a] With a broad initial peak
[b] With decline in the old-growth phase
[c] Stands >60 years disturbed by fire
[d] Pinus, Pseudotsuga, Tsuga, Abies, Larix
[e] Oldest stand disturbed by fire

synthesis in more detail indicates that there is some evidence for a U-shaped curve as well, particularly for the data from Roskoski (1980), which were from a series of harvested stands where much of the live biomass was harvested. A reverse-J pattern of woody detritus mass was also found by Idol et al. (2001) in oak-hickory forests of Indiana with a minimum mass in forests 16–100 years after harvest.

There appears to be some support for the classic model in Russian forests. Wirth et al. (2002a, 2002b) observed successional changes in woody detritus in Siberian pine forests disturbed by fire that are consistent with the reverse J-shape curve with initial woody detritus stores six-fold higher than that found in forests over 100 years of age. Legacy wood in this system had largely decomposed by 100 years, and woody detritus appears to increase between the ages of 100 and 400 years of age, despite the fact that recurring surface fires appear to consume about 75% of the de novo wood.

South American forests observations support the classic model to some degree. Saldarriaga et al. (1988) found a U-shaped temporal pattern in woody detritus following slash-and-burn agriculture in moist tropical forests of Columbia and Venezuela. Although the youngest stands sampled were 9–14 years since clearing, considerably more woody detritus mass was found here than in forests that had been disturbed 20 years before. Interestingly, the accumulation of de novo wood appears to start soon after this point in time because forests disturbed 30 years ago have almost as much woody detritus as those disturbed 9–14 years before. Carmona et al. (2002) found support for a range of curves in temperate forests in Chile, with stands that had been logged having 4–50% of the woody detritus mass of that found in those that had only been burned. In stands with substantial removal of wood, early-successional forests had lower amounts of woody detritus than mid-successional or old-growth forests, suggesting an S-shaped accumulation curve. In forests disturbed only by fire, a reverse J-shaped curve appeared to be followed, with mid-successional forest having the least, and unlogged old-growth intermediate amounts of woody detritus mass.

8.4.2   Studies Not Matching the Classic Model

There have been cases where the reverse-J and U shaped curve for the temporal development of woody detritus mass has not been followed. This often occurs as an artifact of woody components measured or how the data are reported. For example, Brown and See (1981) found little consistency of temporal trends; however, they only considered downed woody detritus. This lack of consistent pattern occurred even when the mass for different forest types was normalized, with some areas exhibiting S-shaped curves, others U-shaped curves, and others having a peak in the intermediate stand ages. This inconsistency might be expected depending on the amount of downed wood removed by disturbance and the fact that disturbances creating standing dead trees would result in major input to downed woody detritus many years after the disturbance. For example, Tinker and Knight (2000) found that

downed woody mass was similar in recently burned or harvested lodgepole pine forests in Wyoming. However, when standing dead material was included, burned forests contained at least twice the mass of woody detritus suggesting that Brown and See (1981) might have seen a reverse J-shape in stands originating from fire had they accounted for snags. Clark et al. (1998) observed a U-shaped pattern of log volume following fire in spruce-fir and pine sub-boreal forests of British Columbia. Snag basal area followed a reverse-J shape in these same forests, but given the different units reported it is difficult to determine what the overall pattern was; in relative terms, logs and snags seemed least abundant in forests of 50–100 years of age.

Another cause for the lack of correspondence to theoretical trends is that only a segment of the succession was examined. For example, Franklin (1982) observed a very gradual increase in woody detritus for forests of 150–1,000 years of age, which is consistent with the later portions of the reverse J-shaped curve. Given the live biomass observed in these stands, it is very likely that the early-successional woody detritus mass would have been four- to six-times higher than they observed in the older ages. In another case, Knohl et al. (2002) observed an exponentially decreasing pattern of woody detritus mass after windthrow in a Russian boreal forest. However, the oldest forest examined was 28 years of age, and thus far younger than required for significant de novo woody detritus to accumulate. A similar decrease in woody detritus over succession was observed by Howard et al. (2004) in harvested southern boreal Jack pine forest of Canada, where mass decreased at least three-fold from an age of 0 to 29 years. Given that de novo woody detritus stores were five-fold higher in a 79-year-old forest that had been disturbed by fire, this might indicate that more of an S-shaped (as opposed to reverse J-shape) curve occurs in these forests following harvest. Shifley et al. (1997) reported that second-growth Missouri hardwood forests contained half the volume of downed wood of old-growth forests. This pattern is consistent with the accumulation of de novo wood, although without additional age classes it is difficult to ascertain. Davis et al. (2003) observed a negative exponential decrease to an asymptote in southern beech forests of New Zealand, and while this might be consistent with a reverse J-shaped curve, it is quite different from the classic version of this curve, with the minimum and oldest forest masses being similar.

In some cases, the peak of initial woody detritus can be quite broad, causing a departure from the classic model. This broad peak can be caused by the nature of the mortality or the presence of decomposition lags. Lambert et al. (1980) observed a variation of the reverse J-shape in a balsam fir forest in New England that was subject to fir-wave mortality. However, the pulse of input was drawn out over a decade by the gradual mortality process. After this pulse occurred, the mass curve displayed a decrease to a minimum in 50 years after the onset of mortality. In fire-killed black spruce forests of Canada, Manies et al. (2005) observed that woody detritus mass remained relatively constant for the first 30 years. This was probably caused by the very low decomposition rate of snags, but once these fell to the ground mass declined rapidly, reaching a minimum 70 years after the fire. Between

70 and 150 years after the fire, a small increase of woody detritus mass indicated a variant of the reverse-J shape.

Not all the U-shaped curves "confirmed" in the literature are strictly supported by the reported data. Sturtevant et al. (1997) reportedly found a U-shaped curve of woody detritus volume in a chronosequence of harvested stands in boreal forest of Newfoundland; however, the curve suggested by their observations is more of an S-shape. This is likely caused by the fact that their youngest stand sampled was 33 years of age and, after 50 years, most of the woody detritus was de novo wood. Had younger forests been sampled, it is most likely their assertion of a U-shaped curve would have been supported directly.

There is some evidence that temporal patterns of woody detritus mass can be quite complex during succession with secondary periods of decline. Harper et al. (2003, 2005) reported that black spruce forests of Quebec do not follow the classic temporal patterns. Those growing on sandy soils appear to follow the reverse J-shape for log volume, but since snags were reported in terms of basal area it is difficult to estimate a total volume pattern. Those forests growing on clay soils show an initial decrease in log volume followed by an increase in intermediate stages, with a decline as forests age further. Combining this data with the snag volume reported in Hély et al. (2000) suggests that the overall pattern of woody detritus abundance is similar. It seems likely that there is a decline in total woody detritus volume associated with paludification (i.e. the process of bog expansion resulting from rising water tables as a consequence of peat growth) given that live biomass in these forests declines from age 100 years to 200 years (Paré and Bergeron 1995). This would be similar to the theoretical pattern observed when NPP declines greatly as stands age (Fig. 8.8). Since paludification also decreases the amount of live wood present at the time of the disturbance, the low amounts present 32 years post-disturbance might be a consequence of this change in NPP as well (Hély et al. 2000). Sturtevant et al. (1997) also suggested that late succession boreal forests in Newfoundland could have a decline in woody detritus mass associated with changes in structure from even- to uneven-aged stands.

8.5   Effect of Management

There is little question that timber harvest, salvage logging, and intensive management (i.e. harvesting over short intervals, thinning, and salvage of mortality) can reduce the amounts of woody detritus found at different stages of stand development as suggested by the basic model presented in Sect. 8.3. While shortening the disturbance regime can reduce the amount of woody detritus, the interval between disturbances must be greatly reduced for this to be the dominant effect. For example, Wright et al. (2002) examined two disturbance regimes in Oregon that differed four-fold in the frequency of fires. Interestingly they had very similar amounts of woody detritus averaged over a landscape. This suggests that the effect of management is due largely to the reduction of legacy wood. Pedlar et al. (2002)

found that recently burned hardwood-conifer mixed forests in Ontario contained three times the woody detritus of those that had been recently clear-cut harvested. However, they also found that pure conifer stands created by management contained one-sixth to one-ninth the volume of woody detritus of mixed forests. Duvall and Grigal (1999) compared chronosequences of naturally disturbed versus managed stands in the Lake States region of the United States and found that the largest relative differences occurred early in succession, with managed (i.e. harvested stands) having one-fifth the amount of woody detritus of natural stands. By the end of the harvest rotation interval examined, managed stands contained one-third the woody detritus biomass of natural stands.

8.6   Consequences for Net Ecosystem Carbon Balance

The amount of legacy wood remaining at the start of the succession has a major impact on the pattern that net ecosystem carbon balance (NECB – Chapin et al. 2006) follows after disturbance. The basic model suggests that if legacy wood is left, the initial values of NECB are negative (a source to the atmosphere); however, as the amount of legacy wood decreases, the source phase (i.e. the period that NECB is negative) is weaker in magnitude (i.e., the absolute size of the flux) and ends earlier (Fig. 8.10). The basic model also predicts that the source phase is shorter but of much higher magnitude than the sink phase. While it is common to think of woody detritus always being a source of carbon to the atmosphere, the basic model predicts that the accumulation of de novo wood actually increases the strength of the carbon sink in the later phases of succession [cf. Chaps. 5 (Wirth and Lichstein) and 21 (Wirth), this volume]. The majority of published studies on forests disturbed by harvest or natural processes indicate an increase in carbon
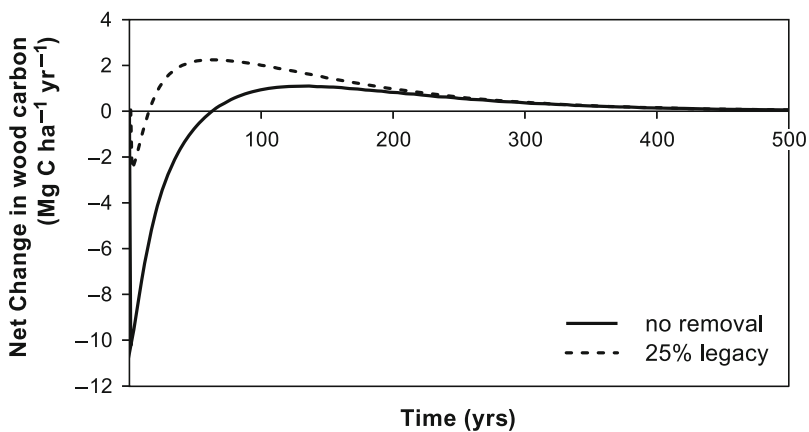
Fig. 8.10 Net change in total woody carbon stores predicted by the basic model for the case when all or 25% of the legacy wood remains

stores associated with accumulation of de novo dead wood during the middle stages of succession (8.2). The simulation experiments conducted here indicate that this pattern is also likely to be true for all cases except when: (1) a fast-decomposing species replaces a slow-decomposing species during succession, or (2) NPP decreases markedly during the latter phases of succession. In both these cases a secondary period of net carbon loss as the forest enters the old-growth stage is possible. At first glance, removing legacy wood appears to create a net sink over the succession, but this conclusion is misleading unless the majority of the wood removed by harvest is permanently stored. A more realistic interpretation would account for the fate of removals in terms of decomposition, losses in manufacturing and use etc., all of which would tend to put the overall forest sector system (i.e. the forest and forest products) in carbon balance.

Unfortunately, few studies have measured atmospheric carbon flux directly after a disturbance. Knohl et al. (2002) measured atmospheric carbon exchange from July to October in a Russian boreal forest that had been windthrown 2 years prior to the study. The decomposition of woody detritus comprised one-third of the total ecosystem respiration and caused these forests to be a source of carbon to the atmosphere. Clark et al. (2004) measured atmospheric flux for a chronosequence of harvest slash pine plantations in Florida and found that recently harvested forests were a strong net source to the atmosphere, but by year 10 forests were net sinks.

Despite the number of chronosequences sampled for woody detritus mass, few studies have reported masses for both live and dead wood. Therefore the ability to check the predictions of the basic model regarding successional patterns of NECB is limited. In the Eurosiberian boreal region, harvested forests remain carbon sources to the atmosphere for their first 14 years (Schulze et al. 1999). Examining the trends in NEP (net ecosystem production) of fire-disturbed Scots pine forests in Siberia based on changes in live and dead biomass (including woody detritus) indicated that forests remained a net source to the atmosphere for 12–24 years and then became net sinks (Wirth et al. 2002b; Fig. 8.11). This analysis also indicated that NEP approached zero when the forest exceeded 300 years of age. In the Pacific North-west, harvested forests remained a net source to the atmosphere for 15 years despite the removal of the majority of the legacy wood (Janisch and Harmon 2002). Using an empirical model, this study estimated that the source phase would have lasted 40–50 years if all the legacy wood had remained. In accordance with Wirth et al. (2002b), Janisch and Harmon (2002) estimated that the sink phase would have lasted until an age of 300 years. It would be expected that the timing of this pattern of source–sink switching would shorten approaching the tropics. This is supported by the findings of Gholz and Fisher (1982) from a 35-year long chronosequence in Florida slash pine forests. In this case, a harvested forest switched from a net source to a net sink with respect to the atmosphere within 3 years, with the source phase having twice the magnitude (i.e. absolute size of the flux) of the sink phase. Based on the rate of woody detritus loss between ages of 9 and 20 years, this rapid pattern of loss may also be true for the tropical post-pasture succession examined by Saldarriaga et al. (1988); however, their chronosequence started 9 years after disturbance and NECB is generally positive after this time.

8.7   Reducing Observational Uncertainties

The simulation model results show that many factors can change the pattern of woody detritus mass over succession relative to the classic model, but that the fundamental pattern shape is determined by the amount of legacy wood remaining. There are observations consistent with the classic model as well as those suggesting that other factors may influence the pattern of accumulation. However, it is also clear that observational studies could be improved to elucidate whether some of the more subtle predictions occur. There are several aspects that would make chronosequence data more useful in this regard:

1. To detect changes in the non-linear curves suggested by the models it is necessary to have more than three to four points in time sampled. The minimum times to sample would be: (1) right after the disturbance, (2) at the lowest point, (3) as the mass approaches the final maximum, and (4) for a very old forest to help check if there is a final decline in mass. Pinpointing these optimal times would be difficult in most systems and so a greater number of stand ages would be preferable. A related comment is that many studies sample chronosequences long after the disturbance occurred, thus making it difficult to determine the overall pattern of woody detritus mass accumulation.

2. Standing and downed debris need to be sampled and reported in the same units (either volume or mass) to quantify the total woody detritus trend. Ideally, tree mass would also be determined to allow to estimate changes in total wood carbon stores over succession. Sampling both standing and downed wood is important since there is no fixed relationship between their abundance, in part because disturbances and subsequent stand development can create a wide range of mixtures. Mass is the most appropriate unit to examine changes in carbon stores as volume is more conservative than mass (Duvall and Grigal 1999) and unless the degree of decay during succession can be estimated, a fixed volume to mass conversion factor, which would give the same relative temporal pattern as volume, must be used. Predicting the state of decay is difficult because it is likely to be highly non-linear and so it is necessary to record at least the average state of decay during sampling (and it is even better to determine this on each piece of wood sampled). Separating woody detritus into legacy and de novo wood is very helpful in creating an empirical model of the system (e.g. Spies et al. 1988) and interpreting the total mass pattern.

3. Chronosequences are a relatively fast way to determine successional changes in woody detritus mass; however, they have several shortcomings. It is extremely important that the productivity, soils, and climate of the stands sampled are as similar as possible. Since this is difficult to achieve, replicate stands of similar age helps to minimize some of these problems. It is also important that the disturbances initiating the succession are comparable. While mismatching disturbances in chronosequence (e.g. Howard et al. 2004; Carmona et al. 2002) can provide insights, the results have to be interpreted very carefully when the amounts of legacy wood differ. While using a time series to observe an entire

forest succession sequence is not realistic in the short-term, more could be learned by examining short-term changes of forests arranged along a chronose-quence (Wirth et al. 2002a). This would result in a vector of change and allow one to quantify NPP as well as mortality inputs and decomposition rates, all of which would provide considerable insight into the processes underlying changes in mass. This approach has been applied to CWD decomposition and changes in forest floor mass to reveal far more details than can be detected using a chronosequence approach alone (Harmon et al. 2000; Yanai et al. 2000).

8.8   Conclusions

Woody detritus is an important, but until recently understudied, part of forest ecosystems. While often considered solely a feature of old-growth forests, woody detritus is present in all forests. The way this material changes over succession follows a predictable pattern, strongly influenced by the nature of the disturbance. The classic model predicts that when disturbances leave most of the legacy wood, the temporal pattern generally follows a reverse-J shaped curve and as legacy wood is removed this evolves to a U-shaped curve; if the entire legacy is removed it follows an S-shaped curve. This suggests that the commonly held view that old-growth forests always contain the maximum amount of woody detritus is not always true – the relative amount in old-growth forests depends strongly on the amount of legacy wood present at the start of succession. There are likely many variations on the classic model predictions; however, the only cases in which the basic shapes are not likely followed include: (1) the replacement of an early-successional species with high decay resistance by a late-successional species with low decay resistance, and (2) a forest in which there is a substantial decline in NPP late in succession. In these two cases there are possible secondary, but minor, decreases in woody detritus mass late in succession that may have implica-tions for carbon sequestration. In the case of repeated harvest, the shorter the interval between disturbances and the more legacy wood that is removed, the lower the average woody detritus mass becomes. Chronosequence studies have confirmed the basic pattern predicted by the simple, classic model, and in at least one case suggest that a secondary decline in woody detritus mass due to decreases in NPP. Field studies using changes in mass and eddy flux also indicate the presence of woody detritus early after disturbance causes forests to be net sources to the atmosphere. The time forests switch from a net source to a net sink is controlled by the amount of legacy wood left and by the rate at which the new forest re-establishes. However, to fully understand these changes and their consequences for forest carbon balances, the temporal resolution of chronosequences needs to be improved and these measures need to be combined with measurements over time.

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Part III
Belowground Processes

Chapter 9
Aboveground and Belowground Consequences of Long-Term Forest Retrogression in the Timeframe of Millennia and Beyond

David A. Wardle

9.1 Introduction

Following the occurrence of a substantial disturbance and creation of a new surface, primary succession occurs. This involves colonisation by new plant species, and their associated aboveground and belowground biota. During this period, substantial ecosystem development occurs (Odum 1969), and this involves the buildup of ecosystem carbon through photosynthesis and nitrogen through biological nitrogen fixation. The initial colonising plant species are short-lived and often herbaceous, but these are replaced over time by those that are larger, woody, more conservative at retaining nutrients, and produce organic matter of poorer quality (Grime 1979; Walker and Chapin 1987). Disturbances that are not sufficiently severe to result in new surfaces being formed can reverse the successional trajectory, resulting in a secondary succession that often operates in a broadly similar way to primary succession though from a later starting point (White and Jentsch 2001; Walker and Del Moral 2001).

Following the initial development of forest during succession, and as trees age, there may be a notable reduction in net biomass productivity. The generality of this phenomenon is under debate (see Chap. 21, by Wirth, this volume), but where it occurs, the decline is usually apparent in the order of decades to centuries following forest stand development (Gower et al. 1996). The mechanistic basis for this decline is unclear, but there are likely to be multiple factors involved (see detailed discussion in Chap. 7 by Kutsch et al., this volume). Some proposed explanations have a plant-physiological basis, such as increasing hydraulic limitation as trees grow taller, shifts in the balance between photosynthesis and respiration, and increasing stomatal limitation as trees age. However, the evidence for or against each of these mechanisms is mixed and no universal explanation emerges (see, e.g. Gower et al. 1996; Magnani et al. 2000; Weiner and Thomas 2001; Ryan et al. 2004, 2006). Other explanations relate to belowground properties and nutrient supply from the soil. For example, as forest stands develop and succession progresses, the rate of mineralisation of nutrients from the soil declines (Brais et al. 1995; De Luca et al.

2002). This is at least partly as a result of a greater proportion of nutrients being immobilised in plant tissue and because of the declining quality of plant litter (Hättenschwiler and Vitousek 2000; Nilsson and Wardle 2005). This reduced soil activity is consistent with changes in the composition of the soil community that have sometimes been observed during succession (e.g. Scheu 1990; Ohtonen et al. 1999). Often the reduction of nutrient availability is driven in part by changes in the forest understorey composition, such as increased densities of dwarf shrubs (Nilsson and Wardle 2005) and mosses (Zackrisson et al. 1997; Bond-Lamberty et al. 2004), which may lock up nutrients or produce litter of poor quality. Regardless of the precise mechanisms involved, it is apparent that at least part of the reduction in forest stand productivity in the order of decades to centuries is frequently associated with the reduced rate of supply of nutrients from the soil, and probably involves changes in the composition of the soil biota as well as the vegetation.

In the prolonged absence of major disturbance, i.e. in the order of millennia and beyond, the decline in forest productivity can be followed by significant declines in forest stand biomass. This decline is often associated with declines in the availability of soil nutrients that occur during pedogenesis (Walker and Syers 1976; Richardson et al. 2004; Vitousek 2004; Wardle et al. 2004; Coomes et al. 2005). We refer to this situation of long-term decline in forest biomass caused by reduction in available nutrients as 'ecosystem retrogression' (Walker et al. 2001; Walker and Reddell 2007). This phenomenon is distinct from the shorter term decline in forest productivity that frequently occurs in the order of decades to centuries and that may have a variety of causes (Gower et al. 1996). Significantly, as ecosystems age in the order of thousands of years without major disturbance, phosphorus availability may become a major factor limiting forest biomass. In a classical investigation of long-term chronosequences on sand dunes and moraines in New Zealand (spanning several millennia), Walker and Syers (1976) showed that as soils age the total amounts of phosphorus declines significantly (presumably through leaching and runoff), and that the remaining phosphorus becomes converted to forms that are increasingly physically occluded or bound in relatively recalcitrant organic compounds, and that are relatively unavailable to plants. This type of pattern has subsequently been shown in other locations and for other ecosystems, e.g. in eastern Australia (Walker et al. 1981) and the Hawaiian islands (Crews et al. 1995; Vitousek 2004). In the long term, greatly reduced availability of nitrogen may also occur, partly because of increased immobilisation, partly because of retention of nitrogen in recalcitrant polyphenolic complexes that are less easily decomposed (Northup et al. 1995, 1998; Wardle et al. 1997), and partly because of leaching losses as dissolved organic nitrogen (see Chap. 16 by Armesto et al., this volume). These changes in availability of key nutrients during retrogression appear to be linked to both changes in soil biota (Williamson et al. 2005; Doblas-Miranda et al. 2008) and forest vegetation composition (Wardle et al. 1997; Nilsson and Wardle 2005).

It is apparent that in forested ecosystems subjected to the absence of disturbance in the order of thousands of years, the initial build-up phase is followed by a decline

in net productivity, and, given sufficient time, by a decline in standing biomass (Richardson et al. 2004; Vitousek 2004; Wardle et al. 2004; Coomes et al. 2005). At least part of this decline is linked to reduced nutrient availability . In this chapter, I will explore the changes that occur in forested ecosystems that have been absent from disturbances for sufficient time for declines in standing tree biomass to occur, i.e. in the order of millennia and beyond. In doing so, I will firstly describe an ongoing study on forested lake islands in northern Sweden where these ideas are being explicitly explored. I will then assess the generalities of these concepts by considering other long-term forested chronosequences around the world. In doing so, I will attempt to determine whether there are general trends that occur aboveground and belowground with regard to how communities and ecosystems respond to long-term ecosystem retrogression.

9.2 Lake Islands in Northern Sweden

The study system consists of an archipelago of forested lake islands in two adjacent lake systems (Lakes Uddjaure and Hornavan), in the boreal zone of northern Sweden (66°55′–66°09′ N; 17°43′–17°55′E). Within this system are over 400 islands that vary in size from a few square metres to over 80 ha. For our studies, we have selected several forested islands in each of three size classes, i.e. 'small' islands (<0.1 ha), 'medium' islands (0.1–1.0 ha) and 'large' islands (1.0 ha). Study islands were been chosen such that their areas are distributed lognormally, and very large islands with obvious signs of human activity were excluded. The selected islands are all of approximately the same age, having been formed by the retreat of land ice 9,000 years ago, and have been subjected to minimal human interference.

Islands are ideal systems for studying the effects of historical fire regimes on large numbers of spatially independent ecosystems (Bergeron 1991). The main extrinsic driver that varies across the islands in our study system is wildfire disturbance through lightning strike; large islands get struck by lightning more often than do smaller ones, and therefore burn more frequently (Wardle et al. 1997, 2003). This is apparent both from analyses of fire scars on trees, and from dating of ^{14}C of the most recent charcoal present in humus profiles (Table 9.1). Island size therefore serves as a surrogate for time since fire and fire frequency. Some large islands have burned in the past century, while others have not burned for the past 5,000 years (Wardle et al. 2003), making the system ideal for investigating the effects of variation of a major agent of disturbance across essentially independent discrete ecosystems. Some large islands have historical fire regimes that are probably comparable to those of Scandinavian boreal forests on the mainland (Zackrisson 1977; Niklasson and Granström 2000), while most small islands have regimes that are consistent with long-term fire suppression or absence.

Fire history is an important long-term determinant of vegetation composition in boreal forests (Payette 1992; Légaré et al. 2005) and, consistent with this, the variation in fire regime across islands has been found to exert important effects

Table 9.1 Changes in selected aboveground and belowground properties (mean values with standard errors in brackets) across an island size gradient in northern Sweden, in which decreasing island size is reflective of increasing ecosystem retrogression. Data from Wardle et al. (1997, 2003, 2004) and Wardle and Zackrisson (2005). Within each row numbers followed by the same letter are not statistically significant at $P = 0.05$ (Tukey's test following one-way ANOVA).

Response variable	Large island (>1 ha)	Medium island (0.1–1.0 ha)	Small island (<0.1 ha)
Disturbance regime			
Time since last major fire (^{14}C data) (years)	585 (233) c	2180 (385) b	3250 (439) a
Number of fire scars caused in past 250 years	0.667 (0.256) a	0.208 (0.085) b	0.143 (0.016) b
Aboveground properties			
Tree biomass (kg m^{-2})	7.39 (0.83) a	5.38 (0.47) a	3.98 (0.62) b
Tree litterfall (g C m^{-2} year^{-1})	37.3 (5.2) a	43.7 (4.0) a	32.3 (4.5) b
Tree productivity (g C m^{-2} year^{-1})	148.1 (15.5) a	152.8 (12.9) a	78.4 (14.7) b
Dwarf shrub biomass (kg m^{-2})	0.365 (0.014) a	0.383 (0.015) a	0.288 (0.019) b
Dwarf shrub productivity (g C m^{-2} year^{-1})	76.8 (3.9) a	72.7 (3.5) a	51.6 (4.8) b
Dominant tree species	Pinus sylvestris	Betula pubescens	Picea abies
Dominant dwarf shrub species	Vaccinium myrtillus	Vaccinium vitis-idaea	Empetrum hermaphroditum
Belowground properties			
Soil polyphenols (µg g^{-1})	175 (6) b	204 (6) a	225 (8) a
Soil respiration (µg CO$_2$-C g^{-1} h^{-1})	4.23 (0.30) a	2.97 (0.28) b	1.81 (0.30) c
Substrate-induced respiration (µg CO$_2$-C g^{-1} h^{-1})	22.9 (1.43) a	14.5 (1.35) b	11.5 (2.13) b
Litter decomposition rate (% loss in 2 years)	45.9 (1.1) a	44.2 (1.0) b	41.5 (1.0) b
Total humus carbon mass (kg m^{-2})	6.4 (1.1) c	16.2 (2.5) b	27.3 (2.5) a
Humus C to N ratio	40.4 (1.18) a	36.0 (1.17) ab	32.9 (0.79) b
Humus C to P ratio	623 (20) b	687 (36) ab	759 (30) a
Humus N to P ratio	15.4 (0.5) c	19.1 (0.9) b	23.3 (1.1) a

on vegetation composition (Wardle et al. 1997; Table 9.1). The largest and most regularly burned islands are dominated by relatively fast-growing early-successional species such as *Pinus sylvestris* and *Vaccinium myrtillus*, and the middle-sized islands are dominated by *Betula pubescens* and *Vaccinium vitis-idaea*. Meanwhile, the small islands are dominated by slow-growing late-successional species such as *Picea abies* and *Empetrum hermaphroditum*. Those species that dominate on large islands tend to allocate carbon to growth while those dominating on smaller islands tend to allocate carbon to the production of secondary compounds such as polyphenolics (Nilsson 1994; Gallet and Lebreton 1995; Nilsson and Wardle 2005). Consistent with this, humus on small islands has a significantly higher concentration of polyphenolics than that on the larger islands (Table 9.1).

Responses of the plant community to island size have important consequences for the belowground subsystem. The poorer quality of litter returned to the soil on small islands, and the higher concentrations of polyphenolics in the humus, leads to significant impairment of soil microbial biomass and activity (Table 9.1). This in turn results in reduced decomposition rates of plant litter in the soil, and lower rates of supply of nutrients from the soil for subsequent plant growth. The concentration of nitrogen in the humus of the small islands is slightly greater than that of the large islands (Wardle et al. 1997), and biological nitrogen fixation by cyanobacteria associated with feather mosses (the main biological form of nitrogen input to the islands) is greatest on the small islands (Lagerström et al. 2007). However, the small islands appear to be more nitrogen limited: test litter placed on the small islands releases nitrogen more slowly than when placed on large islands and the concentrations of plant available forms of nitrogen are lower in soils of small islands (Wardle and Zackrisson 2005). This appears to influence nitrogen acquisition by microbes and plants; the nitrogen concentrations of the microbial biomass and green leaves of at least some plant species are lower on the small than the large islands (Wardle et al. 1997). Despite there being more soil nitrogen (and nitrogen input) on the small islands, it is likely that much of the soil nitrogen on the small islands is not biologically available because it is bound tightly in polyphenolic complexes (Wardle et al. 1997). Concomitant with this reduced availability of nitrogen is reduced availability of phosphorus on the small islands (Wardle et al. 2004), which is a characteristic of retrogressive chronosequences that span thousands of years (Walker and Syers 1976). As a consequence of reduced nutrient availability and plant uptake following the prolonged absence of wildfire, small islands show lower rates of tree and understorey productivity, less litterfall, and lower vascular plant standing biomass (Wardle et al. 1997, 2003; Table 9.1).

The island system provides evidence that reductions in fire frequency, and the ecosystem retrogression that follows, greatly affects ecosystem carbon sequestration. As island size decreases and time since fire increases, the amount of carbon stored aboveground declines. However, because litter decomposition rates are also impaired on the small islands, the amount of carbon stored belowground in the humus increases (note that the mineral soil layer, and hence the amount of carbon stored in it, is negligible). Reduction of decomposition on small islands emerges for at least four reasons (Wardle et al. 2003, Dearden et al. 2006): (1) plant species that

produce poorer quality litter (e.g. *Picea*., *Empetrum*). begin to dominate; (2) pheno-typic plasticity within species, i.e. a given plant species may produce poorer litter quality on a small island; (3) trees produce a greater proportion of poor quality twig litter relative to higher quality foliar litter; and (4) activity of the decomposer microflora declines. As a consequence, some large islands store less than 5 kg C/m^2 in the humus layer (which is often less than 10 cm deep) while some small islands store over 35kg C/m^2 in the humus layer (which is often over 80 cm deep). Because the belowground (rather than aboveground) component stores the majority of carbon in these forests, there is net carbon sequestration over time, of around 0.45 kg C/m^2 for every century without a major fire (Wardle et al. 2003). This indicates that long-term fire suppression significantly contributes to ecosystem carbon storage, and if the pattern identified in this system is representative of northern ecosystems in general, then current fire suppression practices in the boreal zone are likely to play an important role in the global carbon cycle. In this light, a recent study of a long-term (over 2,300 years) chronosequence in the boreal zone of eastern Canada found belowground carbon accumulation rates to be significantly greater than that measured on the lake islands (Lecomte et al. 2006).

The island study is also relevant for addressing the so-called 'diversity-function' issue, which relates to whether plant species diversity promotes key ecosystem processes such as production and decomposition [see Hooper et al. (2005) for a review]. As island size decreases, tree species diversity (Shannon-Weiner diversity index) increases sharply (Wardle et al. 2008; Fig. 9.1), as does total vascular plant species richness (Wardle et al. 2008). However, small islands also have the lowest rates of key ecosystem processes such as decomposition, nutrient mineralisation and aboveground productivity. The resulting negative correlation between plant diversity and process rates suggests that plant diversity is not a key driver of ecosystem processes across the island sequence, because of the overriding importance of other factors that also vary across the sequence such as the traits of the dominant plant species. In particular, the large islands are dominated by rapidly growing plant species that produce litter of high quality, and promote rapid ecosystem process rates. However, these species are also highly competitive and appear to suppress subordinate species through competitive exclusion, reducing total plant diversity. These competitive dominants cannot dominate on the less fertile small islands; this leads to a greater coexistence of species being possible, but also a greater incidence of those plant species that are unproductive, produce litter of a poor quality, and slow ecosystem process rates down.

While traits of dominant plant species may govern ecosystem functioning at the across-island (between ecosystem) spatial scale, biodiversity may have a role in influencing ecosystem processes at more local spatial scales. To investigate this, an ongoing study was set up in 1996 on each of 30 islands and which involves 420 manipulative plots (first 7 years reported by Wardle and Zackrisson 2005); the study involves regularly maintained experimental manipulations of various plant species and functional groups with a particular focus on understorey vegetation. Above-ground, removal of various components of the understorey layer often reduced total plant biomass in that layer. Meanwhile, when belowground properties were considered,
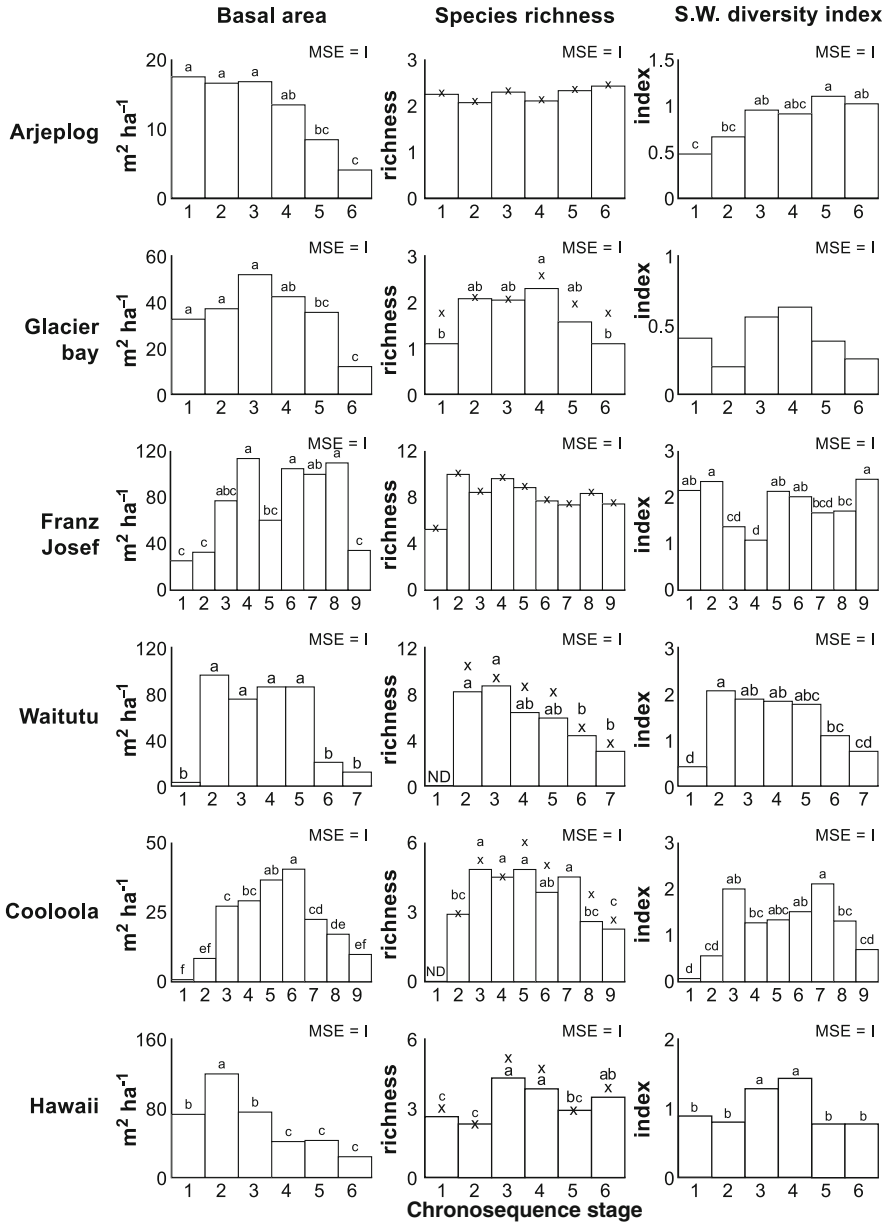
Fig. 9.1 Changes in tree basal area, species richness, and Shannon-Weiner (*S.W.*) diversity indices (mean of all plots for each stage) in response to ecosystem development (*1* = youngest) for each of six long-term chronosequences (see Table 9.2 for timescale of each sequence). For the species richness measures at each chronosequence stage, values represented by *histogram bars* have been corrected for varying total stem density using rarefraction analyses, while the values represented by *crosses* are the raw species richness values not adjusted using rarefraction. Within

two dwarf shrub species (*Vaccinium myrtillus* and *Vaccinium vitis-idaea*) emerged as major ecosystem drivers, but only on large islands. Specifically, experimental removal of these species on large (but not on small) islands adversely affected plant litter decomposition rates respiration, soil microbial biomass, and plant-available forms of nitrogen. This work points to the effects of biodiversity loss (either in terms of functional groups or species) at the within-island scale being context-dependent, and being of diminishing importance with increasing time since wildfire and as retrogression proceeds. These results reveal that, although biodiversity is unlikely to be a major driver of ecosystem properties at the across-island scale, biodiversity loss may play a role at the within-island scale, but that this role may be important only in relative productive earlier successional ecosystems.

It is apparent that as retrogression proceeds in this island system, a range of responses occur both above- and below-ground. Several of these responses are driven in the first instance by the reduced availability of nutrients over time, and in the second instance by changes in the functional composition of the dominant vegetation. Changes in the availability of other resources such as moisture cannot explain our results, because humus depth increases during retrogression, and this involves greater retention of soil moisture with increasing time since fire. Other changes that may occur on these islands during retrogression involve shifts in the communities of microorganisms and above- and below-ground invertebrates, and investigations of the involvement of these organisms are in progress. It is apparent in the long-term absence of disturbance on these islands that high productivity and high biomass forests cannot be maintained beyond around 2,000–3,000 years and that, after this time, increasing nutrient limitation leads to reduced stature of the forest, slowdown of ecosystem process rates, and increasing storage of organic matter belowground rather than aboveground. This type of retrogression resulting from the prolonged absence of wildfire may be a common phenomenon in boreal forests (Asselin et al. 2006), and could ultimately lead to low productivity in forest tundra and taiga communities throughout many boreal forest habitats (see Payette 1992; Hörnberg et al. 1996).

9.3   Retrogressive Successions Elsewhere in the World

While the Swedish lake island system provides evidence of ecosystem retrogression driven by nutrient limitation, the question emerges as to whether this phenomenon is more widespread in nature. Some other studies have also characterised long-term chronosequences that yield evidence of retrogression, and details

Fig. 9.1 (Continued) each panel, *histogram bars* topped by the same letter do not differ significantly at $P = 0.05$ according to the least significant difference test; this test has not been applied to panels for which chronosequence stage effects are not significant according to ANOVA. *ND* Not determined, *MSE* mean standard error. Stages 1 and 2 for the Glacier Bay chronosequence lack trees and are therefore not presented here (taken from Wardle et al. 2008)

of six of these (the Swedish lake island system, and five others) are summarised in Table 9.2. These do not represent an exhaustive list of retrogressive chronosequences , but rather a selection of sequences that have each been well characterised and well studied, and that have previously been used in a comparative study by Wardle et al. (2004) to understand ecosystem decline. These sequences are all very long term and span at least 6,000 (and up to 4.1 million) years. Each chronosequence represents a series of sites varying in age since surface formation or catastrophic disturbance, but with all other extrinsic driving factors being relatively constant. Two of these sequences are in the Boreal zone, i.e. the Arjeplog sequence in northern Sweden (described above) and the Glacier Bay sequence of south-east Alaska (Noble et al 1984; Chapin et al. 1994). Two are in the temperate zone, i.e. the Franz Josef sequence of Westland, New Zealand (Walker and Syers 1976; Wardle and Ghani 1995; Richardson et al.2004) and the Waitutu sequence of southern New Zealand (Ward 1988; Coomes et al 2005). The remaining two are in the sub-tropical zone, i.e. the Hawaiian island sequence (Crews et al 1995; Vitousek and Farrington 1997; Vitousek 2004) and the Cooloola sequence of Queensland, Australia (Thompson 1981; Walker et al 2001). These sequences are formed on vastly different substrates and have been created by different agents of disturbance (Table 9.2). In all six cases, ecosystem development in the long-term has occurred after a catastrophic disturbance event or an event that has substantially re-set the successional clock.

Tree basal area (a surrogate of tree standing biomass) initially increases but eventually shows a sharp decline across each of the six chronosequences, in the order of 2,000–10,000 years following the disturbance that created the chronosequence (Fig. 9.1; Wardle et al. 2004). This is accompanied by changes in forest structure and height for these sequences (Crews et al. 1995; Richardson et al. 2004; Wardle et al. 2003, 2004). This decline in forest stature during retrogression has been shown to be accompanied by reductions in net primary productivity for the Arjeplog and Hawaii sequences (Wardle et al. 2003; Vitousek 2004), and by shifts in respiratory and photosynthetic characteristics of the dominant forest vegetation for the Franz Josef sequence (Turnbull et al. 2005; Whitehead et al. 2005).

The declines in forest biomass and function are almost certainly driven by the aging of the soil and a decline in soil fertility. Importantly, for all six chronosequences, there were general increases over time in the substrate nitrogen to phosphorus, notably in the uppermost layer of humus or, in the case of Cooloola (in which a humus layer is effectively lacking), mineral soil (Fig. 9.2). In all six cases, significant increases in these ratios occurred at around the time that a decline in forest biomass was beginning to occur, indicative of ecosystem retrogression (Fig. 9.1; Wardle et al. 2004). Further, for each chronosequence, the nitrogen to phosphorus ratio during the retrogressive phases became higher than the 'Redfield Ratio' (Redfield 1958), i.e. the ratio that has been previously postulated by aquatic ecologists as the ratio above which phosphorus becomes limiting relative to nitrogen. Consistent with this, there is evidence from several of these sequences for the litter or foliar nitrogen to phosphorus ratio to increase during retrogression (Vitousek 2004; Wardle et al. 2004; Coomes et al. 2005), indicative of increasing relative

Table 9.2 Details of long term forested retrogressive chronosequences around the world that provide evidence of aboveground and belowground limitation by nutrient availability over the order of at least thousands of years (adapted from Wardle et al. 2004). The Arjeplog sequence is the lake island system presented in Table 9.1

Chronosequence	Location	Mean January temperature (°C)	Mean July temperature (°C)	Mean annual precipitation sum (mm)	Cause of chronosequence	Parent material	Duration of chronosequence (years)
Arjeplog, Sweden	65°02′N, 17°49′E	−14	13	750	Islands with varying time since last major fire	Granite boulders; moraine	6,000
Glacier Bay, Alaska	59°N, 136°W	−3	13	1,400	Surfaces of varying ages caused by glacial retreat	Sandstone, limestone, igneous intrusions	14,000
Cooloola, Australia	27°30′S, 153°30′E	25	16	1,400 – 1,700	Sand dunes of varying age caused by aeolian sand deposition	Sand derived from quartz grains	>600,000
Franz Josef, New Zealand	43°25′S, 170°10′E	15	7	3,800 – 6,000	Surfaces of varying ages caused by glacial retreat	Chlorite schist, biotite schist, gneiss	>22,000
Waitutu, New Zealand	46°06′S, 167°30′E	12	5	1,600 – 2,400	Terraces of varying ages caused by uplift of marine sediments	Mudstones and sandstones	600,000
Hawaii	19–22°N, 155–160°W	14	17.5	2,500	Surfaces of varying ages caused by volcanic lava flow	Basalt tephra	4,100,000

Substrate N-to-P ratio
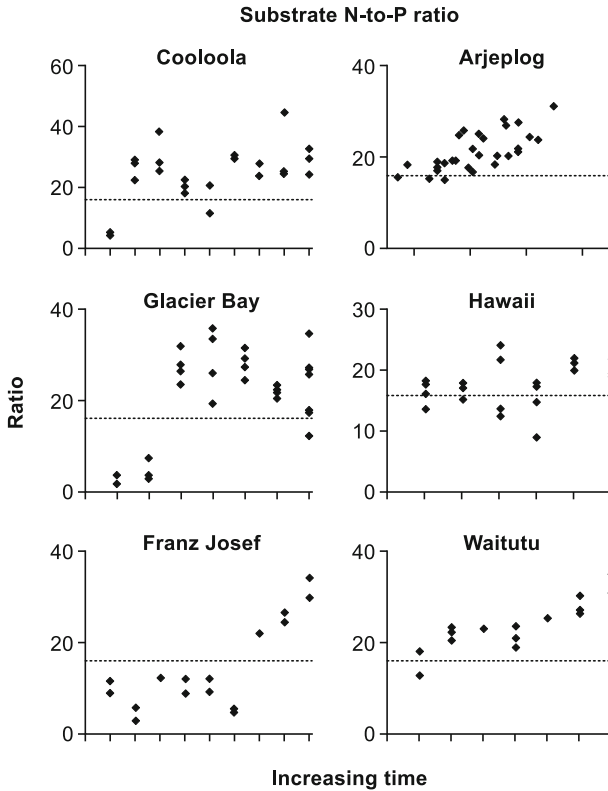
Fig. 9.2 Nitrogen to phosphorus ratios for humus substrate (or uppermost mineral soil substrate in the case of Cooloola) of each of six long-term chronosequences, in relation to increasing time since the catastrophic disturbance that initiated the chronosequence (see Table 9.2 for timescales of each sequence). Values for R^2 between nitrogen to phosphorus ratio and chronosequence stage are: Cooloola: 0.323 (quadratic; $P = 0.011$); Glacier Bay: 0.625 (quadratic; $P < 0.001$); Franz Josef: 0.609 (quadratic; $P < 0.001$); Arjeplog: 0.525 (linear; $P < 0.001$); Hawaii: 0.160 (linear; $P = 0.048$); Waitutu: 0.725 (linear; $P < 0.001$). The Redfield ratio (nitrogen : phosphorous = 16), above which phosphorus is believed to become limiting relative to nitrogen (Redfield 1958), is shown for comparative purposes in each panel as a *dashed line* (adapted from Wardle et al. 2004)

limitation by phosphorus over time. Additionally, a long-term fertilisation study across the Hawaiian chronosequence provides clear evidence of forests responding primarily to nitrogen addition at early stages and primarily to phosphorus addition at late retrogressive phases (Vitousek and Farrington 1997). The available evidence therefore points to long-term retrogression being generally driven by limitation by phosphorus rather than by nitrogen.

Across each of these six chronosequences, we also measured diversity of tree species (Wardle et al. 2008). For these sequences, rarefraction-adjusted tree species richness often peaked coincidentally with tree basal area (a surrogate of tree biomass), and declined during retrogression (Fig. 9.1). This result is in contrast to

theories predicting positive or unimodal responses of tree diversity to biomass or soil fertility (Grace 2001; Grime 2001). The Shannon-Weiner diversity index for trees sometimes showed the same pattern but was least when tree basal area peaked in the Franz Josef and Arjeplog sequences (Fig. 9.1); this was driven by the domination of total basal area by single tree species in both cases. The decline in tree diversity during retrogression was often associated with increased nitrogen to phosphorous ratios in the soil, pointing to these ratios as important controls not only of tree biomass but also of tree diversity.

The producer and decomposer subsystems of terrestrial ecosystems operate in tandem to maintain ecosystem functioning. Measurements performed across each of these chronosequences point to impairment of belowground processes during retrogression. For example, there is evidence that the rate of plant litter decomposition declines across most of these sequences during the retrogressive stages (Crews et al. 1995; Hobbie and Vitousek 2000; Wardle et al. 2003, 2004). Further, measurements of mineral nutrient dynamics in decomposing plant litter points to a general pattern of reduced rates of phosphorus release from litter collected from retrogressive chronosequence stages (Wardle et al. 2004). These reductions are indicative of increased retention of phosphorus in litter for those chronosequence stages for which growth of trees is impaired. Coupled with this are changes in soil biota . Across several of these chronosequences are clear trends of reduced levels of soil microbial biomass and activity (Wardle and Ghani 1995; Wardle et al. 2003, 2004), reduced densities of several groups of soil fauna (Williamson et al. 2005; Doblas-Miranda et al. 2008), and increasing dominance of fungi relative to bacteria (Wardle et al. 2004; Williamson et al. 2005), during retrogression. Because fungal-based food webs encourage nutrient cycles that are less leaky than bacterial-based webs (Coleman et al. 1983), this result is indicative of nutrient cycles becoming increasingly closed and nutrients becoming less available during retrogression. In sum, the available data on belowground processes and organisms across these six chronosequences indicates that ecosystem retrogression has comparable effects on both the aboveground and belowground subsystems, pointing to the likelihood of feedbacks between the two components during retrogression.

The available evidence points to a general pattern of limitation by phosphorus during retrogression, particularly relative to nitrogen. This does not mean that nitrogen is not also limiting during retrogression for at least some chronosequences; evidence of nitrogen limitation during retrogression exists at least for the long-term chronosequences in the boreal zone, i.e. Glacier Bay and northern Sweden (Chapin et al. 1994; Wardle et al. 1997). However, there are plausible grounds for believing that phosphorus should eventually become limiting relative to nitrogen during retrogression. This is because phosphorus is derived from parent material and, at the beginning of primary succession, there is a fixed amount of phosphorus that declines over time in both amount (through runoff and erosion) and availability (through physical occlusion and conversion to less available organic forms) (Walker and Syers 1976; Vitousek 2004; Turner et al. 2007). In contrast, nitrogen is biologically fixed by living organisms and therefore builds up during primary

succession . Therefore, unlike phosphorus, nitrogen can be biologically renewed during succession (including retrogression), and there is evidence of significant biological nitrogen fixation during the retrogression phases for both the Hawaiian chronosequence (Crews et al. 2000) and the Swedish island chronosequence (Lagerström et al. 2007). Further, shrubs capable of symbiotic nitrogen fixation are common in the retrogressive stages of the Cooloola chronosequence. Phosphorous can be renewed during retrogression only by abiotic means such as dust and rainfall input; in this light the extent of decline of ecosystem processes during retrogression for the Hawaiian chronosequence appears to be less than that for the other five, presumably because phosphorus loss is partially replenished by deposition of windblown dust sourced from central Asia (Chadwick et al. 1999).

9.4 Conclusions

This chapter has explored a specific long-term retrogressive chronosequence in some depth, and then considered retrogressive phenomena for other comparable chronosequences around the world. These sequences show a relative consistency of patterns over time despite being located in different climatic zones, based on different parent materials, and formed by different agents of disturbance. Collectively, these chronosequences point to the fact that in the very long-term time perspective (in the order of millennia or beyond) following catastrophic disturbance or creation of a new surface, phosphorus eventually becomes limiting to biological activity relative to nitrogen. This is because, regardless of the specific characteristics of the chronosequence considered, total ecosystem nitrogen builds up over time as it is derived from biological activity, while phosphorus can only diminish because it is derived from parent material at the start of succession.

There is increasing recognition that aboveground-belowground feedbacks are major drivers of ecosystem processes, and that there is an important temporal dimension to these feedbacks (Wardle 2002; Bardgett et al. 2005). With the Swedish lake island system, it has been shown that reduced availability of nutrients during retrogression creates feedbacks through plants producing litter of poorer quality and returning fewer resources to the soil. This in turn impairs decomposer biota and the supply of nutrients from the soil, negatively affecting plant nutrient acquisition and growth. Experimental work on these islands points to the relative influence of specific plant species on these feedbacks also changing during retrogression. Further, changes during retrogression in the balance between aboveground processes such as plant productivity, and belowground processes such as decomposition, have been shown to exert important effects for island carbon sequestration. For the other five chronosequences, it is also apparent that there are important declines in plant productivity, forest stature and photosynthetic capacity during retrogression, that these changes coincide with reduced availability of soil nutrients, as well changes in the

biomass and activity of soil organisms that govern decomposition and nutrient mineralisation processes.

The studies described for the six chronosequences collectively provide evidence that the classic 'climax' view of forest succession does not hold in the long-term perspective, and that in the prolonged absence of major disturbances, high biomass forest cannot be maintained indefinitely. It is, however, important to note that all six chronosequences described in this article are located on flat terrain or terraces in which catastrophic disturbances are infrequent. Many other forests occur on slopes, in valleys, or on floodplains, where they are subjected to more regular disturbances (e.g., erosion; flooding) that regularly make fresh phosphorus-containing parent material available to plant and soil communities (Porder et al. 2007). Studies on long-term retrogressive chronosequences are important for aiding our understanding of the importance of disturbance for the long-term functioning of forest ecosystems and the role of nutrient limitation. But it is important to note that many, perhaps most, forests are subjected to sufficient disturbance in the long-term perspective to prevent them from entering extreme stages of ecosystem retrogression.

Finally, it is apparent from comparing long-term chronosequences (Wardle et al. 2004) that different chronosequences show remarkably similar patterns of retrogression across vastly different types of forested ecosystems, representing the boreal, temperate and subtropical zones. However, whether these sorts of patterns are characteristic of other forest types such as hyperdiverse tropical rainforests (Ashton 1989), non-forested chronosequences, or ancient soils characteristic of much of the tropics, remains an open question and one that merits further investigation.

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Chapter 10
Rooting Patterns of Old-Growth Forests: is Aboveground Structural and Functional Diversity Mirrored Belowground?

Jürgen Bauhus

10.1 Introduction

When we think of old-growth forests, we generally imagine old forests with large trees and possibly a highly diverse forest structure resulting from the death of individual trees and the resulting gap-phase dynamics (Oliver and Larson 1996; Franklin et al. 2002). This is also reflected in the definitions of old-growth forests (see Chap. 2 by Wirth et al., this volume), which normally do not refer to belowground structures and processes. This neglect of belowground aspects, although intriguing, is understandable since so little information is available. It is well known that the species richness, and often also the biomass, of invertebrates, fungi, and bacteria is much higher belowground than aboveground (e.g. Torsvik et al. 1990), yet we know very little about how their diversity and abundance belowground is related to forest age or forest structure. Carbon storage is an important value of old-growth forests, and the carbon stored in soils, forest floor, and belowground biomass often approximates the quantities stored in aboveground biomass (e.g. Trofymow and Blackwell 1998; see Chap. 11 by Gleixner et al., this volume). The turnover of fine roots is believed to be an important driver of soil carbon accumulation, yet little is know about how this process changes with forest age or forest developmental stages found in old-growth forests.

Many of the attributes and values of old-growth forests are related to their aboveground structural diversity (McElhinny et al. 2005). It is therefore interesting to ask whether this structural diversity in old-growth forests is mirrored belowground, and to what extent belowground structural diversity may contribute to functional diversity. To approach these questions, I will ask firstly which attributes may comprise belowground structural diversity, whereby the term belowground encompasses the substrates colonised by roots, the soil and forest floor layers.

10.2   What Comprises Belowground Structural Diversity?

Since belowground structural diversity has not been defined, I will first reflect on the attributes that commonly are used to quantify structural diversity aboveground. Stand structural diversity is a measure of the number of different structural attributes present and the relative abundance of each of these attributes, as summarised by McElhinny et al. (2005) for some forest types. These attributes are responsible for variation in the vertical and horizontal structure of forest stands and are thought to be indicative of biodiversity, i.e. related to the provision of faunal habitat. The range of attributes comprises vertical layering of foliage; variation in canopy density (e.g. caused by gaps); variation in the size and distribution of trees; the height and spacing of trees, and their species diversity and biomass; the cover, height and richness of the understorey including shrubs; and the number, volume and range in decay stages of standing and fallen dead wood (McElhinny et al. 2005). The equivalent belowground attributes that may be important for belowground biodiversity and ecosystem functioning are listed in Table 10.1. In general terms, these structural elements provide horizontal and vertical heterogeneity in belowground structures. In the following, some of the analogies between belowground and aboveground structural elements or parameters will be pointed out and discussed, focussing in particular on the question of whether the structural diversity created by these elements increases with forest age.

Table 10.1 Potential attributes of belowground structural complexity

Contribution to:	Attribute	Quantified as:
Vertical structure	Maximum rooting depth of structural or fine roots	Depth in metres
	Variation in maximum rooting depth between species	
	Vertical distribution of fine or coarse roots	No. of layers, evenness of root distribution in layers/horizons over the profile depth
Horizontal variation	Size and distribution of roots systems	Number, volume
	Size and number of root gaps	Area
	Quantity and size of belowground coarse woody detritus (stumps, old root channels, etc.)	Number, volume and depth
	Pit-and-mound topography	Area covered by these features

10.3 Root Gaps and Horizontal Variation in Rooting Density in Old-Growth Forests

Old-growth forests are the result of the long-term absence of stand-replacing disturbances (see Chap. 2 by Wirth et al., this volume). The old trees may comprise the cohort that developed following the previous stand-replacing disturbance or they may have developed subsequently in gaps created by the death of trees from the disturbance cohort. In any case, by the time an old-growth developmental phase is reached, the disturbance dynamics, until then, will have been dominated by the formation of gaps in most types of forests. Therefore, gaps are an important feature of old-growth forests. They may occupy 5–15% of the stand area in temperate forests (e.g. Runkle 1982; Emborg et al. 2000). These gaps contribute greatly to the vertical structural diversity of old-growth forests and also, through the successional processes triggered within them (e.g. Busing and White 1997; Rebertus and Veblen 1993), to species diversity. Some canopy species may not be able to regenerate in these gaps and are replaced by more shade-tolerant species (Oliver and Larson 1996; Gilbert 1959). However, the prevalence of gap dynamics in old-growth forests leads to a patchwork of developmental stages, creating horizontal variation in canopy height, tree biomass and necromass and/or species composition (e.g. Emborg et al. 2000; Korpel 1995; Franklin et al. 2002). Whether or not the aboveground structural diversity of old-growth forests attributable to gap formation is mirrored belowground depends on whether root gaps are created in the process, and on whether belowground structural elements vary with the developmental stage of the patches. This would, for example, be the case if these gap phases have different levels of fine- or coarse-root biomass, or roots with functional traits or mycorrhizal associations that differ from those found during other developmental stages.

First, I will explore the question of whether aboveground gaps create belowground gaps. Then I will ask to what extent belowground gaps contribute to structural and functional diversity.

Aboveground gaps are created when one or more trees participating in the main canopy layer are removed or killed. While the foliage of trees within the crown is confined to a reasonably small projected ground area around the trees, the same is not true for roots. These are far more wide-reaching than the branches (Stone and Kalisz 1991), and so roots tend to overlap much more than crowns. For example, Büttner and Leuschner (1994) found complete spatial overlap of the root systems of the co-occurring species *Quercus petraea* and *Fagus sylvatica*. Consequently, when one tree or a small group of trees is removed or killed, the soil beneath them remains partially occupied by the root system of neighbouring trees. Thus, in most cases, "root gaps" do not represent patches with no live roots, but may be characterised as zones of reduced root competition.

Runkle (1982) and Brokaw (1982) have defined canopy gaps. These have a certain minimum size, and extend from the top of the canopy through all vegetation layers to a certain height above the ground. We can distinguish between the actual canopy gap, between the edges of crowns, and the expanded gap between tree

stems. Since we usually have no zone without roots, it is very difficult and certainly impractical to define a root gap in the field. Thus, attempts to identify root gaps have focussed on the ground areas within the perimeter of aboveground canopy gaps. Also, when root gaps have been studied, the focus was usually on fine roots, which are responsible for belowground competition for soil resources.

The picture that emerges from the few available studies of root gaps is far from clear. This is certainly due, in part, to the fact that the results are from different gap sizes and that root measurements are from different soil depths and times since gap creation. Many of these studies are from tropical forests, and, in most cases, only the general gap area was analysed rather than the fine root distribution in relation to distance to the gap perimeter. When fine root biomass between root gaps and intact adjacent areas was compared, a reduction could be observed in most cases (Fig. 10.1). This reduction in fine root biomass was usually not more than 60% (mostly between 20 and 40%). The reduction in live fine roots following canopy creation could be very fast, for example, a 40% reduction in a subtropical wet forest system (Silver and Vogt 1993). However, when medium-term fine root growth between these two areas was compared, root gaps more often showed an increase than a decrease, possibly indicating a reasonably fast recovery of fine root biomass. Unfortunately, very few studies provide information on the process of root gap closure with time. Bauhus and Bartsch (1996) used in-growth cores to compare the fine root growth of *Fagus sylvatica* at the centre and perimeter of 30 m diameter gaps within an undisturbed ca. 160-year-old forest in the Solling area of Germany. Fine root growth in the stand was 390 g m^{-2} (0–30 cm soil depth) over a 12-month period (Fig. 10.2).
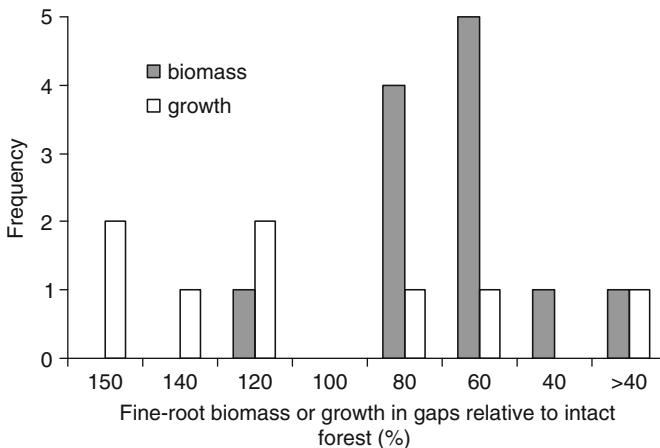
Fig. 10.1 Reduction or increase in fine root (<2 mm diameter) biomass or growth observed in root gaps associated with canopy gaps in different forest ecosystems, where fine root biomass was compared to that of intact adjacent forest. Note that the time since gap creation differs between studies (Bauhus and Bartsch 1996; Silver and Vogt 1993; Ostertag 1998; Denslow et al. 1998; Wilczynski and Pickett 1993; Cavelier et al. 1996; Sanford 1990; Battles and Fahey 2000)
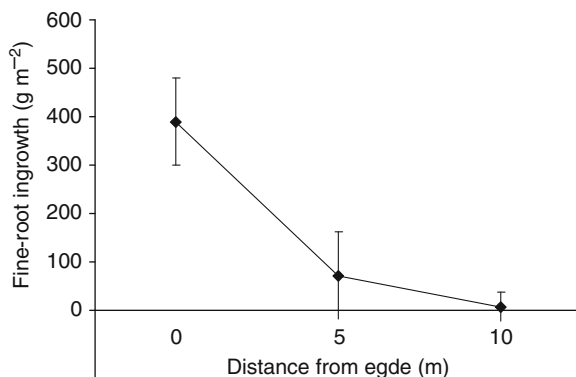
Fig. 10.2 Fine root biomass production over a 16-months period determined by the ingrowth-core method in an undisturbed European beech forest (0 m) and at different positions (5 and 10 m from the edge) within 30 m diameter gaps (0–30 cm soil depth) (after Bauhus and Bartsch 1996)

At a distance of 5 m from the edge trees into gaps fine root production over the same period declined to 15–130 g m^{-2}, whereas in the centre of gaps it was negligible. Similarly, Müller and Wagner (2003) found the greatest fine root growth in gaps only 2.2 m from the edge of the gap in a 35-year-old spruce (*Picea abies*) forest, while no live fine roots were found beyond 7.4 m from the gap edge. These studies show that root gaps can persist for a substantial period of time, if gaps are not, or only slowly, recolonised by other vegetation, as was the case in the two studies cited above. However, fine root biomass may recover rapidly when gaps are large enough to be recolonised by fast-growing understorey or shrub species (Bauhus and Bartsch 1996). Jones et al. (2003) showed that belowground gaps in *Pinus palustris* forests closed quickly because understorey vegetation compensated for the absence of pine fine roots, in particular in gaps with higher soil moisture and nitrate concentrations than in the surrounding forest. Campbell et al. (1998) also found a rapid recovery of non-tree roots in small experimental gaps in mixed boreal forests in Québec. Whether the speed of recolonisation depends on the contrast in soil nutrient and water availability between the root gaps and surrounding soil, such that the root gaps represent rich patches, is not clear (e.g. Ostertag 1998). Higher concentrations of nitrate and phosphate in soils of root gaps as compared to undisturbed areas might facilitate colonisation by pioneer species (Denslow et al. 1998). Once saplings have established in gaps, fine root growth in them might be higher than in the undisturbed surrounding forest (Battles and Fahey 2000).

The occurrence of fine root gaps is related to the horizontal distribution of fine root mass of individual trees. Models of fine root distribution of single trees indicate that the biomass over the entire soil profile is greatest near the stem and declines with distance from the tree (Nielsen and Mackenthun 1991; Ammer and Wagner 2005). However, other studies have indicated that the spatial distribution of roots around stems does not follow such a symmetrical pattern but may be related more to soil nutrient availability (Mou et al. 1995). Large-crowned trees have more fine root

biomass and a greater maximum extent of the root system than small trees with little foliage. Therefore, the reduction in fine root biomass following the removal or death of individual trees will be greatest in the immediate vicinity of the stump. Owing to the lack of studies on this topic, we know neither what size of aboveground gap is required to create a root gap in stands of different tree dimensions, nor what reduction in fine root density is required to have a situation one might call a root gap. However, some studies have quantified the distance from the gap edge at which fine root growth ceases (Bauhus and Bartsch 1996; Jones et al. 2003). In addition to a significant reduction in fine root density or growth, root gaps should be characterised by changes in the level of resources such as soil moisture and nutrients, which would allow colonisation of the gap area by vegetation that previously could not become established under competition from trees occupying the area.

A number of studies have demonstrated that belowground ecosystem processes can change dramatically in gaps (Denslow et al. 1998; Parsons et al. 1994), supporting the notion that the structural diversity in old-growth forests also leads to functional diversity. For example, reduced root competition by mature trees and increased precipitation in gaps lead to higher levels of soil moisture in gaps (e.g. Bauhus and Bartsch 1995; Ritter and Vesterdal 2006). Depending on the microclimatic and soil conditions in gaps, this may or may not lead to increased decomposition of organic matter (e.g. Bauhus et al. 2004). Increased mineralisation of nutrients and, owing to reduced uptake, increased availability of nutrients can lead to high losses via leaching (Bartsch et al. 2002; Ritter and Vesterdal 2006; Parsons et al. 1994) or in gaseous forms (Brumme 1995). Both processes commonly are associated with changes in soil microflora (e.g. Bauhus et al. 1996), which is often reflected in increased nitrification rates (e.g. Parsons et al. 1994). Von Wilpert et al. (2000) documented a rapid and very high increase in seepage water nitrate concentrations at a soil depth of 180 cm following the removal of a single *Picea abies* tree in a pole-sized stand. Their results showed that such dramatic changes in nutrient transformation processes, equivalent in magnitude to changes following clearfelling, can occur even in very small gaps, probably as a result of the rapid turnover of mycorrhizal fungi. Therefore, although most gaps in old-growth forests are small, and only a few gaps are large (Runkle 1982; Butler-Manning 2007), it can be assumed that most, if not all, gaps leave a belowground signal in the form of root gaps, which contribute to the functional diversity of old-growth ecosystems. These patches, with their higher soil moisture and greater nutrient availability, can be colonised by species that were either absent or present in low abundance in undisturbed parts of old-growth stands. These different species might in turn support a different soil microfauna and microflora than would dominate under undisturbed conditions, thus contributing to belowground biodiversity.

While it is likely that roots gaps are formed when aboveground gaps are created, it is not clear whether the vegetation patches of different ages that developed subsequently in gaps also differ in their belowground biomass. There are indications that fine root growth of saplings in gaps exceeds that of the surrounding stand matrix (Battles and Fahey 2000). For fine roots, the biomass of even-aged stands may be indicative of that found for similar stand developmental phases in patches of

old-growth forests. However, owing to the onerous nature of such a task, few studies have compared different age classes of the same species on comparable sites and at the same soil depth. Where this has been done for the same ecosystem (Idol et al. 2000), it was shown that fine root growth, mortality and decomposition in 4-year-old stands was as high, if not higher, than in 10-, 29-, or 80- to 100-year-old stands of an oak-hickory forest. Where data on fine root biomass from the literature have been compiled, such analyses do not reveal clear temporal patterns of fine root biomass with stand age, and even show contradictory trends for different species. In their analysis of published studies, Leuschner and Hertel (2003) showed that the fine root biomass of *Fagus sylvatica* appeared to decline with age, whereas fine root biomass in *Picea abies* stands increased with stand age. It is conceivable that in spruce stands, owing to the low quality of litter and associated accumulation of forest floor mass with age (Meiwes et al. 2002), nutrients become more growth-limiting with age, hence necessitating the maintenance of more fine roots for nutrient capture in older stands compared to young stands. This age-dependent increase in fine root biomass has also been observed in *Abies amabilis* forests in the Washington Cascades in the United States (Grier et al. 1981), or for a chronosequence of a tropical montane *Quercus* forest in Costa Rica, ranging from an early-successional stage to old-growth (Hertel et al. 2003). In both cases, this increase in fine root biomass also coincided with an increase in forest floor thickness and greater fine root biomass in the forest floor layer but not in the mineral soil, lending support to the idea that the increase may be linked to the immobilisation of nutrients. Cavelier et al. (1996) reported that fine root biomass in the surface mineral soil of early-successional stages from a tropical montane cloud forest did not differ from that in a mature forest. However, the fine root biomass (<5 mm) growing in a root mat above the mineral soil surface on logs and branches was higher in the 20-year-old and the mature forest than in the young secondary forest. They assumed that, in this extremely moist environment, fine root density saturation and oxygen limitation in the surface mineral soil leads to an expansion of the root system "aboveground". The increasing heterogeneity of the micro-topography with stand age facilitated this process.

However, this pattern of increasing fine root biomass with age cannot be generalised, as demonstrated for fine root biomass in chronosequences of the species *Fagus sylvatica*, *Picea abies*, and *Quercus cerris* (Claus and George 2005). In these cases, fine root biomass peaked at around 20–30% of the mature age of each species, and at levels of 150–200% of the fine root biomass at stand maturity. In their study, however, two of three sites had almost no forest floor, whereas at the third site, differences in fine root biomass resulted from differences in forest floor thickness. The pattern observed in the latter study mirrors the temporal dynamics commonly observed for foliage biomass or leaf area index, suggesting that, for these stands, the ratio of foliage biomass to fine root biomass is maintained at a similar level with stand age. This may be a more general pattern in situations where nutrient and water availability do not decrease with age. However, Uselman et al. (2007) found that the fine root production and turnover increases with forest age from 77 years to over 850 years in a successional sequence at

Mt. Shasta, California, while the aboveground litterfall declines. Owing to the paucity of published data on fine root biomass in chronosequences, it remains speculative whether age-related increases in fine root biomass or production are related to decreasing nutrient or water availability. Therefore, it is also not possible to state whether the spatial heterogeneity in fine root density associated with patches of different ages is higher in old-growth forests than in younger, regrowth stands. At sites where an accumulation of forest floor material with stand age occurs, it is likely that gaps, and subsequent development of even-aged groups in these gaps, contribute to a diversification of forest floor conditions and thus rooting patterns. Ponge and Delhaye (1995) demonstrate how relationships between stand developmental phases and forest floor development in an old-growth European beech forests influence earthworm communities. The presence of different age classes or age-related vegetation communities may also influence the distribution of soil microflora and microfauna, which can be age- and species-specific.

The coarse root biomass of individual trees is closely related to their size. As trees become older and taller they need to be firmly anchored, and they need to support an increasingly far-reaching network of fine roots. Coarse root biomass of individual trees is therefore commonly predicted through allometric relationships to measures such as tree diameter at breast height (e.g. Bolte et al. 2004) or by using root-shoot ratios (Mokany et al. 2006). The relationship between aboveground and root biomass declines with tree biomass and stand age (Mokany et al. 2006). However, the declining trend in these relationships is confined largely to young ages and small values for stand biomass. Above 30 years or 100 t ha^{-1}, root:shoot ratios remain surprisingly constant. This means that, for most situations, belowground biomass is closely related to the age or biomass of stands and patches. Therefore, old-growth forests, which are often characterised by a high spatial heterogeneity of aboveground biomass (Korpel 1995; Butler-Manning 2007), should also have a high spatial heterogeneity of belowground biomass. However, it is not yet clear what relevance this spatial heterogeneity of belowground biomass has for ecosystem function (cf. Chap. 11, Gleixner et al., this volume). The belowground equivalent of large old trees, which are an important feature of old-growth, is their large root systems. Analogous to dead wood in the crowns of old living trees, with its particular importance to species such as woodpeckers or xylobiotic arthropods, the large root systems may generate large coarse dead roots, which provide belowground habitat and substrate. Eventually, when the aboveground part dies, stumps and structural roots will constitute a large input of woody material. The function of these large dead roots will be discussed further below.

Trees also act as conduits for the input of precipitation and chemical elements into forest ecosystems. Depending on the architecture of tree crowns, different proportions of these factors enter the system in the form of crown drip and stem flow. For smooth-barked species with mostly steep-angled branches such as *Fagus sylvatica*, the proportion of stem flow is so high that the soil at the base of trees exhibits significantly different chemical characteristics than soil further away from the stem. Usually it is substantially more acidified (Koch and Matzner 1993). The quantity of stem flow increases with tree crown size so that the channelling effect

for inputs and the resulting changes in soil chemical conditions is more pronounced for soil at the base of large trees as compared to small trees. Consequently, this phenomenon will also lead to higher spatial belowground heterogeneity in old-growth forests comprising species, where stem flow forms an important part of their input fluxes. When tree species have different influences on nutrient cycles and soils (for the underlying mechanisms see Binkley and Giardina 1998), this can lead to long-lasting spatial patterns in soils (e.g. Boettcher and Kalisz 1990; Fujinuma et al. 2005). We can assume that these patterns are more profound in old-growth forests, where trees are long-lived and tend to maintain these different influences for long periods of time.

10.4   Pit-and-Mound Topography in Old-Growth Forest

In addition to root gaps, small scale gap-phase disturbance in old-growth forests may also lead to heterogeneity in soil conditions, when trees are blown over and their root plates are tipped up (Liechty et al. 1997). Since the risk of windthrow increases with tree height, this phenomenon is more common in taller, older forests than in young forests. In addition, the volume of the pits created by uprooting and the size of the mound resulting from the decay of the root plate are strongly related to tree size (Putz 1983; Clinton and Baker 2000). The importance of this phenomenon differs with forest type, depending on the typical root development of the dominant species, which is often influenced by soil thickness and the soil water regime. In mixed species forests in the Carpathian Mountains and boreal forests in Central Russia, the surface area covered by pits and mounds ranged from 6.5 to 25% (Ulanova 2000). The latter case is obviously the result of a catastrophic windthrow event. In northern hardwood, and hemlock-hardwood old-growth forests in Michigan, the surface area in pit-and-mound topography shaped by recent windthrow events was 27% and 33%, respectively (Liechty et al. 1997).

Both pits and mounds can be associated with important ecosystem functions. The uprooting of trees bares mineral soil, which may be required for the regeneration of species with small seeds or that otherwise have difficulty in germinating and becoming established on thick forest floors (Bazzaz 1996). In addition, the root plates or mounds constitute microsites with higher light availability or reduced competition. For example, Nakashizuka (1989) showed for an old-growth mixed temperate forest with a bamboo understorey that the mounds created through tree fall were more important for tree regeneration – particularly for species with small seeds – than the gaps created at the same time. Often, mounds are characterised by favourable conditions for root growth, which result from the forest floor mixing with mineral soil, increased soil temperature and favourable soil moisture regimes, especially when the surrounding soils are not free-draining (Clinton and Baker 2000). Mounds may also be sites of increased soil faunal activity (Troedsson and Lyford 1973). At the same time, pits represent microsites that accumulate forest floor material and are often moister than their surroundings (Beatty and Stone 1986;

Liechty et al. 1997). Mound disturbance is also very important in boreal or alpine forests, in which nutrients become locked up in the forest floor; the mixing of forest floor with mineral soil remobilises these nutrients. For *Picea sitchensis-Tsuga heterophylla* forests in south-east Alaska, Bormann et al. (1995) calculated that windthrow and associated soil mixing is required every 200 to 400 years to maintain soil fertility (see Chap. 9 by Wardle, this volume).

Although the creation of pit-and-mound micro-topography has some important ecosystem functions and clearly contributes to soil heterogeneity, particularly in old forests, there is no information on its effect on rooting patterns, and little information on its effect on soil biodiversity. However, pits and mounds as well as coarse woody debris (CWD) appear to be important structures in maintaining the diversity of vascular plants in old-growth forests, especially where these have to compete with an understorey of shade-tolerant tree seedlings (Miller et al. 2002). Whether the maintenance of aboveground plant species diversity, through specific associations with belowground micro-flora and fauna, provides positive feedback to belowground biodiversity is uncertain. The diversity of mycorrhizal fungi does not follow patterns of plant diversity (Allen et al. 1995). If mounds are a preferred substrate for tree growth, and hence colonisation by roots, this may also create positive feedback leading to spatial variation in the accumulation of organic matter.

10.5 Old-Growth Structures Harbouring Roots

It has been recognised that so-called "residual structural elements" play an important role in the conservation of biodiversity in managed forests (Franklin et al. 1997). The term describes structures such as standing dead trees (snags), logs on the ground, residual live trees, and undisturbed vegetation patches, which can be found following natural disturbance events in old forests, but which are usually removed or are much reduced when forests are harvested regularly. Franklin et al. (1997) created the term "life-boating" for the retention of these structures in managed forest ecosystems to illustrate the function of these structures as refuges for different taxonomic groups during the re-organisation and aggradation phase of ecosystem development. Interestingly, this concept has been applied so far only to aboveground structures. Therefore, we might ask whether old-growth forests also have belowground structural elements that provide important habitat or are important for ecosystem functions following disturbance. Obvious candidates for such residual structures are root channels. Are there more, deeper root channels in old-growth forests, and what are their functions?

Root channels can be created by soil cracks or by old, decaying roots. Such channels constitute preferential flow paths for seepage water, act as dispersion pathways for microorganisms and invertebrates, and facilitate root movement through the soil and possibly the deep rooting of young trees. Based on measurements of soil microbial biomass and activity, Bundt et al. (2001a) have suggested

that root channels can be continual hot-spots of soil activity. Preferential flow paths appear to be particularly stable in uncultivated or old forest soils (Beven and Germann 1982). They facilitate the transport of immobile nutrients such as phosphorus, which would otherwise move only extremely slowly through the soil matrix, and the illuviation of young soil organic carbon to deep soil layers. They are further characterised by different carbon and nutrient concentrations, and more rapid nutrient cycling (Bundt et al. 2001b). Root channels make up a large proportion of macropores in forest soils (Noguchi et al. 1997). Dell et al. (1983) illustrated how these root channels facilitate the exploration of soil profiles by fine roots of *Eucalyptus marginata* to a depth of 40 m. Unfortunately, there is no information about the extent to which the abundance, or importance, of root channels changes with forest stand age, or about the longevity of such channels. We can imagine that root channels may be more abundant in old-growth forests, since these forests contain more structural roots, which provide channels upon their death and decay. However, the rate of formation of root channels can also be high, if not higher, in selection forests, where single trees or groups of trees are harvested at regular intervals and their stumps remain. Presumably, the length of time since the land became forested is more important for these features than the actual age of the stands. However, it can be assumed that, owing to the absence of soil cultivation, root channels are an important feature contributing to spatial heterogeneity in soil chemical, biological and hydrological properties and processes in old-growth forests (see also Chap. 11 by Gleixner et al., this volume).

While not strictly regarded as contributing to belowground structural diversity, structural features of the forest floor such as CWD, which is often more prominent in old-growth than in younger forests (Chap. 8 by Harmon, this volume), also may contribute to the spatial patterning of roots. This may occur either as the result of soil enrichment through leaching of nutrients from CWD into the mineral soil or by roots colonising CWD directly. Coarse woody detritus is, in most cases, not a favourable substrate for fine root growth (Arthur et al. 1993). While root growth into CWD increases with increasing decomposition stage, the overall fine root abundance is much lower than in mineral soil (Arthur et al. 1993). Nutrient availability in CWD is in most cases lower than in mineral soil, but plants can gain access to these nutrients through mycorrhizal associations (Goodman and Trofymow 1998; Tedersoo et al. 2003). For example, artificial addition of CWD in a subtropical forest increased tree and palm growth as well as fine root biomass (Beard et al. 1995). However, very few studies have examined CWD as a rooting substrate (e.g. Arthur et al. 1993; Vogt et al. 1995). In one such study, Vogt et al. (1995) found that fine roots and mycorrhizal tips in submerged logs in a 50 m wide gap in an old-growth Douglas fir stand were maintained at higher levels than in the mineral soil of the gap (Fig. 10.3). The difference in fine root biomass between submerged logs and logs on the ground is likely due to the difference in log moisture regimes, which must be more favourable in submerged logs. This example points to the importance of CWD in buffering the effects of ecosystem disturbance, in this case for the belowground colonisation of gaps by fine roots. Coarse woody debris is a preferred substrate for some groups of ectomycorrhizal fungi (Tedersoo
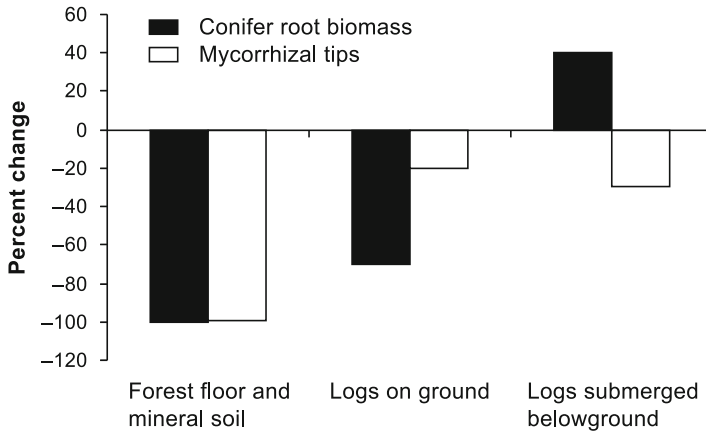
Fig. 10.3 Reduction in conifer fine root biomass and mycorrhizal root tips in different micro-sites in a 50 m gap as compared to Douglas fir old-growth (Vogt et al. 1995)

et al. 2003), and Graham et al. (1994) showed that continual provision of CWD is important for a high level of ectomycorrhizal infections in conifer roots in forest ecosystem soils in the Rocky Mountains. Large amounts of CWD in old-growth forests, and the range of decomposition stages found in such forests (Pyle and Brown 1999), are therefore likely to contribute to the abundance and diversity of mycorrhizal and non-mycorrhizal fungi in these systems.

It is well known that dead wood plays an important role as a safe site for the establishment of seedlings (e.g. Lusk 1995). For example, Narukawa and Yamamoto (2003) showed that the rooting depth of conifer seedlings (*Abies*, *Picea* and *Tsuga*) was related to the depth of decay in logs from boreal and subalpine forests in Japan, presumably related to the increase in water-holding capacity with decay stage. It is conceivable that, in forests where seedling establishment of some species is restricted largely to safe microsites on CWD, the spatial patterning of CWD will create a particular pattern of tree, and thus root system, distribution in the long term (see also Lusk 1995). There may be other particularly important microsites for fine root growth in old-growth forests, such as the skirts around the base of trees created by litterfall, especially bark shedding; however, no information is available on this subject.

10.6 Influence of Stand Age on Diversity of Functional Root Types, Mycorrhizae, and the Vertical Patterning of Root Systems

The functioning of belowground systems is dependent largely on functional root traits, in particular of fine roots, which contribute most to the belowground plant surface area and thus to the interaction with soil and the soil biotic community.

Many belowground plant traits can be summarised by the term "root architecture", which is dependent on genotype and environment. Trees differ in both the architecture of their structural root systems and their fine root systems (e.g. Köstler 1950; Bauhus and Messier 1999). For example, soil exploitation capacity, fine root turnover, the susceptibility to mycorrhizal infection and other important parameters are all related to specific root length (Berntson 1994). Eissenstat (1991) proposed that species with a high specific root length also have the potential for high fine root production rates in favourable soil environments. This was confirmed by Fitter (1994), who found that species with thin fine roots proliferate more strongly in nutrient-enriched soil patches than species with larger mean root diameters. In the context of this chapter, we need to ask whether belowground functional diversity associated with different fine root systems might increase with forest developmental phase, and whether it might differ in old-growth forests from that found in other successional stages. Some old-growth forests are characterised by a high diversity of vascular plants as compared to younger forest developmental phases (Halpern and Spies 1995). This high diversity depends, to a large extent, on the presence of gaps (Runkle 1982; Busing and White 1997). However, whether this high diversity is associated with, or maintained by, a divergence of root functional traits or a complementarity of specific traits is not known. In most situations, the development of forests towards old-growth conditions represents a strong environmental filter selecting for shade tolerant species that can regenerate in the understorey or in gaps. However, shade tolerance often has been linked to low relative growth rates, low specific root length and low root length ratios (root length per unit plant mass; e.g. Reich et al. 1998). Therefore, whereas forest succession develops from communities dominated by shade-intolerant species to those dominated by shade-tolerant species, the highest diversity of functional types of fine root systems may actually be found in intermediate stages. Examples of this can be found in boreal and temperate regions, but may not apply to tropical and subtropical forests. There is obviously insufficient information about this aspect to provide a conclusive answer to the question posed above.

The question of whether mycorrhizal diversity increases with stand age has recently been reviewed by Johnson et al. (2005). For a long period, the general perception was influenced by the ectomycorrhizal succession hypothesis (Mason et al. 1982; Danielson 1984), which postulated that a sequential successional replacement of ectomycorrhizal fungi occurs throughout forest succession. However, this concept was originally developed for birch succession on former agricultural land and has obvious limitations when transferred to successional processes within forests. In forests, e.g. in gaps, it makes sense for seedlings to use the already-existing fungal network, which is fed by older trees, suggesting that it is unlikely that ectomycorrhizal diversity would change with increasing tree age. Therefore, it is not surprising that the few studies that have investigated the relationship between the diversity of mycorrhizal fungi and successional stages, found no consistent trend. Studies on Douglas fir showed no variation in ectomycorrhizal fungal communities with age (Borchers and Perry 1990). However, the number of ectomycorrhizal morphotypes increased with stand age in *Pinus*

banksiana and *Pinus keysia* stands (Visser 1995; Rao et al. 1997). In contrast, in *Pinus sylvestris* stands, ectomycorrhizal species richness varied – but did not increase – with stand age in the forest floor but not in the mineral soil (Johnson et al. 2005). At the level of individual trees, one might expect that, through their far-reaching root network, individual trees will sample the available inoculum in the soil with time. This in turn may lead to a homogenisation of mycorrhizal associations among trees, whereby the most competitive fungi will gradually replace weaker competitors. However, mycorrhizal communities will also be shaped by changes in edaphic factors known to change with stand age, such as the accumulation of CWD and forest floor substrate. The relative importance of these processes is not clear. Based on the scant information available, there is no reason to assume that belowground functional diversity related to mycorrhizal fungi in old-growth stands differs from that of other developmental stages.

Similar conclusions can be reached for the vertical stratification of root systems. Vertical stratification, or the layering of root systems of different tree species, may be an important feature of belowground structural and functional diversity. Since different tree species have different root functional traits, such as fine root turnover, exudation rates, mycorrhizal associations, etc., stratification of root systems may increase the spatial heterogeneity of such traits. The patterns created here may have an ecological function similar to that of vegetation layers aboveground, which can be captured by the diversity in foliage height (MacArthur and MacArthur 1961), an important measure of the vertical distribution of foliage. The distribution of foliage between the top of the canopy and the soil surface is an important determinant of the species richness and diversity of heterotrophs. Fine roots and their associated mycorrhiza are the most important sources of energy for heterotrophic belowground organisms. Hence the vertical distribution of fine roots will also influence the distribution of heterotrophic organisms in soil. There is commonly a strong vertical decline in fine root density from the surface soil to deeper soil layers (Jackson et al. 1996). However, while it has been recognised that trees can extend their roots to great depth (e.g. Dell et al. 1983; Nepstad et al. 1994), there is no indication that fine roots extend to greater depth in old-growth forests. This is also unlikely, since the maximum vertical extent of root systems will probably be related to the transpirational demand of the vegetation, which is not higher in old-growth stands (e.g. Vertessy et al. 1996).

A number of studies have described stratification of root systems (e.g. Mou et al. 1995; Schmid and Kazda 2002). However, whether root stratification of different species increases or decreases with stand age has never been reported in the literature. In studies such as that by Claus and George (2005), fine root biomass in different horizons in stands of different ages may have been reported, but only surface horizons (<30 cm soil depth), and not species mixtures, were investigated. Likewise, the mechanisms responsible for stratification of root systems are not understood. In soil profiles with horizons unsuitable for one species but tolerable for another, e.g. gley horizons with seasonally water-logged conditions, it is easy to picture how stratification might develop, but whether this phenomenon becomes more or less accentuated with stand age has not been investigated. However,

increasing nutrient limitations owing to the accumulation of forest floor material might lead to more pronounced stratification in old-growth forests.

10.7 Conclusions

The general information base about the development of belowground structural and functional diversity with stand age is rather limited. I have found no study that specifically explores this question. A review of the existing literature suggests that horizontal diversity in belowground structures may increase with stand age as a result of gap creation and the development of micro-sites through deposition of CWD on the ground, and the creation of a pit-and-mound relief as well as large stumps. All this may create spatial heterogeneity in resources resulting in spatial patterning of root systems. There is no evidence for any variation in vertical belowground diversity with stand age, except where this may be attributable to the development of forest floors. There is also no evidence to support the notion that the diversity of mycorrhizal fungi might increase with stand age. Whereas, above-ground, the physical space between the soil surface and the top of the canopy is large and increases with stand age, the physical space between the soil surface and the maximum rooting depth is usually much smaller and unlikely to increase with stand age. While much research has focussed on the relationship between above-ground structural diversity and biodiversity, similar relationships, which may exist belowground, still remain largely in the dark, hidden from view.

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Chapter 11
Soil Carbon Accumulation in Old-Growth Forests

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11.1 Introduction

An area of 4.1 billion ha land is covered with boreal, temperate and tropical forest, together comprising up to 80% of the terrestrial aboveground carbon and 40% of total soil carbon (Dixon et al. 1994; Pregitzer and Euskirchen 2004). Forest ecosystems are well studied, mainly because of their importance for timber production during the early economic development of many countries. In the context of global change, however, other ecosystem services like provision of drinking water or carbon sequestration have gained importance. Less is known about these. For ecosystem carbon uptake, it is assumed that biomass production is highest in younger and middle-aged stands but declines with forest age (Pregitzer and Euskirchen 2004) and that long-term soil carbon sequestration is very low (Schlesinger 1990). Both factors suggest that old-growth forests are close to being carbon neutral, i.e. neither storing nor losing carbon. However, these assumptions neglect the fact that root and leaf litter production and the accumulation of coarse woody debris might be highest in old-growth forests, and that soil carbon storage might occur in deeper soil layers rather than in the more often investigated top soils. This chapter will summarise current knowledge regarding soil carbon storage, identifying factors that might affect soil carbon storage in old-growth forests. Finally, the first results relating to soil carbon storage from a case study in a 250-year-old beech forest will be presented.

11.2 Development of Soil Carbon Stocks in Ecosystems

In the long term, accumulation of soil carbon during ecosystem development is driven by the input, decomposition and output of plant-derived carbon. The initial step for most carbon found in soil is autotrophic reduction of oxidised carbon from the atmosphere by plants using energy provided by the sun. In the early stages of ecosystem development during primary succession, e.g. after the retreat of ice in the

late Pleistocene, mainly lower plants such as lichens and mosses produce these reduced carbonaceous compounds and add them to the bare surface. As a consequence, surface rocks are biologically weathered and nutrients for plant growth are provided (Barker and Banfield 1996). First, soil organic matter (SOM) is formed from decomposing biomass and increases the water holding capacity of the surface. Increased nutrient availability and water holding capacity in parallel with temperature increases accompanying ongoing deglaciation, improve growth conditions for plants and enable further progress in ecosystem development, which can be seen in the development of different plant and animal communities and in the formation of soil profiles. Increasing biomass, and therefore litter production, form a litter layer (Oi horizon) of poorly decomposed "fibric" plant litter (Fig. 11.1). Underneath this litter layer, an organic layer of partially degraded, fermented or "hemic" (Oe horizon) plant material develops. No plant structures can be identified in the humic or "sapric" horizon (Oa horizon) above the surface of the mineral layer. Organic matter is also transported into deeper mineral soil layers either by bioturbation or by percolating rainwater. The latter process is critically important for the development of soil profiles and might also enhance carbon storage in the long term. The transport of organic carbon from the O horizons into the upper mineral soil and, in parallel, the export of minerals and metal oxides from the upper mineral soil through percolating soil water form a mineral-depleted A horizon in the upper mineral soil. Below the A horizon, an often brownish or reddish mineral-enriched B horizon forms due to the precipitation of leached weathering products, i.e. iron oxides/hydroxides and/or humic substances, from the percolating stream of soil water. Underneath the developed soil profile the unaltered parent substrate remains in the C horizon.

The main initial sources for soil organic matter in natural systems are leaf litter input to the soil surface and root litter and exudate inputs within the soil profile. As a global average, over 60% of the root biomass is found in the top 20 cm of the soil (Fig. 11.2). Root biomass decreases logarithmically with depth and only 14% is found below 40 cm. The gradient in soil carbon is much smaller. Only 40% organic carbon is located in the top 20 cm soil, and this also decreases logarithmically; however, 36% soil carbon is still found at depths below 40 cm and therefore soil carbon is enriched relative to root biomass (as a proxy of root input) with soil depth. The non-linear distribution pattern of root biomass and soil carbon may result on the one hand from the depth-depending decomposition of biomass and increased substrate use-efficiency of soil microorganisms in deeper soil layers (Witter and Kanal 1998), and on the other hand from the higher sorption capacity of "cleaner" mineral surfaces at deeper soil layers. The spatial variability of root input in the soil of a forest stand is known to be influenced inter alia by water availability, nutrient status, stand density and species composition. Stand age per se has no direct effect on the vertical and horizontal distribution of roots (see Chap. 10 by Bauhus, this volume) and might therefore only indirectly influence soil carbon accumulation. In the upper 20 cm soil profiles, the decomposition of biomass, and hence the decomposer community, i.e. the soil macro-, meso- and micro-organisms, appears to exert a stronger control on carbon storage. In general, soil organisms decompose

O_i

O_e

O_a

A

B

C
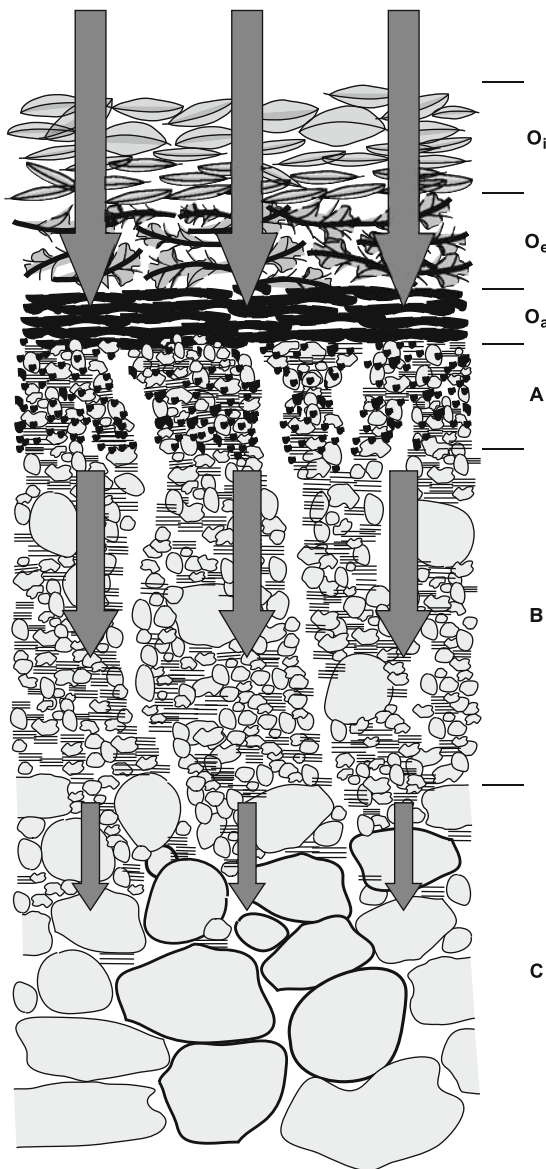
Fig. 11.1 Terminology of soil horizons in a depth profile. *Oi*, *Oe* and *Oa* organic layers; *A* mineral layer with organic carbon and leached minerals; *B* mineral layer with precipitation of oxides/hydroxides and/or carbon; *C* unaltered parent substrate. *Arrows* indicate the decreasing water flow down the soil profile

plant input like litter and root exudates, and release most of the assimilated carbon back to the atmosphere again as CO_2. Some of the plant-derived plant litter remains untouched above the soil, i.e. acid-generating conifer litter forming raw humus, but most of the litter-derived carbon remaining in the soil is transformed to SOM by the action of soil organisms (Gleixner et al. 2001). The complex process of SOM formation is achieved by the trophic networks (Ekschmitt et al. 2008) in the soil and can be influenced by the composition of the decomposer community, which in
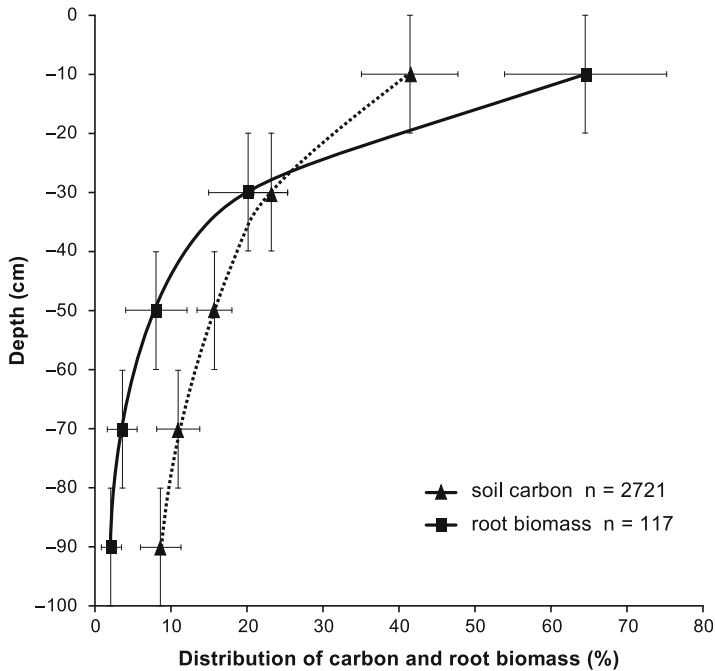
Fig. 11.2 Distribution of soil carbon and root biomass in depth profiles of the world's major ecosystems. *y-Error bars* sampling interval, *x-Error bars* standard deviation from 11 biomes summarising 2,721 soil samples and 117 root biomass samples (Jobbagy and Jackson 2000)

turn might be influenced by stand age. In general, shredding organisms, like earthworms or woodlice, break litter into small pieces and extract digestible compounds. This process increases the surface area of litter and inoculates decomposing microorganisms, which degrade indigestible compounds externally (Gleixner et al. 2001). Soil animals like nematodes, woodlice, collembola or mites feed on these nutrient-rich microorganisms and predators hunt microbe-feeding soil animals in the soil. Finally, decomposers mineralise dead soil animals, closing the element cycle of carbon in soil.

In summary, the formation of soil carbon depends on (1) the amount, quality and distribution of input material; (2) the activity of decomposers and the decomposition rate; and (3) carbon transport to deeper soil layers.

11.3 Soil Carbon Storage in Old-Growth Forests

11.3.1 Effects of Quantity and Quality of Input Material

In general, the stock of carbon in soils is correlated to the mean annual temperature and the mean annual precipitation, and thus indirectly to net primary production (NPP) (Amundson 2001). Sun et al. (2004) analysed 36 forest stands from three

forest sites in Oregon with NPP ranging from 180 to 1,200 g C m^{-2} year^{-1}. They found a tight relationship between NPP and carbon stored in the soils across sites but not within sites (Fig. 11.3). Thus, this trend was driven mostly by the difference in NPP between sites, which in turn was correlated to the amount of precipitation supplied to the different ecosystems. No effect of stand age on soil carbon stocks could be detected within sites. Along the chronosequences, high initial soil carbon stocks were lost in young stands but increased again in two out of the three cases in old growth forests (Sun et al. 2004). Only the site with the lowest productivity also lost carbon in the mature stand. The authors suggested that legacy carbon is decomposed and de novo carbon is formed as a consequence of ecosystem development. It was concluded that the ratio of necromass carbon to total ecosystem carbon decreases with stand age and remains constant in old-growth forests. However, the oldest stands per site consistently exhibited increasing ratios per site, suggesting a continuous necromass build-up (Sun et al. 2004).

Such a build-up of necromass could be driven by the litter quality, e.g. lignin is thought to be more stable to microbial decomposition than cellulose. Comparing three different sites with Douglas fir in Oregon, each comprising an chronosequence of young stands, secondary forest and old-growth forest, Entry and Emmingham (1998) found consistent age-related trends in the composition of litter and SOM. Litter in young stands contained up to 80% structural carbohydrates, i.e. cellulose (Fig. 11.4). This contribution decreased with age and old-growth forest litter contained only about 40% structural carbohydrates. At the same time, the contribution of lignin increased from less then 10% in young stands to 40% in old-growth stands. This change in the chemical composition of the litter layer coincides with the higher content of twigs and reproductive structures. The input of litter almost doubled, from 200 to 400 g m^{-2}, from a 20-year-old stand to an old-growth stand (Klopatek 2002). It follows that higher amounts of less degradable input may be provided in old-growth forests and this could benefit soil carbon storage. Soil organic matter, however, did not follow the chemical trend observed for litter
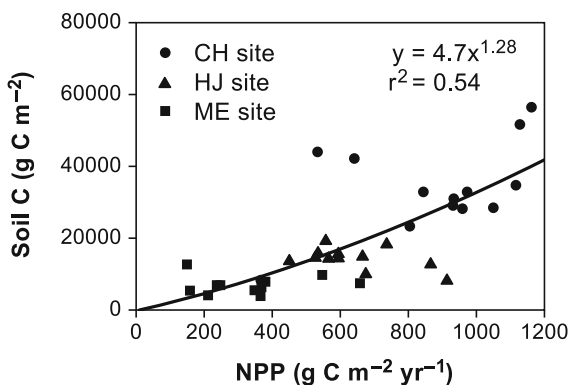
Fig. 11.3 Effect of net primary production (NPP) on the formation of soil carbon (Sun et al. 2004). Sampling sites: *CH* Cascade Head, OR; *HJ* HJ Andrews LTER site, OR; *ME* Metolius; OR
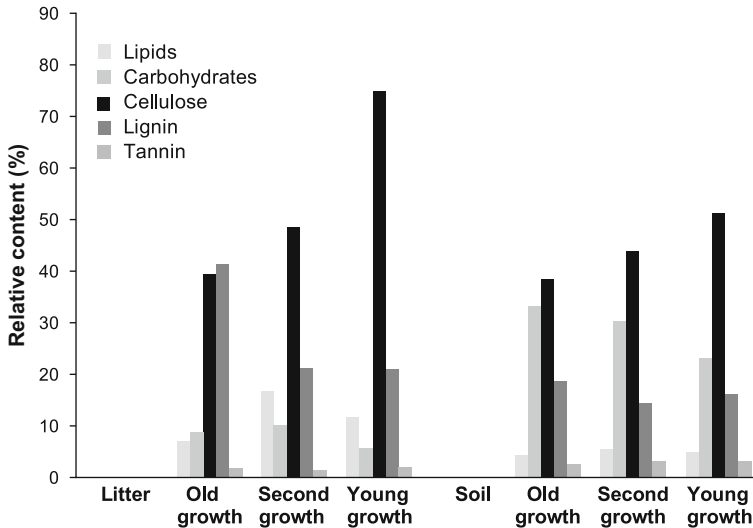
Fig. 11.4 Composition of soil organic matter relative to forest age class (Entry and Emmingham 1998)

(Entry and Emmingham 1998). As in the litter, structural carbohydrates, such as cellulose and hemicellulose, also decreased slightly with age in old-growth forests from 60% to 40%; however, lignin was not affected and remained constant at about 20% in all three age classes (Fig. 11.4). Most striking was the increase in non-structural carbohydrates with age from 20% to 40% in old-growth forests. The origins of these non-structural carbohydrates is unclear, but they are most likely constituents of bacterial cell walls (Gleixner et al. 2001). The chemical similarity of SOM of different age is supported by results from mass-spectrometric investigations (Hoover et al. 2002). Comparing SOM from a chronosequence after stand-replacing fires with an > 600-year-old virgin beech-hemlock site in Pennsylvania, no difference in the chemical composition between the virgin and the youngest site could be detected. In the upper 30 cm soil, a clear trend of decreasing recent, i.e. plant-related, carbon and an increase in humified carbon was observed. Results from litter studies suggest that, in the long term, the amount of input carbon drives soil carbon accumulation. The chemical composition of input carbon is of minor importance as all plant-derived chemical structures can be decomposed and transformed by soil microorganisms into SOM. However, environmental conditions such as acid-generating conifer litter or water-saturated soil can influence the decomposer community and decomposition processes, and hence litter accumulation followed by lower carbon input into the mineral soil and the build-up of organic layers can be expected.

11.3.2   Effects of Organic Matter Decomposition and Soil Respiration

A wide range of methods is available to measure the decomposition of organic matter. Mechanistic approaches measuring the activity of different enzymes (Sinsabaugh et al. 1991; Stemmer et al. 1999; Ekschmitt et al. 2008), balance methods using litter bags (McClaugherty et al. 1985; Joergensen 1991; Smith et al. 2002), differences in the total litter layer (Vitousek et al. 1994), or respiration methods (Zimov et al. 1996; Gower et al. 1997; Janssens et al. 2000; Pumpanen et al. 2004) can be applied. Each type of method has specific advantages and disadvantages. The most integrative values for decomposition of SOM and litter are obtained using soil respiration measurements. The major disadvantage of this method is the additional contribution of root and rhizospheric respiration. Given the fundamental importance of respiration processes for total ecosystem carbon balance and for the global carbon balance of the atmosphere (Houghton and Woodwell 1989; Raich and Schlesinger 1992; Schimel 1995), we will review the current literature on soil respiration in order to evaluate the effect of decomposition on soil carbon storage.

11.3.2.1   Soil Respiration in Forest Ecosystems and Within-Site Spatial Heterogeneity

Like productivity or total soil carbon content, soil respiration is related to climatic gradients. Cold or dry biomes like tundras or deserts have the lowest mean rates of soil respiration at between 60 and 220 g C m^{-2} year^{-1}. Ecosystems with high temperatures and high moisture availability like tropical rain forests have the highest rates, i.e. in the order of 2,000 $\pm$ 1,000 g C m^{-2} year^{-1} (Raich and Schlesinger 1992; Adachi et al. 2006; Sotta et al. 2006). Consequently, we compared the major controls on biome-specific soil respiration rates for (sub-) tropical, temperate and boreal forest. Varying soil respiration rates within the same biome, and even within the same measurement site, are commonly observed (Raich and Schlesinger 1992). This spatial heterogeneity in soil respiration causes high uncertainty of total annual fluxes. Several factors are known to contribute to this heterogeneity, e.g. high variability of soil structure (Bouma and Bryla 2000), soil moisture (Rapalee et al. 1998), bacterial and fungal distributions (Gömöryová 1994), root density (Hanson et al. 2000; M. Mund et al., manuscript in preparation), SOM content, wind speed at the soil surface and pressure patterns (Janssens et al. 2000; Martin and Bolstad 2005). The importance of each factor may be site-specific, biome-specific and even age-dependent. Unfortunately, knowledge of age trends relative to soil respiration is very sparse. Only Campbell and Law (2005) have investigated soil respiration across three climatically distinct chronosequences at four different age classes, but age-related trends were not consistent between forest types. However, in order to estimate the decomposition rate for different sites and differentially aged

stands, it is important to gain appropriate knowledge of the "within-site" heterogeneity of soil respiration. In the following paragraphs, we assess the importance of factors that control soil respiration and summarise the implications of spatial heterogeneity of soil respiration for old-growth forest carbon balances.

In tropical and subtropical forest soils, water content is suggested to be the main driver of the variability in soil respiration (Sotta et al. 2006). This can be caused either directly by both topographical features and the size distribution of soil particles influencing the water content, or indirectly by the water-dependent distribution of roots and decomposing microorganisms. The main mechanisms seem to involve the fact that these high rainfall biomes sites have higher water contents as a consequence of high precipitation, thus leading to lower oxygen influx. The lack of oxygen prevents root growth and suppresses microbial decomposition, and therefore is associated with slower CO_2 efflux rates. Therefore, decomposition is higher at drier sites and carbon accumulation might occur at wetter sites.

In temperate coniferous, broad-leaved and mixed forest, soil respiration seems to be driven primarily by the amount of fine roots of trees and understorey (M. Mund et al., manuscript in preparation). Although soil respiration near the trees is higher in young stands than in old stands, due to the higher root biomass the total soil respiration is higher in old stands (Soe and Buchmann 2005). Furthermore, soil respiration is positively influenced by the amount of carbon available for decomposition, whereas high soil moisture reduces the soil respiration rate. In contrast to the tropical system, low water content in summer often slows down root respiration and microbial activity (Saiz et al. 2006).

In boreal forest, soil respiration is driven mostly by the amount and C/N ratio of the litter or the underlying brown moss layer, highlighting the importance of litter layers for boreal ecosystems (Rayment and Jarvis 2000). The loss of the litter layer due to disturbances like fire generally leads to lower respiration rates (Shibistova et al. 2002). Like in tropical forests, sites with high soil moisture content, or even with anaerobic site conditions, have lower respiration rates (Rayment and Jarvis 2000). Higher temperatures in summer increase spatial variability in soil respiration; however, this effect was due mostly to higher root activity and not temperature effects *per se* (Khomik et al. 2006).

11.3.2.2   Heterotrophic Respiration in Old-Growth Forests

In order to overcome the uncertainty of soil respiration introduced by the high spatial variability that is mostly induced by autotrophic contributions related to roots and the low temporal coverage of respiration measurements, heterotrophic respiration may be calculated from the difference between independently measured NPP and net ecosystem productivity (Pregitzer and Euskirchen 2004). For boreal, temperate and tropical ecosystems, the estimated amount of annual heterotrophic respiration was slightly lower than soil respiration measurements in the corresponding ecosystems (see above). This discrepancy might be due to different scaling methods. Most interestingly, Pregitzer and Euskirchen (2004) observed a
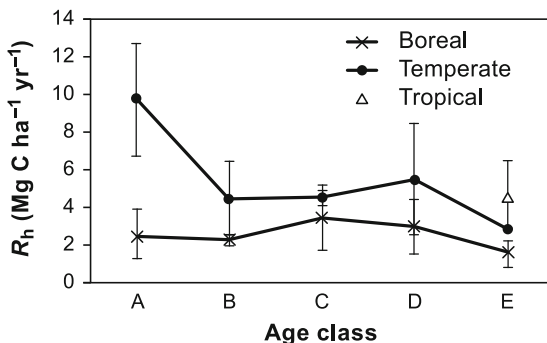
Fig. 11.5 Heterotrophic respiration across all age classes in boreal, temperate and tropical biomes (Pregitzer and Euskirchen 2004)

continuous decline in heterotrophic respiration with increasing stand age classes (Fig. 11.5). They suggested that disturbances associated with stand replacement, like fire or harvest, caused high heterotrophic respiration rates in young stands and that this legacy effect levels off in old-growth stands. This is supported by similar respiration rates of girdled and non-girdled trees 2 years after girdling (Ekberg et al. 2007). Unfortunately, no direct observations along chronosequences are available to support this observation. However, the decline in respiratory losses from young stands to old-growth forests would overcompensate for the decline in NPP, and suggests additional carbon is available for sequestration or drainage.

11.3.3 Drainage of Dissolved Carbon from Forest Ecosystems

Losses of dissolved or particulate carbon with precipitation percolating to the groundwater might be an important process, either to transport carbon to deeper soil layers for storage or for the removal of carbon from the ecosystem. The latter process was reviewed for 42 forest ecosystems having temperate, boreal or alpine climates and covering all major soil types (Michalzik et al. 2001). Both conifer and broadleaf forests were analysed; however, no age-dependent data were used. The highest carbon losses, of between 10 and 40 g C m^{-2} year^{-1}, were found underneath the Oa horizon, supporting the notion that decomposition of leaf and root litter is the main source of dissolved carbon losses (Ekberg et al. 2007; Uselman et al. 2007). However, the total amount of litter or coarse woody detritus [see Chaps. 5 (Wirth and Lichstein) and 8 (Harmon), this volume], which is higher in old forest, was negatively correlated to carbon export, suggesting enhanced gaseous carbon losses due to priming of microbial decomposition (Steinbeiss et al. 2008a). The total export rate of dissolved carbon decreased strongly in the mineral A and B horizons, and less then 10% carbon transferred from the Oa horizon was exported to the unaltered parent material, i.e. to the C horizon (Michalzik et al. 2001). In a two-phase sorption equilibrium, carbon is reactively transported to deeper soil layers.

Carbon is thereby partly transformed to SOM and partly respired by soil micro-organisms (Steinbeiss et al. 2008a). In total, dissolved losses of carbon from forested upland ecosystems are rather small and almost negligible.

Only one study could be found that investigated dissolved carbon exports in relation to stand age. Peichl et al. (2007) studied a chronosequence of white pine (*Pinus strobus*) afforestations in southern Ontario starting from carbon-depleted agricultural land. The annual export of dissolved organic carbon decreased from an initial 7 g C m^{-2} $year^{-1}$ 2 years after afforestation to 2 g C m^{-2} $year^{-1}$ in 65-year old sites. These data suggest that losses of dissolved carbon in old-growth forests are negligible.

11.3.4   Soil Carbon Stock Changes

As with soil respiration, the large spatial variability in soil carbon strongly limits the detection of carbon stock changes in the soil. In addition to changes in the carbon concentration of mineral soil, changes in soil bulk density also have to be considered. The latter, however, is controlled mostly by physical processes like swelling, shrinking or freezing, by biological processes like digging soil fauna or penetrating roots, or by chemical factors like the total concentration of carbon in the soil. Most of these factors change over the course of the year and are difficult to compare. Therefore changes in carbon concentration have proven to better reflect changes in carbon stocks (Steinbeiss et al. 2008b). Additionally, time series investigating changes at identical sites are very rare (Sect. 11.4; Zhou et al. 2006; Kelly and Mays 2005).

Pregitzer and Euskirchen (2004) compared carbon stocks determined for different forest stands separated according to age classes. In general, for temperate, boreal and tropical soil, they consistently found mean carbon stocks in the order of 10,000 g C m^{-2}. In boreal and tropical forests, the carbon stocks of young stands were 10% and 50% lower, respectively, than the mean across all age classes. In temperate forests, 10-year-old stands had slightly higher carbon stocks that initially decreased and then started increasing again at a stand age of about 30 years. The highest carbon stocks were always found in the oldest stand age class. This effect was strongest in boreal systems where, on average, the soil carbon stocks found in old-growth forests were twice those found in young stands. The analysis of Pregitzer and Euskirchen was the first systematic global meta-analysis of age-related changes in carbon stocks but has two main limitations: First, stands from individual investigations and chronosequences were pooled into broad age classes irrespective of site quality and hydrology. The results are therefore influenced by the interaction between site quality and age. For example, forests on poor soils develop more slowly and therefore tend to dominate the older age classes. This potentially introduces a bias towards lower accumulation rates in old forests. Second, the age range was rather limited and, in fact, for temperate and tropical forest no data from stands older than 200 years were included. Third, differences in the depth to which the carbon stocks were quantified were not corrected for.

In the following, we present a meta-analysis that avoids these problems. Using data from the literature, we take two approaches. In a first step (age-class approach),

we repeat the analysis of Pregitzer and Euskirchen based on age-classes but use only data from upland chronosequences (i.e. excluding hydromorphic sites) and standardise the soil carbon stocks by extrapolating shallower profiles down to 1 m depth using the biome-specific functions for vertical carbon distribution derived by Jobbagy and Jackson (2000). In addition, all data points within a chronosequence were standardised by dividing by the mean of the chronosequence. This approach increased the comparability of data from different biomes and enabled us to better take into account the effect of NPP on soil carbon stocks (see above), the effect of land use change in afforestations (Post and Kwon 2000), and to exclude the effect of high carbon accumulation in water-saturated lowland soils.

In a second approach (chronosequence approach), absolute changes in carbon stocks were calculated within specified developmental stages (pioneer phase: 0–100 years; transition phase: 101–200 years; early old-growth: 201–400 years; and late old-growth; see Chap. 5 by Wirth and Lichstein, this volume, for an identical approach for biomass and woody detritus). Only chronosequences extending beyond a maximum age of 150 years were considered and additional data from primary succession studies were included. In contrast to the age-class approach, data from the organic layer were also included where available and no depth extrapolation was applied. Spline functions were fit to the chronosequence data and the stock changes were calculated as the difference between fitted values for the upper and lower age boundaries divided by the duration of the respective developmental stage.

11.3.4.1 Age-class approach

Compared to the analysis by Pregitzer and Euskirchen (2004), this approach resulted in a much better agreement of the total soil carbon stocks with NPP estimates for the different biomes (Table 11.1). In general, the lowest median carbon stocks of 4,980 (sd 4,153) g C m^{-2} were found for different sites in boreal forests at 0–100 cm soil depth. This contrasts with the much higher findings of Pregitzer and Euskirchen (2004), where, unfortunately, some of the mineral soil carbon data used for boreal forests also contained the forest floor. Intermediate median carbon stocks of 9,347 (sd 2,652) g C m^{-2} were found in temperate deciduous forests; 9,961 (sd 8,614) g C m^{-2} in temperate coniferous forests; and were highest, i.e. in the order of 13,420 (sd 4,366) g C m^{-2}, in tropical evergreen forests. To compare individual chronosequences within biomes, we calculated changes in chronosequences relative to the mean carbon stock of the investigated depth (Fig. 11.6). We found a significant increase in soil carbon stocks of 35% and 5% with age for temperate deciduous ($P < 0.001$) and tropical evergreen forest ($P = 0.031$), respectively. Forests dominated by boreal conifers lost up to 24% mineral soil carbon with age; however, this age-trend of carbon stocks was not significant. No clear pattern emerged for temperate coniferous forests. Initially, these forests gained up to 20% carbon, but it was lost again in the oldest age class (Fig. 11.6). The decline in mineral soil carbon stocks in boreal forests is probably due to the parallel build-up of a thick organic raw humus layer above the mineral soil

Table 11.1 Soil organic carbon (SOC) stocks in the mineral soil of boreal, temperate and tropical forest chronosequences

Reference	No.	Depth (cm)	Age (years)	SOC Measured depth (g m^{-2})	SOC 0–100 cm (g m^{-2})
Boreal coniferous forest					
Wirth et al. 2002	1	25	12	2,216	4,585
			53	1,201	2,484
			95	1,030	2,131
			266	900	1,863
			Mean	1,337	2,766
	2	25	2	1,369	2,832
			14	1,724	3,567
			28	934	1,932
			31	1,155	2,389
			95	2,520	5,213
			Mean	1,540	3,187
			67	876	1,813
			130	1,814	3,753
			138	1,566	3,239
			200	693	1,433
			204	1,599	3,308
			383	797	1,649
			Mean	1,224	2,533
	4	25	14	1,779	3,681
			26	1,714	3,547
			48	2,677	5,539
			215	1,232	2,548
			238	2,144	4,436
			235	1,509	3,122
			244	2,760	5,710
			Mean	1,974	4,083
Van Cleve et al. 1983	1	20	55	4,000	8,000
			70	14,000	28,000
			77	5,000	10,000
			95	7,300	14,600
			134	5,500	11,000
			Mean	7,160	14,320
			1	2,400	10,520
			4	2,100	9,205
			12	2,600	11,396
			14	2,700	11,835
Yermakov and Rothstein 2006	1	10			
			22	2,300	10,081
			27	2,300	10,081
			36	2,100	9,205
			52	1,900	8,328
			72	2,000	8,766

(*continued*)

Table 11.1 (Continued)

Reference	No.	Depth (cm)	Age (years)	SOC	
				Measured depth (g m^{-2})	0–100 cm (g m^{-2})
			Mean	2,267	9,935
Trumbore and Harden 1997	1	40	30	1,800	2,400
		40	90	2,900	3,867
	2	40	34	8,630	11,507
		40	117	4,300	5,733
			Mean	4,408	5,877
Pennock and van Kessel 1997	1	45	3	5,770	8,138
			13	6,240	8,800
			80	4,410	6,220
			Mean	5,473	6,954
			boral		
			Median	2.120	4,980
			SD	2,376	4,153
Temperate deciduous forest					
Hoover et al. 2002	1	30	15	4,100	6,401
			128	6,200	9,679
			192	7,000	10,928
			250	8,800	13,738
			Mean	6,525	10,187
Entry and Emmingham 1998	1	10	15	470	1,402
			65	870	2,595
			185	1,350	4,027
			Mean	897	2,675
Schöning and Kögel-Knabner 2006	1	35	62	6,400	9,298
		40	111	5,600	7,670
		55	169	6,500	7,828
			Mean	6,167	8,265
			30	4,363	9,947
			62	4,092	9,329
Mund 2004	1	15	111	3,221	7,343
			141	4,177	9,523
			153	4,307	9,819
			Mean	4,032	9,192
			38	4,373	9,969
			55	4,112	9,374
	2	15	85	4,161	9,486
			102	4,598	10,482
			171	4,367	9,956
			Mean	4,322	9,853
			122	4,735	10,795
	3	15	123	3,440	7,842
			168	4,329	9,869
			Mean	4,168	9,502
	4	15	147	4,763	10,859

Table 11.1 (Continued)

Reference	No.	Depth (cm)	Age (years)	SOC Measured depth (g m^{-2})	SOC 0–100 cm (g m^{-2})
			131	5,098	11,622
			153	4,510	10,282
			Mean	4,790	10,921
Gerighausen 2002	1	20	22	3,155	6,074
			61	3,366	6,480
			170	3,682	7,089
			180	3,702	7,127
			Mean temperate broadleaf	3,476	6,693
			Median	4,245	9,347
			SD	1,733	2,652
Temperate coniferous forest					
Klopatek 2002	1	20	20	15,700	30,226
			40	17,450	33,595
			500	9,740	18,751
			Mean	14,297	27,524
Law et al. 2003	1	100	23	6,918	6,918
			9	12,686	12,686
			16	5,380	5,380
			69	4,060	4,060
			56	7,634	7,634
			89	7,868	7,868
			105	9,699	9,699
			93	6,906	6,906
			96	7,361	7,361
			190	5,556	5,556
			251	4,122	4,122
			316	6,496	6,496
			Mean	7,057	7,057
Rothstein et al. 2004	1	100	1	3,800	3,800
			2	4,050	4,050
			4	4,210	4,210
			7	3,840	3,840
			12	4,660	4,660
			14	5,030	5,030
			22	4,380	4,380
			27	5,080	5,080
			36	4,010	4,010
			52	4,240	4,240
			72	3,690	3,690
			Mean	4,272	4,272
Smithwick et al. 2002	1	100	150	36,550	36,550
			225	19,540	19,540

(*continued*)

Table 11.1 (Continued)

Reference	No.	Depth (cm)	Age (years)	SOC Measured depth (g m^{-2})	0–100 cm (g m^{-2})
			400	3,670	3,670
			750	1,160	1,160
			455	12,250	12,250
			Mean	14,634	14,634
Smithwick et al. 2002	2	100	300	26,260	26,260
			470	10,900	10,900
			500	5,990	5,990
			550	7,560	7,560
			700	5,470	5,470
			750	9,590	9,590
			750	10,930	10,930
			1000	7,810	7,810
			1000	20,480	20,480
			1200	11,660	11,660
			Mean	11,665	11,665
Boone et al. 1988	1	30	25	3,740	5,839
			53	3,980	6,213
			84	3,700	5,776
			225	3,330	5,198
			Mean	3,688	5,757
			temperate coniferous		
			Median	9,361	9,361
			SD	4,916	8,614
Tropical evergreen broadleaf					
Davis et al. 2003	1	10	10	2,980	10,802
			25	3,200	11,600
			125	3,340	12,107
			150	4,200	15,225
			Mean	3,430	12,434
de Camargo et al. 1999	1	100	12	10,300	10,296
			300	10,200	10,196
			Mean	10,250	10,246
Williams et al. 2008	1	30	3	4,250	7,620
			8	4,500	8,068
			15	5,000	8,965
			25	4,500	8,068
			300	7,900	14,164
			Mean	5,230	9,377
Bashkin and Binkley 1998	1	20	15	6,240	14,169
			300	7,830	17,779
			Mean	7,035	15,974
Raich et al. 1997	1	5	110	2,480	15,609
		8	136	985	4,229

Table 11.1 (Continued)

Reference	No.	Depth (cm)	Age (years)	SOC Measured depth (g m^{-2})	0–100 cm (g m^{-2})
		1	136	257	7,102
		22	300	6,990	14,982
		15	300	7,360	20,077
			Mean	3,614	12,400
Street 1982	1	30	13	7,220	12,945
			300	9,660	17,320
			Mean	8,440	15,133
Brown and Lugo 1990	1	50	23	9,000	12,317
			40	9,000	12,317
			40	11,000	15,054
			42.5	12,000	16,423
			55	14,500	19,844
			100	15,200	20,802
			300	13,000	17,791
			Mean	11,957	16,364
	2	25	35	7,500	14,911
			50	9,000	17,893
			300	4,500	8,947
			300	6,000	11,929
			Mean	6,750	13,420
Reiners et al. 1994	1	10	5	1,400	5,075
			9	1,300	4,712
			9	1,900	6,887
			12	2,100	7,612
			12	2,200	7,975
			300	1,400	5,075
			300	1,700	6,162
			300	2,800	10,150
			Mean	1,850	6,706
Smith et al. 1998	1	20	23	11,700	26,566
			36	9,200	20,890
			63	9,300	21,117
			36	9,500	21,571
			300	10,600	24,069
			Mean	10,060	22,843
Guariguata et al. 1997	1	30	16	7,700	13,805
			16.5	7,900	14,164
			17	11,400	20,439
			300	8,700	15,598
			300	9,100	16,316
			300	11,600	20,798
			Mean tropical	9,400	16,853
			Median	7,035	13,420
			SD	3,258	4,366
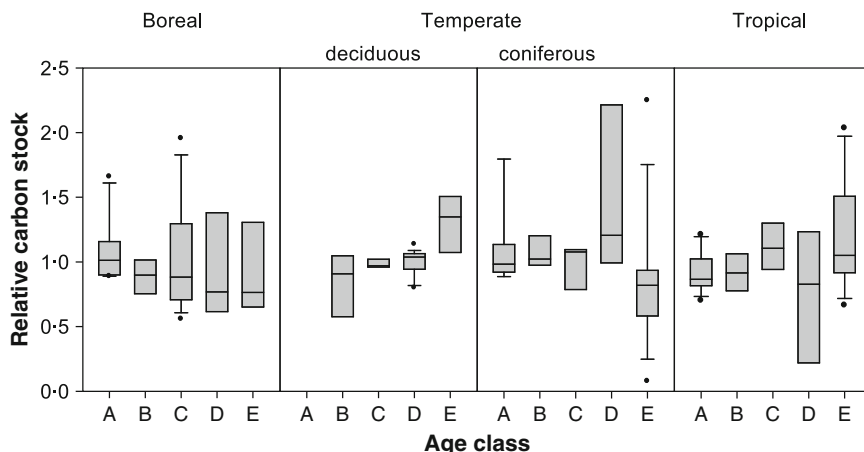
Fig. 11.6 Development of soil organic carbon (SOC) stocks in age-class of chronosequences relative to the mean SOC stocks of individual chronosequences (data from literature, see Table 11.1). Age classes in years: boreal coniferous forests *A* 0–20, *B* 20–40, *C* 40–100, *D* 100–200, *E* >200; temperate deciduous forests *A* 0–15, *B* 15–40, *C* 40–100, *D* 100–190, *E* >190; temperate coniferous forests *A* 0–20, *B* 20–40, *C* 40–90, *D* 90–190, *E* >190; tropical evergreen forests *A* 0–20, *B* 20–40, *C* 40–90, *D* 90–190, *E* >190; significant increase of SOC with stand age in temperate deciduous- and tropical evergreen forests (P <0.05); not significant decrease of SOC with stand age in boreal- and temperate coniferous forests (P >0.05)

(cf. Chap. 13 by Bergeron and Harper, this volume). The consequence of this are two-fold: the low pH of the organic layers negatively effects both litter decomposition and bioturbation, and the acidic soil solution forces the development of carbon- and nutrient-depleted eluvial horizons via a podzolation process. As a consequence, carbon accumulation occurs in deeper B horizons that are often below the investigated soil depth. These results from the improved age-class approach suggest that temperate deciduous and tropical evergreen forests continuously accumulate soil carbon until the highest age-class (>190 or 200 years). Conifer-dominated boreal and temperate forest potentially also accumulate carbon in old-growth forests, but here carbon is found in thick organic soil layers that are not protected against disturbances and carry the dangers of nutrient lock-up and ecosystem retrogression (cf. Chap. 9 by Wardle, this volume).

11.3.4.2 Chronosequence approach

The high variability in rates of carbon stock changes (ΔC_{SOM}) was the most notable feature of the chronosequence data (Table 11.2, Fig. 11.7). Variability was most pronounced in the boreal and temperate coniferous sequences where both negative and positive rates were estimated for all developmental stages; values of ΔC_{SOM} ranged from –14 to +57 g C m^{-2} year^{-1}. Mean values of ΔC_{SOM} decreased with latitude from the boreal (between 1.4 and 2.5 g C m^{-2} year^{-1}) to the tropics

Table 11.2 Boreal, temperate and tropical forest chronosequences of soil carbon extending beyond a stand age of 150 years. Labels refer to the panel numbers in Fig. 11.7. ΔC Change in soil carbon stocks (g C m^{-2} year^{-1}), *Pioneer* pioneer phase (1–100 years), *Transition* transition phase (101–200 years), *EOG* early old-growth phase (201–400 years), *LOG* late old-growth phase (401–600 years), *bc* boreal coniferous, *tec* temperate coniferous, *teb* temperate broadleaved, *trb* tropical broadleaved, *sol* complete column was measured, + including organic layer

Sequence	Biome	Location	Forest type	Depth (cm)	Minimum age (years)	Maximum age (years)	ΔC_{SOM} Pioneer	ΔC_{SOM} Transition	ΔC-EOG	ΔC-LOG	Reference
1	bc	Central Siberia	*Pinus sylvestris*, Vacc. type	25+	10.6	265	0.6	0.5	0.5		Wirth et al. 2002
2	bc	Central Siberia	*Pinus sylvestris*, lichen type	25+	1	379	−0.8	−2.5	−3.1		Wirth et al. 2002
3	bc	Central Siberia	*Abies sibirica, Picea obovata*	25+	67	320	4.5	9.5	8.3		C. Wirth, unpublished data
4	tec	Oregon, USA	*Pseudotsuga menziesii*	10+	28.9	185	7.6	7.8			Entry and Enningham 1998
5	tec	Washington, USA	*Pseudotsuga menziesii*	20+	21.4	400	−14.2	−14.1	−13.8	−14.3	Klopatek 2002
6	tec	Oregon, USA	*Tsuga heterophylla*	30+	24.4	223	−0.1	0.2	0.9		Boone et al. 1988
7	tec	California, USA	Mixed conifer	20+	1	300[a]	4.4	−1.8	−1.9		Black and Harden 1995
8	tec	California, USA	Mixed conifer	sol	47	400	57.2	14.6	6.2	1.8	Sollins et al. 1983
9	tec	Oregon, USA	*Pinus ponderosa*	100+	7.6	317	−8.5	−14.3	−14.2		Law et al. 2003
10	tec	Fichtelgebirge, Germany	*Picea abies*	30	8	172	7.6	0.4			Mund 2004
11	teb	Leinefelde, Germany	*Fagus sylvatica*	15	35	153	−0.6	−1.5			Mund 2004
12	teb	Hainich, Germany	*Fagus sylvatica*	15	43	170	−0.4	0.7			Mund 2004
13	teb	Leinefelde, Germany	*Fagus sylvatica*	70+	29	179	4.5	4.2			Mund 2004
14	teb	Patagonia, Chile	*Nothofagus pumilo*	30	31.44	300[a]	1.8	1.2	−0.6		Weber 2001
15	teb	Pennsylvania, USA	Mixed deciduous	30+	11.8	400	6.2	7.1	6.6	6.9	Hoover et al. 2002
16	teb	Maine, USA	Mixed deciduous	+	2.7	200	7.1	5.9			Covington 1981

17	teb	New Zealand	*Nothofagus solandri*	10+	8.8	200	8.2	8.2			Davis et al. 2003
18	trb	Paragominas, Brazil	Mixed tropical	100	9.8	300[a]	–0.1	0.0	0.0		de Camargo et al. 1999
19	trb	Hawaii, USA	*Metrosideros polymorpha*	5	100	400		0.3	1.6	1.7	Raich et al. 1997
20	trb	Kompiai, New Guinea	Mixed tropical	30	4.6	300[a]	28.3	28.1	25.0		Street 1982
21	trb	Porce, Colombia	Mixed tropical	400	7.3	300[a]	11.8	12.0	11.7		Sierra et al. 2007
22	trb	Puerto Rico, USA	Mixed tropical	50	21.8	300[a]	60.6	1.8	2.0		Brown and Lugo 1990
23	trb	Para, Brazil	Mixed tropical	20	22.1	300[a]	2.4	1.5	1.5		Smith et al. 1998
24	trb	Sarapiqui, Costa Rica	Mixed tropical	30	14.2	300[a]	2.7	2.8	2.4		Guariguata et al. 1997

[a] An estimated age of 300 years was assigned if simply the stage "old-growth" was indicated. This is approximately the age of tropical stands referred to as old-growth found in the literature (see Chap. 2 by Wirth et al., this volume)
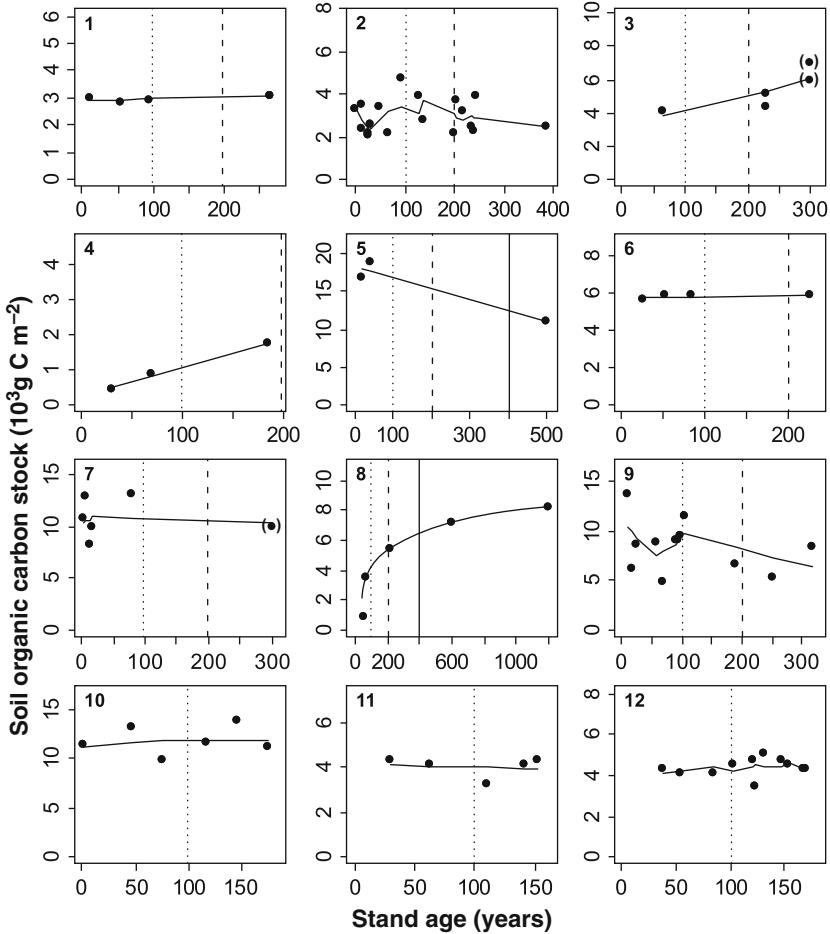
Fig. 11.7 Chronosequences of soil organic carbon stocks extending to stand ages beyond 150 years. Data were taken from the literature (see Table 11.2) and where necessary digitised from figures. The individual trajectories were fitted with Friedman's super smoother (subsmu-function in R – with parameters span = 0.2 and bass = 10). *Vertical lines* delineate the successional stages 'pioneer', 'transition', 'early old-growth' and 'late old-growth' (see text). The intersections between *smooth lines* and *vertical lines* were used to calculate the changes in biomass carbon stocks during the successional stages. The numbers *1–24* indicate the sequences described in detail in Table 11.2. Points in brackets indicate stands that were labelled 'old-growth'; these were assigned the mean age of old-growth sites of 300 years according to Wirth et al. (Chap. 2, this volume)

(between 6.3 and 17.6 g C m^{-2} year^{-1}). Except in the tropics the overall magnitude of ΔC_{SOM} was low. Using the biome-specific values of NPP from Luyssaert et al. (2007) for the four biomes (boreal coniferous: 331 g C m^{-2} year^{-1}, temperate coniferous: 355 g C m^{-2} year^{-1}, temperate broadleaved: 738 g C m^{-2} year^{-1} and tropical evergreen: 863 g C m^{-2} year^{-1}), it becomes clear that only a small fraction
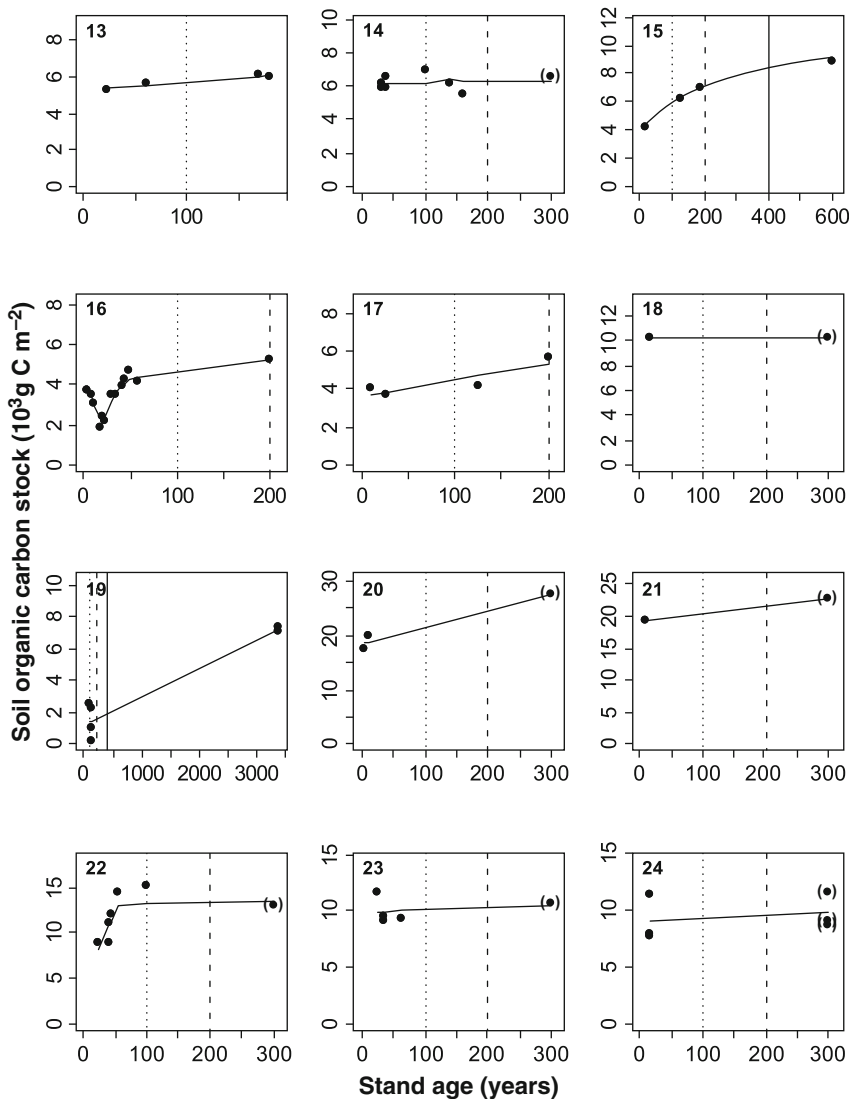
Fig. 11.7 (Continued)

of the annual NPP accumulates in the soil even if we use the maximum rates per phase (0.76%, 2.2%, 0.5% and 2%, respectively). With the exception of temperate coniferous forests, the chronosequences tended to accumulate carbon during the early old-growth phase at rather low rates of between 2 g C m^{-2} year^{-1} (boreal coniferous), 3 g C m^{-2} year^{-1} (temperate broadleaved), and 6 g C m^{-2} year^{-1} (tropical). Data for the late old-growth phase are too scarce to allow any interpretation.

It should be noted here that these chronosequence-based estimates of ΔC_{SOM} are much lower than those estimated with other methods (cf. Table 11.4). Comparing developmental phases within biomes, there was no clear age-trend for the chronosequences of boreal and temperate broad-leaved biomes. In the temperate coniferous sequences there was a shift from carbon sequestration during the pioneer phase ($\Delta C_{SOM} = 7\,g\,Cm^{-2}\,year^{-1}$) to carbon losses ($\Delta C_{SOM} = -4.5\,g\,C\,m^{-2}\,year^{-1}$). In the tropical sequences, ΔC_{SOM} dropped from 17.6 to 6.3 g C m^{-2} $year^{-1}$ and thus remained positive. The results need to be treated with caution however, since most of the cited chronosequence studies did not consider soil layers below 30 cm and thus miss the potentially important subsoil carbon accumulation. Another more laborious way of quantifying soil carbon stock changes in old-growth forests are geo-referenced soil samplings repeated at the same location and with a depth resolution of at least 1 m in order to investigate the effect of soil profile development and potentially important carbon storage in deeper soil layers. An example of such a study is given in the next section.

11.4 Case Study of Soil Carbon Sequestration in a 250-Year-Old Beech Forest

A case study investigating soil carbon sequestration in an old-growth forest was performed in the Hainich National Park (NP), Germany. This site is fully equipped to obtain a full carbon balance and, in addition, historical data on past carbon export from the site were available.

11.4.1 Site Description and Experimental Setup

The study site is located within the Hainich NP ($50°14'$ N, $10°00'$ E, 440 m a.s.l.) in Thuringia, central Germany. European beech (*Fagus sylvatica*, 65%) and ash (*Fraxinus excelsior*, 25%) of up to 250 years of age are the dominating trees (Knohl et al. 2003). The aboveground stem carbon pool is 13,000 g C m^{-2} (Mund 2004), coarse woody debris is 1,350 g m^{-2} (Cotrufo et al. 2002), and litter production is, on average, 170 g m^{-2} $year^{-1}$ (Mund 2004). The annual litter production decomposes almost completely within 1 year (Soe and Buchmann 2005).

Soils are 50–60 cm deep fertile cambisols (clay loam) underlain by a limestone bedrock. The soil is characterised by a large clay content (40%), sand (4%) and a thin litter layer. The A-horizon is 5–15 cm deep and followed by a clayish T-horizon.

From April 2005 to April 2006, soil CO_2 efflux was determined from 79 collars in randomised locations using a double nested approach. The CO_2 efflux was determined biweekly employing a closed chamber method using an infrared gas analyser. Carbon export via downward water flux was measured at four collection systems that were installed in 2001 along the slight slope of the study area. Soil

water was collected biweekly with glass suction plates (1–1.6 µm pore size) at 5, 10 and 20 cm. Soil carbon concentrations were measured at 80 points distributed on a random grid over the whole measurement site. Soils were sampled at the same location (within the spatial autocorrelation distance) in July 2000 and in July 2004 with a Puerkhauer auger. Total carbon and organic carbon concentrations were analysed with an elemental analyser. Soil density was determined independently at 100 sampling points using an 87-mm-diameter soil column cylinder (M. Schrumpf, personal communication). For stock calculations, the mean bulk density for each depth segment measured in 2004 was also applied for the year 2000. The spatial distribution of the carbon stocks and the stock changes have been regionalised using ordinary kriging with a geographic information system (GIS).

11.4.2 Historical Carbon Export

The historical management and especially the historical carbon export of the study site for the time period 1815–2007 have been analysed using all available archived information, including maps, operation plans and forest regulations (Schenk 1999). The bulk of the biomass was exported as construction wood, and firewood, and regulated litter-use was also documented.

From 1815 to 1920 the forest was managed as a coppice-with-standard forest, in which only coppice and selected trees were harvested. The 260 ha area was divided into 13 units and every year one unit of 20 ha was harvested according to a management plan. The carbon export for wood averaged 125 ± 31 g m^{-2} year^{-1} and for litter 30 g m^{-2} year^{-1} (Table 11.3). In 1920, the forest changed to a high forest and management was restricted to selected removal of single trees. In this phase the carbon export initially decreased to 68 g m^{-2} year^{-1} and increased 20 years after conversion up to 120 g m^{-2} year^{-1}. Between 1950 and 1960, the increment of growth was harvested and 254 g C m^{-2} year^{-1} exported. In 1960 large parts of the Hainich forest became a military training area. Mund (2004)

Table 11.3 Carbon export from the Weberstedter Holz study site in the Hainich National Park (NP), Germany, during the time period 1830–2007

Time period	Management	C-export (g C m^{-2} year^{-1})	Total C-export (g C m^{-2})
1830–1920	Coppice-with-standards forest	125 ± 31	10,400
1830–1920	Litter use	29	2,610
1920–1939	Selection forest	68	1,365
1940–1949	Selection forest	120	1,200
1950–1959	Selection forest	254	2,540
1960–1989	Selection forest – extensive management	65	1,950
1990–2007	No management	–	–
1830–2007		110	20,065

describes extensive management and a carbon export of 2 m^3 ha^{-1} $year^{-1}$, which is equivalent to 65 g m^{-2} $year^{-1}$. With the conversion of the area to a National Park in 1990 the management, and consequently the carbon export, stopped completely. Thus, a total of 20,065 g C m^{-2}, i.e. an average of 110 g C m^{-2} $year^{-1}$, has been lost by historical silviculture in the last 177 years.

The historical management of the Hainich site was moderate and no ruinous exploitation occurred. Compared with contemporary management of forests, the amount of historical C-export in the Hainich NP was low, and soil carbon pools are thought not to have been depleted by historical management.

11.4.3 Soil Respiration in Hainich NP

In 2006, mean and median CO_2 efflux (mean from all collars and all measurements) was 623 and 593 g m^{-2} $year^{-1}$. Rates from individual collars ranged from 295 to 1,298 g m^{-2} $year^{-1}$. These rates are well within the range reported by other research groups working in temperate forests (Hanson et al. 1993; Reiners 1968; Savage and Davidson 2001; Martin and Bolstad 2005). For all measurements, Q_{10} was 3.9, indicating a large temperature dependency of soil respiration. Temperature dependency of soil respiration was highest at low soil moisture, declining from 4.1 at 0–30% and 3.6 at 30–60% to 2.3 at 60–90% soil moisture. These values represent the average values for temperate deciduous forests listed by Chen and Tian (2005). The dependency of soil respiration to soil moisture followed an optimum function, with highest rates at 45–50% when soil temperature was low (0–12°C) and at 35% during times of high soil temperature (>12°C).

In beech-dominated areas of the forest, there was no correlation between potential fine root biomass and soil respiration for the entire season. However, during the leaf-sprouting phase, a high potential fine root biomass increased soil respiration ($r^2 = 0.19$, $P = 0.02$). In ash-dominated parts of the forest, high soil respiration was correlated with elevated potential fine root biomass for the entire year (r^2: 0.48, $P = 0.01$) as well as during the leaf-sprouting phase ($r^2 = 0.37$, $P = 0.03$).

11.4.4 Carbon Export to the Liquid Phase

To determine carbon export from the surface soil to the liquid phase, dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) in soil water samples were analysed biweekly. In addition, the vertical flux of soil water was determined and the water balance of the system modelled (Wetzel 2005). For this purpose, 13 Tensiometers (FDR-probes) were located along the slope profile of the study site, parallel to the four intensive measurement points for soil water. Starting in January 2002, soil moisture was measured for a whole year at high frequency (Fink et al.
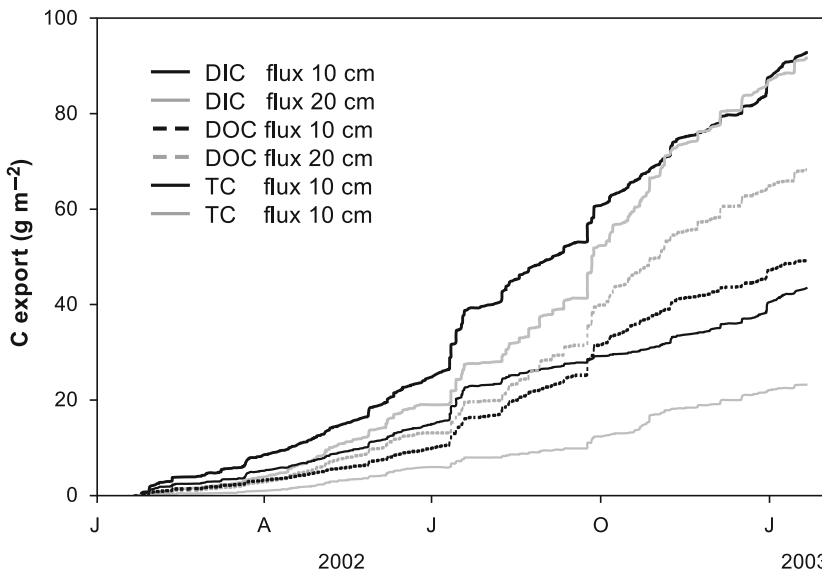
Fig. 11.8 Export of dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and total carbon (TC) at 10 and 20 cm soil depth in 2002 at the water collection system within the study site 'Weberstedter Holz' in the Hainich National Park (NP), Germany

2004). The export of DOC at 10 cm soil depth reached 6.8 g m^{-2} and at 20 cm, 5 g m^{-2} (Fig. 11.8). Thus 28% DOC was lost by mineralisation and sorption processes. Compared to DOC export in similar forest ecosystems (Michalzik et al. 2001), the values in the Hainich NP are low. DIC export increased with soil depth from 2.3 g m^{-2} at 10 cm to 4.3 g m^{-2} at 20 cm. In total, the export of carbon was about 9 g m^{-2} per analysed soil depth in 2002.

In relation to the large amount of carbon stored in the soil of the Hainich NP, carbon exported via water flux contributed only a small fraction.

11.4.5 Development of Carbon Stocks

The concentration of soil organic carbon (SOC) measured for all 80 plots was distributed normally for all depths. The SOC concentration decreased continuously with increasing soil depth from 5,038 g m^{-2} at 0–10 cm to 1,255 g m^{-2} at 50–60 cm in 2000, and from 4,622 g m^{-2} at 0–10 cm to 1,377 g m^{-2} at 50–60 cm in 2004 (Fig. 11.9). This amount is in agreement with the SOC inventory data of Mund (2004) in the Hainich NP and with other temperate old-growth forests (Reichle 1970; Tate et al. 1995; Liechty et al. 1997; Hoover et al. 2002). In the upper 20 cm, 500 g SOC m^{-2} was lost within the years 2000 and 2004, which might be due to the
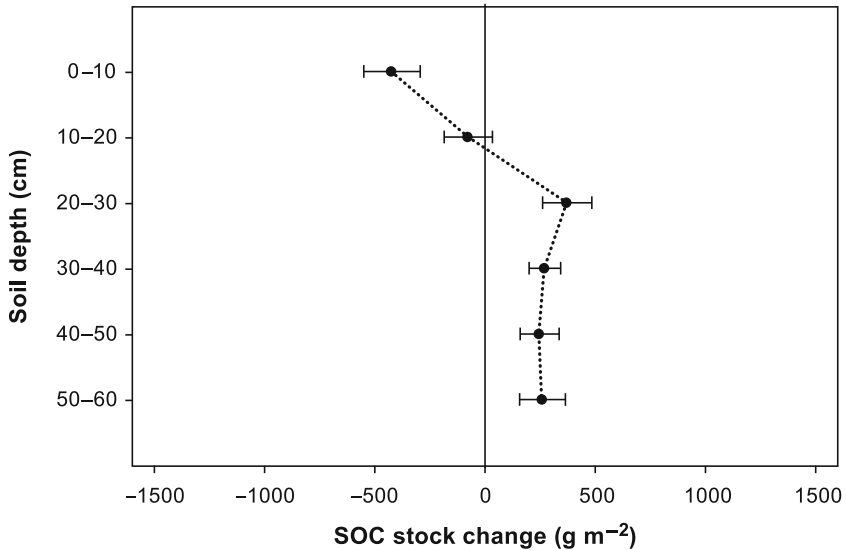
Fig. 11.9 Changes in SOC stocks between 2000 and 2004 at the study site 'Weberstedter Holz' in Hainich NP. *Error bars* Standard error (20–30 cm $P > 0.05$)

unusual climatic conditions in the year 2003. A heatwave, and hence particularly water limitation, negatively affected the gross primary productivity of the biosphere and the carbon balance (i.e. ecosystem respiration; Reichstein et al. 2007). Hence the input of organic material into upper soil layers was low to negligible. However, at a soil depth of 20–60 cm, 1,150 g SOC m^{-2} accumulated within 2000 and 2004. The greatest sequestration (270 g m^{-2}) occurred at 20–30 cm depth, directly below the major SOC loss horizon (Fig. 11.9). We assume that the sequestration of SOC in deeper soil layers might be (1) the result of downward transport processes of organic material (i.e. DOC) from the upper soil layer and/or (2) a permanent increase in fine roots, especially in deeper soil layers, to compensate for drought stress. The production of fine roots at 20–30 cm depth is greater in autumn with 56 g m^{-2} than in spring with 43 g m^{-2} (A. Claus, FORECAST, personal communication). Consequently, these two processes should result in a continuous accumulation of organic carbon and continuous growth of the soil profile downwards. In summary, soil in the beech forest of the Hainich NP stored 650 g SOC m^{-2} in 4 years, which is equivalent to 165 g SOC m^{-2} $year^{-1}$.

The spatial distribution of the carbon stocks and the storage of SOC in our study area is very heterogeneous (Fig. 11.10). The upper soil layer especially is exposed to climatic conditions and influenced by digging animals, roots and fine roots. The majority of fine roots is distributed in the upper soil layer (0–10 cm, 260 g m^{-2}), with fine roots decreasing continuously with increasing soil depth (20–30 cm, 50 g m^{-2}; A. Claus, FORECAST, personal communication). The most diverse spatial distribution of stored SOC occurs at a soil depth of 20–30 cm, where we
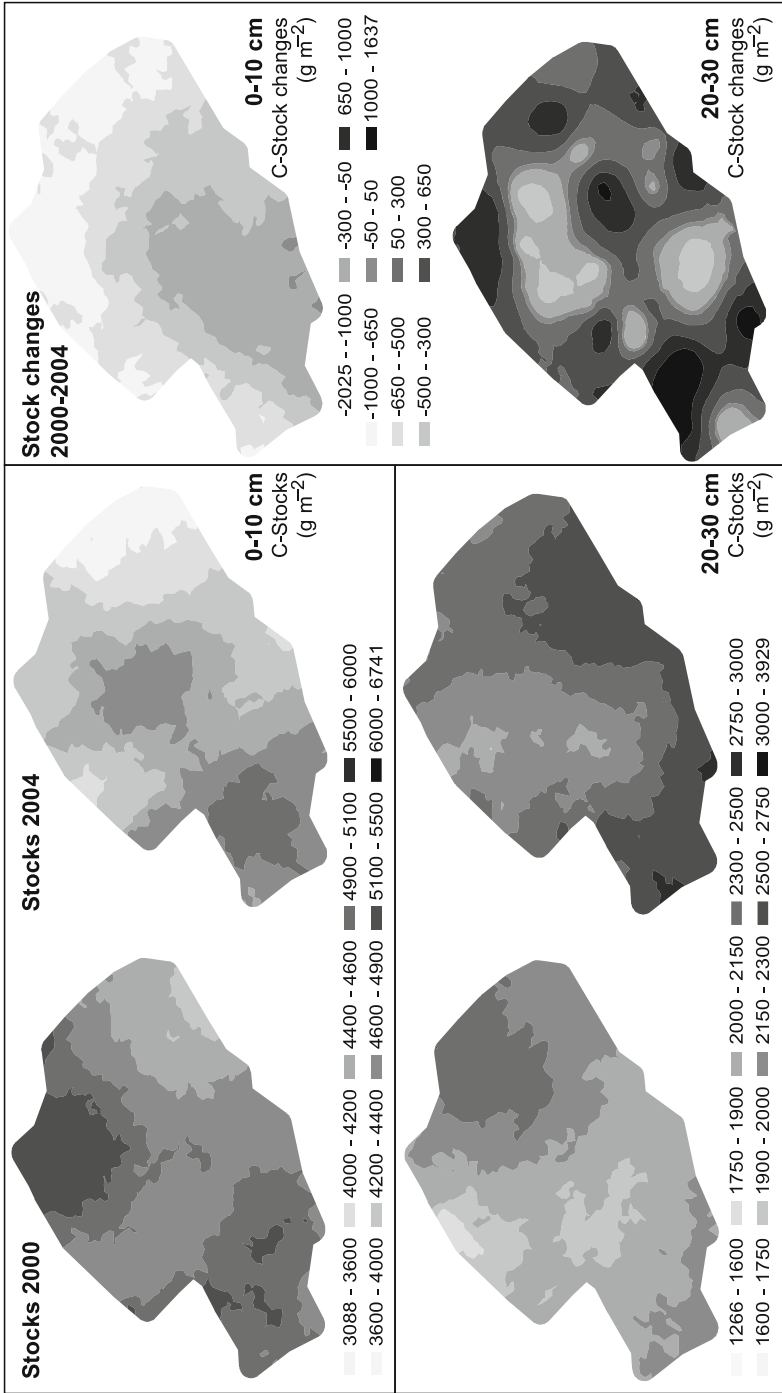
Fig. 11.10 Spatial distribution of SOC stocks and stock changes at different soil depths within the study site 'Weberstedter Holz' in Hainich NP

also found the highest accumulation between 2000 and 2004. This suggests that particulate transport, such as particulate organic matter or growth of roots, drives this storage.

11.5   Discussion of Carbon Stock Changes

Soil carbon sequestration rates (ΔC_{SOM}) obtained from different regions and through different methods differ substantially (Table 11.4). It appears that chrono-sequence estimates (range: –4.5 to 17.6 g C m^{-2} year^{-1}) are in the same range as estimates based on a carbon balance approach (range: –5 to 19 g C m^{-2} year^{-1}), but are generally much lower than estimates based on repeated sampling (range: 32 to 165 g C m^{-2} year^{-1}). There were also pronounced differences between biomes but different methods yielded different rankings. Values of ΔC_{SOM} were highest in the tropics and lowest in the boreal according to the chronosequence approach in Sect. 11.3.4 irrespective of stage, whereas the analysis by Pregitzer and Euskirchen (2004) suggest that tropical rates are highest during the pioneer stage but lowest during the transition stage.

The median values of ΔC_{SOM} within stages (across different methods) pro-gressed from the pioneer stage to the late old-growth state in the following order: pioneer 14.8 $\pm$ 25.6, transition 8.4 $\pm$ 17.6, early old-growth 21.0 $\pm$ 57.0, and late old-growth 6.9 $\pm$ 19.7 g C m^{-2} year^{-1}. Thus differences between developmental stages were generally low and not significant. The errors were large and resulted mostly from discrepancies between methods. The study by Schlesinger (1990) was based on data from long-term primary successions in the order of several thousand years. It is likely that these systems have already lost soil carbon as a consequence of ecosystem retrogression (see Chap. 9 by Wardle, this volume) or simply by disturbances such as fire or erosion. Nevertheless, as a whole, the data suggest that the soil in forests remains a small-to-moderate carbon sink well into the old-growth stage. The few estimates based on repeated sampling (Sect. 11.4; Homann et al. 2005; Kelly and Mays 2005; Zhou et al. 2006) even suggest substantial rates in old-growth forests that may be in the range of the aboveground litterfall. It should be noted that Homann et al. (2005) detected changes only in the forest floor organic matter, but not in the mineral soil. Furthermore, the case study presented above and the study by Kelly and Mays (2005) inferred changes in carbon stocks from changes in measured carbon concentrations assuming constant bulk densities over time (see first paragraph in Sect. 11.4.2). Given that soil carbon concentrations tend to be negatively correlated with soil bulk density, this assumption of a constant density may lead to a slight overestimation of carbon sequestration. However, Zhou et al. (2006) consider this effect, and their high sequestration rates were obtained despite a reduction in bulk density.

The reasons for differences between estimates from chronosequence and from repeated sampling can be manifold. Forest ecosystems that are influenced by recurring disturbances the remove carbon, such as fire, are in a permanent stage

Table 11.4 Carbon storage in the mineral soil in forests of different developmental stages in different biomes estimated with different methodologies

Source	Biome[a]	Method[b]	Soil depth (cm) [c]	Carbon storage (g m^{-2} year^{-1})[d]
Pioneer stage				
Chronosequences (Sect. 11.3.4)	Bor-c	C	Var	1.4 ± 2.8
	Temp-c	C	Var	7.7 ± 23.3
	Temp-b	C	Var	3.8 ± 3.6
	Trop-b	C	Var	17.6 ± 23.5
Post and Kwon (2000)[e]	Temp	PS	Var	24 ± 22
	Trop	PS	Var	69 ± 85
Pregitzer and Euskirchen (2004)[f]	Bor	C	Var	18.6
	Temp	C	Var	–5.5
	Trop	C	Var	76
Liski et al. (2002)[g]	Various	CB	N.I.	19 (0–107)
Median ± SD				14.8 ± 25.6
Transition stage				
Chronosequences (Sect. 11.3.4)	Bor-c	C	Var	2.5 ± 6.3
	Temp-c	C	Var	–1.0 ± 10.6
	Temp-b	C	Var	3.7 ± 3.6
	Trop-b	C	Var	6.6 ± 6.3
Pregitzer and Euskirchen (2004)[f]	Bor	C	Var	56
	Temp	C	Var	31
	Trop	C	Var	8
Homann et al. (2005)[h]	Temp-c	RS	0–15+	32
Trumbore and Harden (1997)[i]	Bor-c	CB	0–40+	–5 to 12
Median ± SD				8.4 ± 17.6
Early old-growth stage				
Chronosequences (Sect. 11.3.4)	Bor-c	C	Var	1.9 ± 5.8
	Temp-c	C	Var	–4.5 ± 9.1
	Temp-b	C	Var	3.0 ± 5.1
	Trop-b	C	Var	6.3 ± 9.1
Kelly and Mays (2005)[j]	Temp-b	RS	0–15	76
Case study (Sect. 11.4)	Temp-b	RS	0–60	165
				21.0 ± 57.0
Late old-growth stage				
Schlesinger 1990	Bor	LC	N.I.	4.9 ± 5.9
	Temp	LC	N.I.	4.2 ± 4.1
	Trop	LC	N.I.	2.4 ± 0.1
Zhou et al. 2006[k]	Temp	RS	0–20	61 (54–68)
Chronosequences (Sect. 11.3.4)	Various	C	N.I.	–1.0 ± 9.1
Median ± SD				6.9 ± 19.7

[a]Biome: *Bor-c* Boreal coniferous, *Temp-c* temperate coniferous, *Temp-b* temperate broadleaved, *Trop-b* tropical broadleaved

[b]Method: *RS* Repeated soil sampling, *C* chronosequence approach, *CB* carbon balance approach, *PS* paired sampling of forest and surrounding agricultural soil

[c]Abbreviations: *N.I.* not indicated, + including forest floor, *Var* variable

[d]Bootstrap medians were calculated as measures of central tendency for the chronosequence estimates of C_{SOM} as well as for all data in developmental phase

[e]Based on a meta-analysis of SOC accumulation during forest regrowth after agricultural abandonment. Accumulation rates were determined as the difference in C_{SOM} between forests and surrounding agricultural control sites

[f]Based on forest SOC stock observations arranged in chronosequences (see text)

[g]Soil carbon sequestration rates under European forests calculated with a carbon balance model driven by litter input rates derived from large-scale forest inventories. Since the mean age of forest in Europe is well below 100 years, this study is assigned to the pioneer phase

[h]Repeated measurements of old-growth forest carbon stocks in 13 second-growth Douglas-fir stands between 1969/1970 and 1995. There were no changes in the mineral soil carbon but a significant accumulation of organic layer carbon in the forest floor

[i]Net carbon sequestration rates in deep organic layers in *Pinus banksiana* and *Picea mariana* forests calculated using the carbon balance approach based on input and turnover rates

[j]Repeated measurement after 26 years at 11 sites in a mixed oak forest. The region was forested before the establishment of the state park in 1930, but the site was subject to woodland grazing and timber harvest prior before that date

[k]Repeated measurement after 25 years with 20 replicates in an undisturbed sub-tropical old-growth forest (>400 years). Range shows the 95% confidence interval of the change in carbon stocks

of recovery. Such ecosystems follow a steeper carbon trajectory than suggested by chronosequence fits as in Fig. 11.7, which cut through the characteristic zig-zag pattern of carbon stock changes created by repeated carbon losses and subsequent recovery of pools (Wirth et al. 2002). Alternatively, most stands might be forced into a transient steeper trajectory because of ubiquitous carbon dioxide and nitrogen fertilisation. The discrepancy may thus reflect a transient imbalance caused by higher litter production rates. Furthermore, the chronosequence approach has its limitations in cases where the temporal sampling density is low. Many of the tropical sequences in Fig. 11.7 compare only young and old-growth systems, often without indicating the exact age of the old-growth stage (in which case it was assigned an age of 300 years according to Wirth et al., Chap. 2, this volume). A linear interpolation probably misses non-linear dynamics along the sequences, and it is likely that this approach underestimates old-growth carbon sequestration rates, since young stands may have stocks of legacy carbon that are decomposed and restocked with *de novo* carbon thereafter.

11.6 Conclusions

Based on the evaluation of the existing literature and results from the case study in the Hainich NP, we are able to draw the following conclusions:

- Soils in old and old-growth forests may play a key role in carbon sequestration. Estimated accumulation rates vary depending on the methods used and the soil depth considered. Chronosequence studies suggest low carbon accumulation rates (and sometimes even losses) in the order of a few grams carbon per square metre per year. Studies using repeated soil inventories tend to yield far higher rates

$(84 \pm 57 \, \mathrm{g\,C\,m^{-2}\,year^{-1}})$. The nature of this discrepancy remains unclear. Several possible explanations, including methodological biases, conceptual differences and the influence of nitrogen deposition on litter production, were discussed. Clearly, four studies using repeated sampling is not enough and more such studies are needed to quantify carbon sequestration rates in old-growth forests under undisturbed conditions and to resolve the above-mentioned discrepancies.

- Several mechanisms have been suggested that allow soil carbon sequestration during the old-growth stage. These range from a deterioration in litter quality, increases in litter production rates, to progressive particulate organic matter transport into deeper soil layers where the sequestered carbon is sheltered from the environmental variability that may otherwise cause recurring flush-type carbon losses. Most important for carbon storage are biologically controlled processes, i.e. transport of plant carbon into mineral soil followed by its transformation to SOC, and the renewed decomposition of soil carbon. These processes are strongly controlled by environmental parameters like oxygen and water content, nutrient availability, soil pH, and summer and winter temperatures, but not by stand age. Therefore old-growth forests are able to store soil carbon with the minimum rate of soil depth-profile growth.
- On the global scale, soil carbon accumulation seems to be related primarily to carbon input to the soil, and latitudinal patterns in NPP are mirrored by similar patterns in soil carbon stocks. However, the type of ecosystem, i.e. broadleaf versus conifer, and induced effects on litter quality, has a distinct effect on the sustainability of the stored carbon. Conifer-dominated systems tend to store large amounts of less-decomposed plant carbon, mainly in superficial organic horizons from where it may quickly disappear following fire, erosion or climatic extremes. Broadleaved forests tend to store a higher fraction of carbon in deeper layers of the mineral soil where it is protected against short-term climate variability and recurring disturbances.

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Chapter 12
Is There a Theoretical Limit to Soil Carbon Storage in Old-Growth Forests? A Model Analysis with Contrasting Approaches

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12.1   Introduction

Apart from the intrinsic worth that nature and forests have due merely to their existence, old-growth forests have always provided a number of additional values through their function as regulators of the water cycle, repositories of genetic and structural biodiversity and recreational areas [see e.g. Chaps. 2 (Wirth et al.), 16 (Armesto et al.), and 19 (Frank et al.), this volume]. In the context of climate change mitigation, carbon sequestration has become another highly valued function of natural and managed ecosystems. In this context, the carbon sequestration potential of old-growth forests has often been doubted and contrasted with the high sequestration potential of young and short-rotation forests, although there can be substantial carbon losses from forest soils following clear-cutting (cf. Chap. 21 by Wirth, this volume).

The question of long-term carbon uptake by old-growth forests has lead to much scientific debate between the modelling and experimental communities in the past. Classical soil carbon turnover models, favoured by certain factions of the modelling community, where soil carbon is distributed among different pools, and decays according to first-order kinetics with pool-specific turnover constants, logically lead to steady state situations. Here, the total input equals the total efflux of carbon and there cannot be a long-term uptake of carbon by ecosystems. However, this theoretical deduction from first-order kinetic pool models seems to contradict a number of observations where long-term carbon uptake has been perceived or at least cannot be excluded (Schlesinger 1990; and see Chap. 11 by Gleixner et al., this volume).

This mostly theoretical chapter will address this apparent contradiction from a more conceptual modelling point of view. A number of modelling approaches to soil carbon dynamics will be reviewed and discussed with respect to their prediction of long-term carbon uptake dynamics. These modelling approaches can be classified into three broad categories: classical first-order decay models with fixed decay rate constants; quality-continuum concepts where it is assumed that, during decay, the quality and decomposability of soil organic matter decreases gradually; and

microbe-centred models where decay depends on the abundance and activity of microbes, which themselves depend on substrate availability (and environmental conditions).

It will be evident that the above-stated modellers' view is strongly contingent on first-order reaction kinetics paradigms, and that there exist both old and recent alternative model formulations predicting that, under certain conditions, soil carbon pools never reach a steady state.

12.2   Observations of Old-Growth Forest Carbon Balance

The carbon balance of old-growth forests is directly accessible via repeated biometric measurements of pool sizes (and component fluxes), through measurements of ecosystem-atmosphere CO_2 exchange (assuming that non-CO_2 fluxes and carbon losses to the hydrosphere are negligible), or indirectly via pool changes along chronosequences (assuming space-for-time substitution is valid). Recently, Pregitzer and Euskirchen (2004) have reviewed such studies, coming to the conclusion that there is a clearly age-dependent net ecosystem productivity in forests. Micrometeorological measurements often indicate a continuation of a strong sink function of forest ecosystems over centuries, while biometric measurements reveal lower net ecosystem carbon uptake. Both methodologies have their specific systematic errors, as discussed elsewhere (Belelli-Marchesini et al. 2007; Luyssaert et al. 2007), but provide strong indications that long-term carbon uptake by old-growth forests is possible [see e.g. Chaps. 5 (Wirth and Lichstein), 7 (Knohl et al.), 14 (Lichstein et al.), 15 (Schulze et al.), and 21 (Wirth), this volume]. In another convincing example, Wardle et al. (2003) show that an increase in carbon stocks in humus may continue for millennia; a sequestration rate of at least $5 - 40$ g m^{-2} year^{-1} was inferred from a chronosequence study with natural island forest sites that have had very different frequencies of fire disturbance depending on island size (see Chap. 9 by Wardle, this volume). Other studies and reviews have also revealed long-term carbon sequestration by soils (Syers et al. 1970; Schlesinger 1990). There are, however, at least two reasons to question if it is possible at all to experimentally determine the existence of a limit to carbon storage. Firstly, there is the question of the time required to reach a potential steady state. Ågren et al. (2007) show that it is likely that a steady state for soil carbon requires several millennia of constant litter input, a period well exceeding the time since the last glaciation in many areas. Secondly, anthropogenic disturbances during the last century may have disrupted previous steady states; current levels of nitrogen deposition in particular may have increased forest growth and induced a transient in forest carbon storage (see also Sect. 18.4 in Chap. 18 by Grace and Meir, this volume).

12.3   Is There a Theoretical Limit to Soil Carbon Storage?

12.3.1   Classical Carbon Pool Models

The classical paradigm of soil organic carbon modelling builds upon so-called first-order reaction kinetics, where the absolute rate of decay is proportional to the pool size (Jenny 1941):

$$\frac{dC}{dt} = -k \cdot C(t) \tag{12.1}$$

Usually, soil organic matter is then divided into several conceptual kinetically defined pools with individual decay rate constants k, and constant coefficients that determine the transfer between different pools. The simplest useful model that exhibits these pool-specific rate constants and transfer coefficients is the introductory carbon balance model proposed by Hénin and Dupuis (1945) or Andrén and Kätterer (1997) as depicted in Fig. 12.1. More complex models differ mostly in the number of carbon pools (Parton et al. 1988; Jenkinson et al. 1991; Hunt et al. 1996; Parton et al. 1998; Liski et al. 1999) and obey the general mathematical formulation as linear systems:

$$\frac{dC_i}{dt} = I_i - k_i C_i + \sum_j k_j h_{ij} C_j$$

or

$$\frac{d\mathbf{C}}{dt} = \begin{pmatrix} I_1 \\ \cdot \\ \cdot \\ \cdot \\ I_n \end{pmatrix} - \begin{pmatrix} k_1 C_1 \\ \cdot \\ \cdot \\ \cdot \\ k_n C_n \end{pmatrix} + \begin{pmatrix} 0 & h_{12} & \cdot & \cdot & h_{1n} \\ h_{21} & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ h_{n1} & h_{n2} & \cdot & \cdot & 0 \end{pmatrix} \cdot \begin{pmatrix} k_1 C_1 \\ \cdot \\ \cdot \\ \cdot \\ k_n C_n \end{pmatrix} = \mathbf{I} - \mathbf{KC} \tag{12.2}$$

where I_i is the input from primary production into each pool, k_i is the decay rate constant, and h_{ij} is the transfer coefficient from pool i into pool j. Where more pools are introduced, the larger the number of potential parameters (growing with the square of pools) and, consequently, the more flexibly the model can simulate carbon trajectories from long-term experiments. However, regardless of model complexity, all models relying on first-order kinetics predict a limit to carbon storage in the soil, i.e. given a quasi-constant carbon input to the soil, a dynamic equilibrium (steady-state) will be asymptotically reached with the equilibrium pool sizes of each being equal to $K^{-1}I$ (symbols as in Eq. 12.2). If input ceases, all pools will decrease to zero with infinite time. The length of time required for the asymptotic approach to steady state clearly depends on the smallest decay constant (the smallest real part of
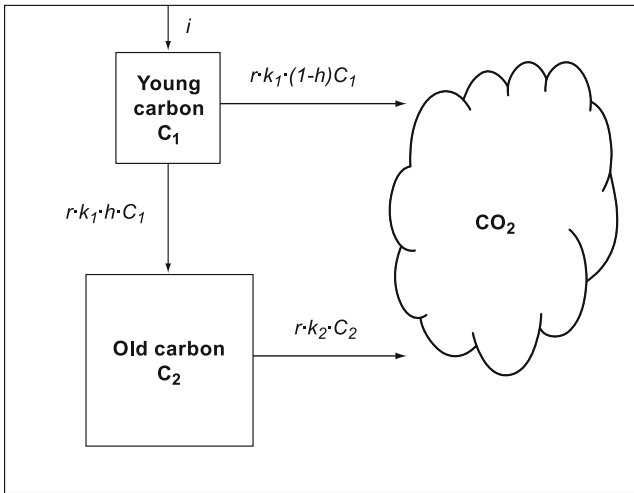
Fig. 12.1 Flow representation of the introductory carbon balance model (ICBM)

eigenvalues to matrix K). Hence, with sufficiently small decay rate constants, long-term sequestration of carbon in the soil can be modelled. Nevertheless, a theoretical limit to carbon sequestration remains a feature of this class of models. Climatic variability of the parameters around some mean value does not change this conclusion but complicates the calculation of the now quasi-steady state. One important assumption with this model is the constant rate of litter input. In a closed system with a limited amount of other essential elements (nutrients), increasing sequestration of carbon in soil pools would also imply sequestration of nutrients in the soil. This leaves less nutrients for vegetation, resulting in decreased litter production. With a decreasing nutrient:carbon ratio in the soil, soil carbon sequestration could go on forever.

12.3.2 Alternative Model Concepts of Soil Carbon Dynamics

The models following the classical paradigm as discussed above have two fundamental properties in common: (1) the intrinsic decay rate constants are constant in time, i.e. k_i varies at most around some constant mean as a result of varying environmental conditions such as soil temperature and moisture – in other words the properties of a pool are constant in time; (2) the decomposition of one carbon pool depends only on the state of the pool itself (i.e. the system is linear), not on other pools or microbial populations that are in turn influenced by other pools or nutrients. Relaxing either of these two assumptions leads to models where there is no theoretical limit to carbon sequestration, as discussed in the following sections.

12.3.2.1 Non-Constant Intrinsic Decay Rates

Consider an amount of carbon entering the soil at some point in time, and that the decay rate of this carbon cohort decreases over time (e.g. as a result of chemical transformation or bio-physical stabilisation). For simplicity, we assume that the half life, τ, of this cohort increases linearly over time, i.e. half life $\tau = \tau_0 + \beta t$. The dynamics of a single pool that does not receive any input would then be described by the following equations, where k is a function of time t.

$$C(t) = C_0 \cdot e^{-k(t) \cdot t}, \ k(t) = \frac{\ln(2)}{\tau_0 + \beta \cdot t} \tag{12.3}$$

In contrast to the single pool model, here decomposition slows over time. Although it does not become zero, complete decomposition of the substrate will never be reached, even given infinite time, since the cohort will reach an asymptotic size greater than zero:

$$C(t) \overset{t \to \infty}{\to} C_0 \cdot e^{\frac{\ln(2)}{\beta}} > 0 \tag{12.4}$$

Equation 12.4 shows that this change to a dynamic k leads to a very different dynamic, where carbon does not decay completely but stabilises at a certain amount. It is evident that, if new carbon is continually added to the system, this would lead to an infinite accumulation of carbon. This very simple theoretical 'model' thus shows that a relaxation of the first-order kinetic model can allow long-term carbon sequestration. Another formulation, which also leaves an indecomposable residue, is the asymptotic model favoured by Berg (e.g. Berg and McClaugherthy 2003).

Conceptually, one could regard the models above as very special cases of the "continuous-quality" model (Bosatta and Ågren 1991; Ågren and Bosatta 1996; Ågren et al. 1996), which postulates the existence of litter cohorts with defined quality q, where biomass quality diminishes by a function of q during each cycle. Both the microbial efficiency e and the growth rate u then depend on q, and the carbon dynamics of a homogeneous substrate is described as:

$$\frac{dC(t)}{dt} = -f_C \cdot \frac{1 - e(q)}{e(q)} \cdot u(q) \cdot C(t) \tag{12.5}$$

with f_C being the fraction of carbon in microbes. The expression on the right hand side of this equation is related to first-order kinetics; however, the rate constants depend on q, and q changes (decreases) over time. Depending on how fast $e(q)$ goes to zero, a single cohort may disappear completely or leave an indecomposable residue. Soil organic matter then consists of the residues of all litter cohorts that have entered that soil. If each litter cohort leaves an indecomposable residue, there will be an infinite build-up of soil organic matter if the litter input can be sustained. However, even if every litter cohort eventually disappears completely, there will be

a finite or infinite build-up of soil organic matter depending upon how rapidly $u(q)$ approaches zero with q relative to the behaviour of $e(q)$, and how rapidly the quality of a litter cohort decreases. For a more detailed discussion, the reader is referred to the literature cited above.

12.3.2.2 Rate Constant Dependent on Factors other than Pool Size

The decomposition models discussed above assume that the decay of a pool depends only on its own properties (first-order reaction kinetics). However, in (bio-)chemistry other reaction kinetics are more common, since the likelihood of multiple reactants coming together for a reaction often depends on the concentration of several reactants. Moreover, in biological systems, hence also the soil, reactions are catalysed by enzymes, so that reaction velocities may also depend on the activity of these. Fontaine and Barot (2005) turned the first-order reaction kinetics model of passively decaying soil organic matter (C_s) upside down by hypothesising that the decay of soil organic matter depends only on the microbial pool size (C_{mic}). The concept has been extended to differentiate between r- and K-strategists and interactions with the nitrogen cycle, but already their simplest formulation (Fig. 12.2) yields to a soil carbon pool never reaching steady state. The system can be described by the following two coupled differential equations (symbols as in Fig. 12.3):

$$\frac{dC_s}{dt} = (s - a) \cdot C_{mic}$$
$$\frac{dC_{mic}}{dt} = i + (a - s - r) \cdot C_{mic}$$

(12.6)

For time going to infinity the following equations can be derived:

$$\frac{dC_s}{dt} = \frac{i \cdot (s - a)}{-a + s + r}$$
$$C_{mic,ss} = \frac{i}{-a + s + r}$$

(12.7)

Hence, while the microbial pool reaches a steady state, the soil carbon pool continues to increase or decrease linearly with a rate related to carbon input, microbial efficiency and mortality rates. A possibly more realistic representation might be to include a limitation of the carbon decay by microbes and the carbon pool itself. For instance, a generalisation of the introductory carbon balance model (Fig. 12.1) would be the following two equations:

$$\frac{dC_1}{dt} = I - k_1 \cdot C_1$$
$$\frac{dC_2}{dt} = h \cdot k_1 \cdot C_1 - \left[\left(\frac{C_1}{C_2} \right)^{\alpha} \cdot k_2 \right] \cdot C_2$$

(12.8)
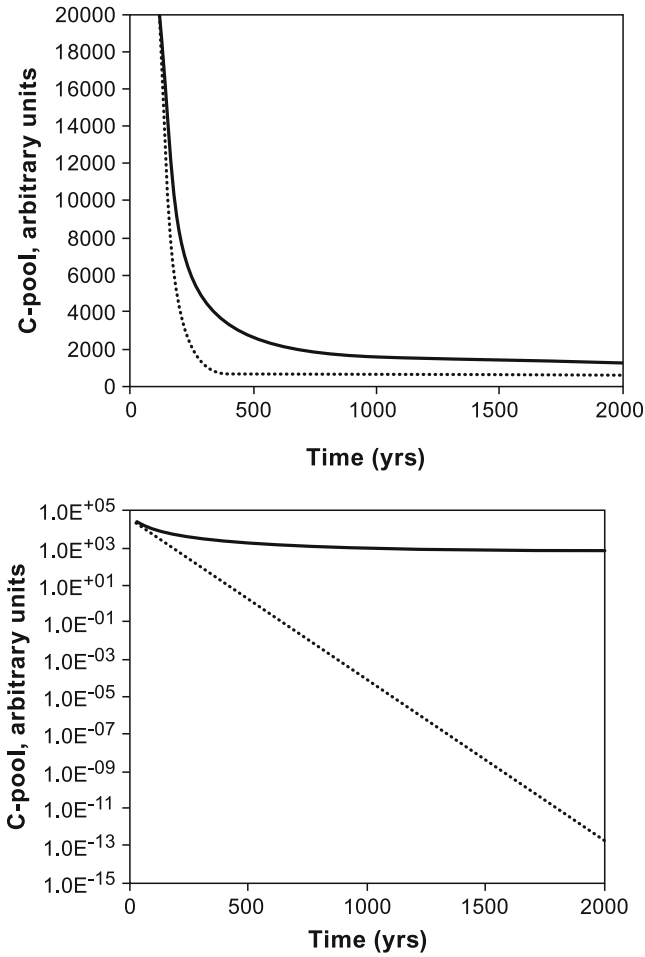
Fig. 12.2 Single pool vs single cohort decomposition dynamics (without input to the pool/cohort). *Solid line* According to first order reaction kinetics with $k = 0.02$ year^{-1} (i.e. a half time of 35 years), *dotted line* according to Eq. 12.5 with the same initial half time $\alpha = 0$ and $\alpha = 0.15$. *Upper panel* Linear y-axis, *lower panel* logarithmic

Fig. 12.3 Decomposition model, where the decay of soil carbon (C_s) does not depend on its own pool size, but on the microbial pool (C_{mic}), which itself depends mainly on the input of fresh material (i). *r, s, a* Rate constants that describe utilisation of substrate by microbes and their mortality. After Fontaine and Barot (2005)
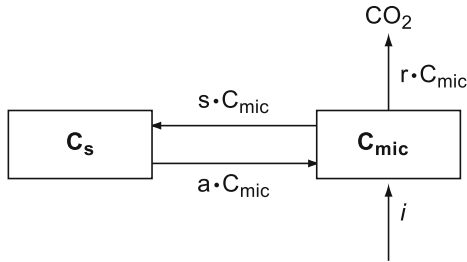
with the only difference being that the decay constant of the slow pool (C_2) is now dependent on the ratio of fresh (supports biomass) and slow pool sizes, parameterised with the exponent α.

Over longer time periods ($t \gg 1/k_1$), the fast pool can be considered as being in steady state (i.e. $C_{1,ss} = I/k_1$), the dynamics of the slow pool can be described by

$$\frac{dC_2}{dt} = h \cdot I - \left[\left(\frac{I/k_1}{C_2} \right)^{\alpha} \cdot k_2 \right] \cdot C_2 = h \cdot I - \left(I/k_1 \right)^{\alpha} \cdot k_2 \cdot C_2^{1-\alpha} \qquad 12.9$$

with the long-term dynamics depending on the parameter α. With $\alpha \neq 1$ the system is behaving simply as a classical first-order kinetic pool model, asymptotically reaching a steady state, while with $\alpha = 1$ the dynamics becomes analogous to those presented by Fontaine and Barot (2005), where the decay rate is independent of C_2 and the pool size increases linearly over time, never reaching a steady state.

Hence, whether or not a steady state is reached can be built into the model formulation a priori, but will in certain cases depend on specific parameter values. The classical pool models are such that steady states will always be reached, whereas Berg's asymptotic model always produces a non-steady state. Both the generalisation of the ICBM suggested above and the Fontaine-Barot model allow for finite and infinite soil organic matter stores. However, both share the unsatisfactory property of being structurally unstable in the sense that it is only for one single parameter value that the generalisation of the ICBM model leads to anything other than finite soil organic matter stores and the Fontaine-Barot model lacks steady state (there will either be an infinite amount of soil organic matter or none at all). Of the models discussed here, the continuous-quality model is the most general in that it allows all possibilities and is stable over large ranges of parameter values. One challenge is to discriminate the models with observed data as indicated in Fig. 12.4. The single-pool first order model can be excluded, as has long been known (Jenny 1941; Meentemeyer 1978). However, the two alternative models and the different parameterisations of the generalised ICBM model (gICBM) can barely be distinguished over the first 300 years in time. In fact, the gICBM model with $\alpha = 1$, which is analogous to the simplest Fontaine and Barot model, is almost indistinguishable over the whole time series (data not shown).

12.3.3   Complicating Factors not Considered

Even simple model formulations, which all bear some plausibility and have been applied in various studies, yield different predictions of whether long-term carbon uptake in forest soils is possible or not. Furthermore, there are certainly a number of additional factors that easily introduce further interactions that may result in additional non-steady state trajectories. Although beyond the scope of this theoretical chapter, we will briefly mention some of these, including references to the literature:
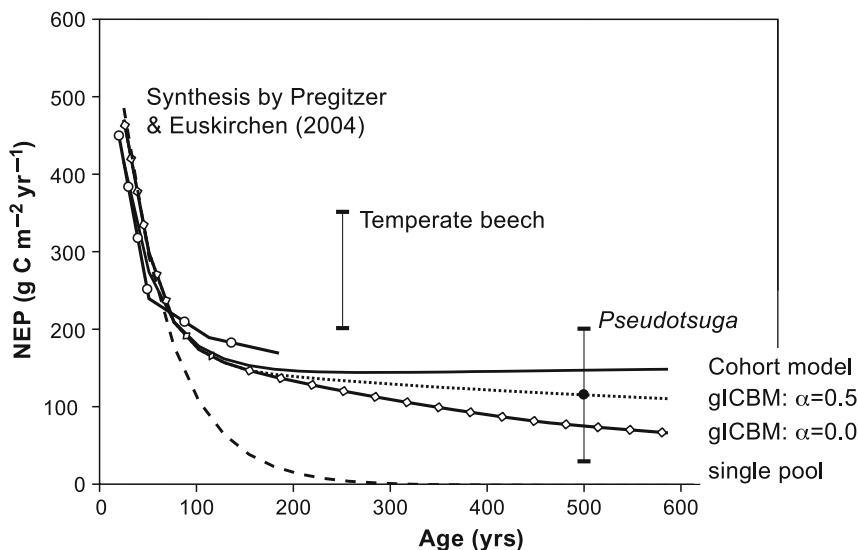
Fig. 12.4 Trajectory of net ecosystem productivity (NEP) as predicted by different types of models with some observed values as in Fig. 12.2. *Dashed line* One pool first-order kinetics model, *solid lines* results from the generalised ICBM model (gICBM) with varying α (cf. Fig. 12.2 and text) and the cohort model. The *line/open circles* contains averaged data from Pregitzer and Euskirchen (2004), and is augmented by two example studies from Knohl et al. (2003) (temperate beech) and Paw U et al. (2002)/Harmon et al. (2004) (*Pseudotsuga*) for illustrative purposes

- Interactions with the nitrogen cycle might lead to retardation of decomposition through either a limitation or excess of nitrogen (e.g. Berg and Matzner 1997; Magill and Aber 1998; Zak et al. 2006).
- Several carbon stabilisation mechanisms via interactions with the mineral soil matrix have been discussed (e.g. Torn et al. 1997; von Lutzow et al. 2006). It is not clear to what extent such interactions are included in model parameters.
- Transport of carbon into deeper layers where unfavourable conditions for decomposition prevail (e.g. energy or oxygen limitation). A particular example is that of peatlands, where the addition of new litter can push the underlying soil organic matter below the water table thus drastically altering environmental conditions (e.g. Frolking et al. 2001).
- Fires can produce very stable carbon compounds (e.g. charcoal) (Czimczik et al. 2003; Gonzalez-Perez et al. 2004).

12.4   Perspectives for a New Generation of Models

It is probably impossible to determine experimentally whether soils have a non-limited capacity to store carbon, not only because it can take several thousands of years to reach a potential steady-state but also because anthropogenic disturbances

and climatic changes may have disrupted previous steady states. Moreover, as discussed in Sect. 12.1.3.2, it is not possible to discriminate the different models on the basis of long-term observations of organic stocks. Indeed, such observations are sparse and the variability of measurements precludes testing of the different models. However, these limitations will not prevent us from evaluating the storage capacity of the ecosystems, but such evaluation requires understanding and modelling of the mechanisms controlling long-term carbon accumulation in soils, and testing of these models at the mechanism scale. In the following, we present two tracks of research and experiments that could substantially improve the quality of predictions of future models.

12.4.1 Models Connecting the Decay Rate of Soil Carbon to the Size, Activity and Functional Diversity of Microbe Populations

The use of the classical first-order reaction kinetic, which assumes that the decay rate is limited by the size of the carbon pool, is relevant when describing the decomposition of energy-rich litter compounds. Indeed, these compounds induce a rapid growth of microbes and the reaction velocity is quickly limited by the amount of remaining substrate (Swift et al. 1979). However, this limitation does not apply to the recalcitrant fraction of soil organic matter (Schimel and Weintraub 2003; Fontaine and Barot 2005). In contrast, the decay rate of recalcitrant carbon seems limited by the size of the microbe population since less than 5% soil carbon compounds are colonised by soil microbes, and the increase in microbe populations induced by the supply of fresh carbon accelerates the decomposition of soil carbon (Paul and Clark 1989; Kuzyakov et al. 2000). Some recent theoretical work has shown that including microbial dynamics and functional diversity in models profoundly changes predictions and allows some important empirical results, such as the long-term accumulation of carbon in ecosystems, to be explained (Fontaine and Barot 2005; Wutzler and Reichstein 2007). These results should stimulate the building of a new generation of models connecting microbial ecology to biogeochemical cycles, and lead these two fields to combine their scientific knowledge. A first step towards such models is to find an equation where the decay rate of recalcitrant carbon is controlled by the size of active microbe populations. Several equations are possible, such as this adapted version of the Michaelis–Menten equation:

$$\frac{dC_s}{dt} = \frac{a \cdot C_{mic} \cdot C_s}{K + C_s} \qquad\qquad 12.10$$

which assumes that the decay rate of soil carbon can increase infinitely as microbial biomass (C_{mic}) increases, and the ratio-dependent equation (Arditi and Saiah 1992),

$$\frac{dC_s}{dt} = \frac{a}{\frac{K}{C_s} + \frac{1}{C_{mic}}} \qquad 12.11$$

which considers that the size of the soil carbon pool (C_s) and the size of microbial biomass (C_{mic}) limit the decay rate. In these equations, a is the consumption rate of recalcitrant carbon by the decomposers, and K is a constant. The type of equation and the value of parameters greatly influence the predictions of models (Arditi and Saiah 1992; Schimel and Weintraub 2003). However, it is now possible to manipulate the size of the microbial biomass and to measure the decay rate of recalcitrant old soil organic matter thanks to a recent method based on the supply of dual-labelled (^{13}C and ^{14}C) cellulose (Fontaine et al. 2007). Moreover, the size of the soil organic matter pool can be manipulated by diluting soil with sand. This means that it becomes feasible to determine how the size of soil carbon pool and that of microbe populations co-limit soil carbon decay rate and to discriminate between different equations. Determining the value of parameters requires that populations of soil organic matter decomposers be identified among all other populations stimulated by the addition of cellulose. Again, the recent development of molecular methods such as the sequencing of microbial DNA and the possible separation of [13]C- and ^{12}C-DNA makes such identification possible (Radajewski et al. 2000; Bernard et al. 2007). Therefore, we suggest that microbiologists and geochemists should set up joint experiments under controlled conditions in order to build a more realistic and microbe-oriented mathematical description of recalcitrant soil carbon decomposition.

12.4.2 Determining the Mechanisms Stabilising Recalcitrant Soil Carbon

Although little is known about the stability of soil carbon compounds, a central question is whether the stabilisation of soil carbon necessarily involves a chemical or physical linkage with soil minerals. If soil carbon persists only when it is bound to soil minerals, and these exist in forms that microbes cannot access, then the storing capacity of soils is limited. Indeed, the amount of carbon that minerals can fix depends on the specific area of these minerals (Eusterhues et al. 2005), which determines the number of binding sites available and the cationic exchange capacity of the minerals (Wattel-Koekkoek and Buurman 2004), which in turn determines the strength with which carbon is retained. More globally, theory predicts that the storing capacity of many soils worldwide has reached its maximum. Moreover, this capacity is likely to decrease due to a decreasing capacity of minerals to fix carbon induced by the weathering of minerals (Torn et al. 1997).

Other theories and experiments, however, suggest that the stability of soil carbon also results from biochemically recalcitrant compounds (Ågren and Bosatta 1996;

Stout et al. 1981; Blondeau 1988; Fontaine et al. 2007). These compounds may persist in soils because the acquisition of energy from such substrates cannot sustain microbial activity. Under such circumstances, theory predicts that soils have no limited capacity to accumulate soil carbon (Fontaine and Barot 2005; Wutzler and Reichstein 2007).

We conclude that the storing capacity of soils depends greatly on the mechanisms involved in the stabilisation of organic carbon and that these mechanisms should be explicitly described in future models. Further research is needed to determine whether a linkage between organic carbon and minerals is necessary to stabilise carbon over a long-term timescale. It would be particularly interesting to measure the turnover of free recalcitrant soil carbon using ^{14}C methods and to determine which factors limit this turnover. Moreover, the ^{14}C dating of soil carbon pools indicates that, irrespective of the mechanism of carbon stabilisation (mineral stabilisation vs biochemical stabilisation), the decomposition of organic carbon is slowed but not stopped in surface layers. This result can be explained by the fact that some microbe populations are able to degrade recalcitrant compounds with their enzymes because they use fresh carbon (litter, exudates) as a energy source (Fontaine et al. 2007). Future theoretical and experimental studies are needed to understand the benefit for microbes of decomposing these recalcitrant compounds, and the factors that could modulate the use of such substrates by the soil microbial community. This means that understanding the capacity of soils to store carbon finally requires an understanding of microbial ecology and biology.

12.5   Conclusions

As shown here, several possible formulations of soil carbon dynamics allow situations where a steady state of soil carbon is never reached. Hence, from a theoretical point of view, there is no justification for excluding the possibility of long-term old-growth forest carbon uptake as has sometimes been suggested from the classical pool model perspective. Rather, we need initiatives and experimental designs that can distinguish between – and potentially exclude – the modelling paradigms that currently co-exist. Since there are already indications that classical first-order kinetic carbon models have severe limitations (because they do not adequately describe the role of soil biota and the interaction between microbes, soil organic matter and soil minerals), the results and predictions from these models – at least in forests – should be approached carefully, with critical assessment of the limitations, and they should not be used for long-term extrapolation. Nevertheless, their merit for assessments and short-term predictions is undoubted (e.g. Kätterer and Andrén 1999; Falloon et al. 2000). There is also a clear need to start to examine the fundamentals of how decomposers attack soil organic matter and to what extent decomposer biomass is dependent upon total soil organic matter or only a fraction of it. The Fontaine-Barot model (Fontaine and Barot 2005) is one example of a

model that takes a different perspective. The models by Weintraub and Schimel (2003) and Neill and Gignoux (2006) are two other alternatives, as discussed together with other models in Wutzler and Reichstein (2007).

From a scientific-theory perspective the example of soil carbon storage in old-growth forests reminds us that models should never be confounded with the truth and that they must be critically examined and tested again and again. Otherwise models can turn into fairy tales.

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**Part IV
Biomes**

Chapter 13
Old-Growth Forests in the Canadian Boreal: the Exception Rather than the Rule?

Yves Bergeron and Karen A. Harper

13.1   Introduction

Fire is one of the most important ecological processes in North American boreal forests (Johnson 1992; Payette 1992). Forest fire regimes, defined by fire frequency, size, intensity, seasonality, fire type and severity (Weber and Flannigan 1997) have a significant influence on many boreal forest attributes. Fire regimes affect the distribution of species (Asselin et al. 2003; Le Goff and Sirois 2004), age-class distribution of stands (Bergeron et al. 2001), characteristics of wildlife habitats (Thompson et al. 1998), vulnerability of forests to insect epidemics (Bergeron and Leduc 1998), and net primary productivity and carbon balance (Peng and Apps 2000; Wirth et al. 2002).

Our understanding of the fire regimes that burn forests throughout the Canadian boreal zone is still fragmentary, making it inappropriate to generalise about fire frequency for the entire region. For example, it has often been assumed that large-scale fires that produce even-aged stands are not only omnipresent but frequent in boreal forests. However, it has become increasingly evident that short fire cycles apply only to parts of the boreal forest, and that the regional situation is considerably more complex (Bergeron et al. 2004). Nonetheless, the assumption of frequent large-scale fires has been used to justify the use of clear-cut harvesting with short rotations in most boreal forests, resulting in a reduction in the proportion of older forest stands.

One important consequence of the variability in fire frequency in the boreal zone is the amount of forests that can reach the status of old-growth forests between fire events. As the time needed to reach old-growth is difficult to define (see Chap. 2 by Wirth et al., this volume), we adopt a pragmatic definition and consider forests over 100 years after disturbance as old-growth. The post-fire cohort of trees is usually no longer dominant after 100 years and normal harvesting rotations are less than 100 years in most boreal forests. In this chapter, we discuss (1) the relative abundance of old-growth in the Canadian boreal forest, (2) the prevalence of old-growth attributes in older forests compared to younger post-fire stands, and (3) the

implications of the importance and uniqueness of old-growth boreal forest in the context of current forest management.

13.2   Abundance of Old-Growth Forests

We calculated the proportion of forests of different ages in different boreal forest regions using historical fire frequencies (or fire cycles, i.e. the inverse). We assumed a constant fire frequency and a fire hazard independent of stand age (as commonly reported for boreal ecosystems controlled by stand-replacing fires; Johnson 1992) to predict the proportion of forest that can reach a defined age class (Fig. 13.1). Historical burn rates were determined from a literature review using available forest fire history studies in North American boreal forest (Bergeron et al. 2004; Fig. 13.2). Most of these studies used dendrochronology to estimate time since fire, and represent the average fire frequency over the last 300 years. Current fire frequency (last 50 years) from a Canada-wide database (Stocks et al. 2002) was used for the Boreal cordillera, Taiga cordillera, Taiga plain and Hudson plains ecozones (Ecological Stratification Working Group 1996) since no studies on historical fire frequency were available for these areas. Average age of the forest (time since fire) or, if not available, fire cycle before large clear-cutting activities began were used to estimate historic burn rates. The average age of the forest was preferred to the historic fire cycle because it integrates climatically induced changes in fire frequency over a long period, and because it is easier to evaluate than a specific fire cycle (Bergeron et al. 2001). The inverse of average age (or fire cycle) was used as an estimator of the annual historic burn rate.

The average fire cycle for different ecozones (Table 13.1) is highly variable, ranging from 52 years in the western boreal shield to 813 years in the Hudson plain ecozone. Differences are due mainly to a drier climate in the west since the dominant tree cover is relatively similar across the Canadian boreal biome (conifers; except for aspen, which dominates the boreal plain).
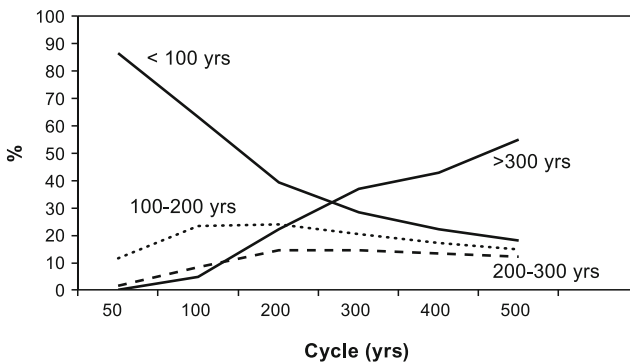
Fig. 13.1 Proportion of forests older than 100, 200 and 300 years for increasing fire cycles

Fig. 13.2 Location of the 18 studies (see Bergeron et al. 2004 for specific references) used to estimate fire frequency throughout ecozones of the Canadian boreal forests. Current fire frequency (last 50 years) was used for ecozones where no long-term studies were available

Table 13.1 Historical fire frequency (% of the area burnt per year) and – in parentheses – its inverse the fire cycle) together with the proportion of forests older than 100, 200 and 300 years for the Canadian boreal ecozones

Ecozones	Historical (% year^{-1})	Area (km^2)	% Area > 100 years	% Area > 200 years	% Area > 300 years
Montane Cordillera	0.99 (101)	490,184	37	14	5
Boreal cordillera[a]	0.39 (255)	470,502	68	46	31
Taiga cordillera[a]	0.20 (495)	267,029	82	67	55
Taiga plain[a]	0.70 (142)	645,014	49	24	12
Boreal plain	1.48 (68)	733,170	23	5	1
Hudson plains[a]	0.12 (813)	374,482	88	78	69
Taiga shield west	0.85 (118)	631,679	43	18	8
Boreal shield west	1.92 (52)	946,260	15	2	<1
Boreal shield east	0.77 (131)	931,062	47	22	10
Taiga shield east	0.6 (166)	758,763	55	30	16
Total		6,148,148	45	24	15

[a]Current fire frequency (last 50 years) was used for these ecozones as no long-term studies were available

Using relationships between fire cycle and age-classes (Fig. 13.1), we then compiled the expected proportion of forests over 100, 200 and 300 years old that would be present in different parts of the Canadian boreal forests given no additional

or anthropogenic disturbances (Table 13.1). The results show that, despite a large variation from east to west, a large proportion of the boreal landscape is composed of forests over 100 years old. Assuming these studies are representative of the different ecozones, and taking into account the size of the ecozones, forests over 100, 200 and 300 years since fire should cover 45%, 24%, and 15%, respectively, of the boreal landscape in Canada. Since most dominant tree species in boreal forests are short-lived, we can conclude that a significant proportion of Canadian boreal forests is composed of stands dominated by the late-successional species typical of old-growth forests. Although significant everywhere, these proportions are distributed unevenly in Canada. As fire cycles are longer in eastern Canada, old-growth forests are more abundant.

These estimates of the amount of older forests are conservative since they include only those areas that were spared from fire by chance; they do not include patches of old-growth forest that can be found inside fire perimeters or associated with fire breaks (Cyr et al. 2005). The proportion of fire skips inside burnt perimeters can range between 5% and 10% of the burnt areas (Eberhart and Woodard 1987; Kafka et al. 2001), and some skips, mainly those associated with wet areas, can be spared for several fires. Moreover, our study does not include differences due to topography or vegetation that could locally influence the presence of old-growth forests. These should be taken into account in any regional assessment of the abundance of old-growth forests.

13.3   Characteristics of Old-Growth Boreal Forests

It is clear from the proportions of forests in different age classes that all stages of development are present in boreal forests. This diversity of stands of different ages most likely contributes to regional biodiversity by providing stands with different habitat features (Harper et al. 2002). In order to identify the unique features of old-growth forests, it is important to understand stand development, and the changes in structure and composition of forest stands following a disturbance. Here we focus on the old-growth stage, although we assess trends throughout stand development to determine when typical old-growth attributes may be prominent.

The final old-growth stage is thought to be characterised by distinctive composition, structure and processes compared to younger stages of development. To summarise the main features reviewed in this volume (see Chap. 2 by Wirth et al., this volume), old-growth forests are considered to be compositionally complex with a high diversity of long-lived shade-tolerant tree species (Spies and Franklin 1988; Kneeshaw and Burton 1998; Wells et al. 1998; Moessler et al. 2003). Typical old-growth structural attributes consist of abundant large or old structural elements including trees, snags and logs (Spies and Franklin 1988; Kneeshaw and Burton 1998; Wells et al. 1998), high structural diversity, particularly of tree ages or sizes and of decay stages of snags and logs (Kneeshaw and Burton 1998; Wells

et al. 1998; Moessler et al. 2003), a complex, heterogeneous spatial pattern with abundant canopy gaps, and a wide range of tree spacing and patchiness (Kneeshaw and Burton 1998; Wells et al. 1998). Old-growth is often described as steady state or climax forest with a stable accumulation of biomass and a net growth close to zero (Kneeshaw and Burton 1998; Wells et al. 1998; Moessler et al. 2003), dominated by small-scale disturbances with tree regeneration in gaps (Kneeshaw and Burton 1998; Moessler et al. 2003). Other processes associated with old-growth characteristics include slow tree growth and high understorey productivity (Kneeshaw and Burton 1998; Wells et al. 1998).

Old-growth forests, particularly old-growth boreal forests, may not share all these characteristics. Rather than judging the 'old-growthness' of the final stage of development of boreal forests using definitions (Wells et al. 1998) or an old-growth index (Spies and Franklin 1988; Kneeshaw and Burton 1998), we assess the uniqueness of old-growth forests in the Canadian boreal for the ensemble of old-growth characteristics listed above and described in the literature for vegetation structure and composition. Here we define old-growth forests as the final stage of development along a chronosequence rather than by a lack of human disturbance, stand age relative to forest management or aesthetic attributes. We focus on types of boreal forest in Canada for which there have been studies of stand development. By examining trends in forest structure and composition with time since fire in different types of Canadian boreal forests, we ask the question: are these old-growth attributes characteristic of the oldest stage of development in boreal forests?

13.3.1 Old-Growth Black Spruce Boreal Forest

Old black spruce forest in the Clay Belt region of northeastern Ontario or in northwestern Quebec appears to be an exception to what we commonly perceive as old-growth even at first glance. The aesthetic vision of a tall majestic forest with large trees, large broken stumps and large logs that serve as substrate for regenerating seedlings does not apply here. But how many of the old-growth attributes apply when we examine trends in forest structure and tree species composition through different stages of stand development?

In black spruce forests in the Clay Belt region, there can be a transition in tree species composition from shade-intolerant deciduous species such as *Populus tremuloides, Betula papyrifera* and *Pinus banksiana* to shade-intolerant *Picea mariana* with some *Abies balsamea* (Harper et al. 2002, 2003). However, in sites dominated by *Picea mariana* immediately after fire, structural development is not accompanied by a change in species composition. Other old-growth attributes related to species composition do not apply to this ecosystem. Tree species diversity is much lower in older black spruce forests compared to young and intermediate-aged forests (Fig. 13.3a). Indeed, most forest stands in this region contain over 75% *Picea mariana* (Harper et al. 2002, 2003). There were also fewer understorey
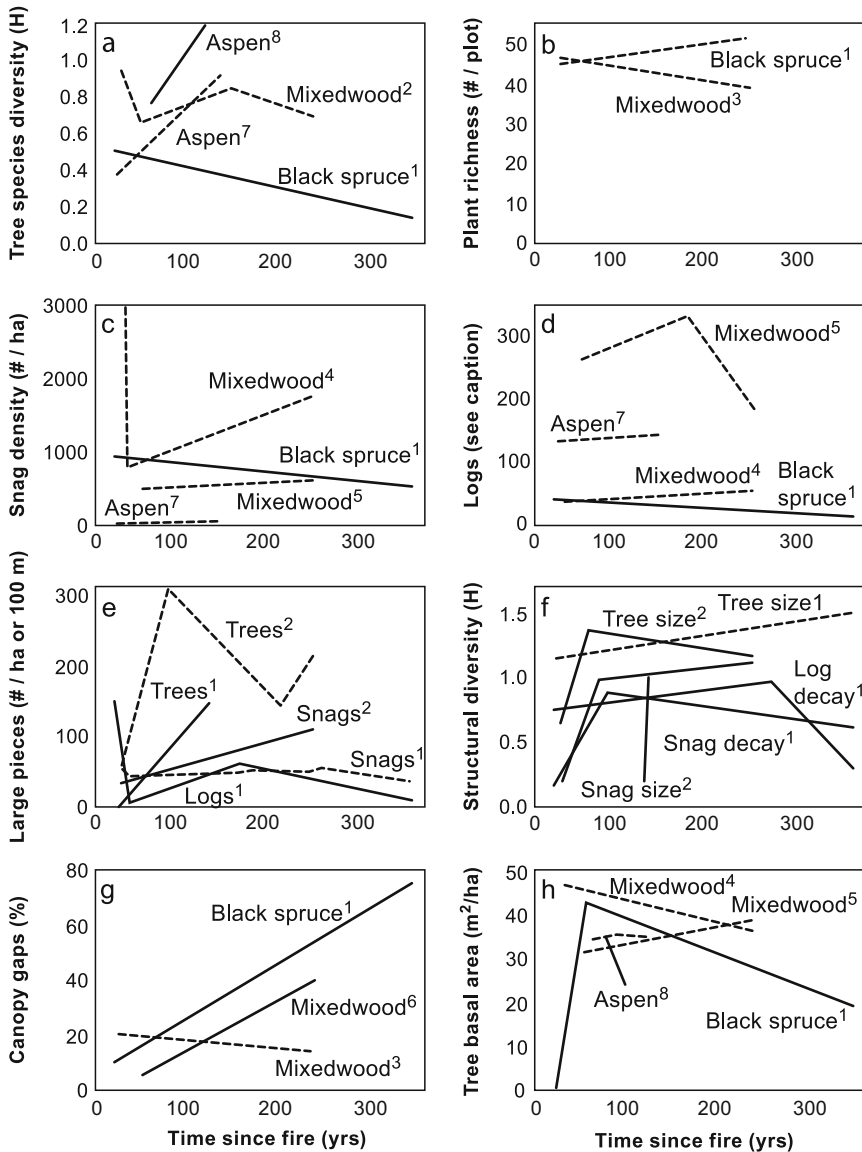
Fig. 13.3a–h Trends in typical old-growth attributes with time since fire for different types of boreal forest. **a** Tree species diversity calculated using the Shannon index based on live tree basal area except for aspen[7], which was based on the density of trees ≥ 10 cm diameter at breast height (dbh). **b** Understorey species richness calculated as the total number of vascular species in a plot. **c** Density of snags of unspecified size for black spruce[1] and mixedwood[4], ≥ 5 cm dbh for mixed-wood[5] and ≥ 10 cm dbh for aspen[7]. **d** Abundance of logs calculated as the number per 100 m for black spruce[1], log load in tons ha^{-1} for mixedwood[4], the number ≥ 5 cm diameter ha^{-1} for mixedwood[5], and the number ≥ 11 cm diameter ha^{-1} for aspen[7]. **e** Density of large components (≥ 20 cm dbh or diameter) for black spruce[1] and mixedwood[2] **f** Structural diversity

species in the oldest age class and none exclusive to old-growth (Harper et al. 2003); the overall non-significant trend of increasing vascular plant richness (Fig. 13.3b) masks a peak in the intermediate age classes (Harper et al. 2003). The development of a thick *Sphagnum* moss layer in old-growth black spruce forest can hinder establishment of some vascular plants while favouring reproduction of *Picea mariana* through layering (Boudreault et al. 2002; Harper et al. 2003).

Older black spruce forests lack some of the key structural old-growth attributes of abundant deadwood and large structural components. The density of both snags and logs decreases during stand development (Fig. 13.3c, d). Likewise, the abundances of large trees, snags and logs decrease towards old-growth and were highest in intermediate stages (Fig. 13.3e). Paludification – the process in which the development of thick moss and organic layers lowers soil temperature, increases soil moisture and decreases nutrient availability (Van Cleve et al. 1983; Paré and Bergeron 1995; Gower et al. 1996; Fenton et al. 2005) – likely contributes to the different structure of old-growth black spruce forest. Due to the decrease in site productivity (Simard et al. 2007), *Picea mariana* trees that establish in later stages tend to be smaller and less numerous, leading to overall lower abundance of deadwood and large trees (Harper et al. 2003, 2005). Structural diversity for tree sizes (also for Quebec's Côte Nord, Boucher et al. 2006), snag decay classes and log decay classes also decrease in the later stages of development, resulting in less diverse old-growth (Fig. 13.3f).

Old-growth black spruce forest is more spatially heterogeneous compared to younger forests. Old-growth attributes of more abundant canopy gaps (Fig. 13.3g), a wide range of tree spacing as indicated by greater gap size diversity, more fine-scale heterogeneous tree cover and understorey patchiness were all present in older black spruce forests relative to younger forests (Harper et al. 2006). During stand development, gaps of different sizes formed by tree mortality and common small-scale disturbances such as spruce budworm and windthrow are filled in slowly due to poor regeneration and growth, leading to greater gap abundance and clumping of trees at fine scales (Harper et al. 2003, 2006).

Processes in the final stage of development of black spruce forests are unique to the boreal rather than typical of old-growth. Tree basal area, an indication of productivity, is lower in older forests (Fig. 13.3h). Low tree basal area is likely

Fig. 13.3 (Continued) calculated using the Shannon index on trees of different sizes and on snags and logs in different decay stages for black spruce[1] and on trees and snags of different sizes for mixedwood[2]. **g** Proportion of canopy gaps. **h** Tree basal area. *Lines* Best-fit linear or piecewise linear regression curves to data from different studies as indicated by superscripts: *1* Harper et al. (2003, 2005 or 2006); *2* Bergeron (2000); *3* DeGrandpré et al. (1993); *4* Hély et al. (2000); *5* Park et al. (2005); *6* Kneeshaw and Bergeron (1998); *7* Lee et al. (1997); *8* Hill et al. (2005). Data were from tables or values reported in the text except for *1* and *2* where data were available from the authors. *Solid* and *dashed lines* indicate regressions that are significant and non-significant ($P=0.05$), respectively. The number of pieces for the linear regressions was decided subjectively based on visual inspection of the data. The number of sites is as follows: $n = 91$ for *1*, $n = 8$ for *2*, $n = 8$ for *3*, $n = 48$ for *4*, $n = 6$ for *5*, $n = 7$ for *6*, $n = 3$ for *7*, $n = 10$ for *8*

due to slower growth since increased mortality would have resulted in greater deadwood abundance, which was not observed. Although low productivity is considered uncharacteristic of old-growth forest (e.g. Wells et al. 1998), it may be globally widespread in the long term (after thousands of years, Wardle et al. 2004). The decrease in tree basal area and changes in other structural attributes in the final stage of development (Harper et al. 2005; Lecomte et al. 2006a) indicate that older black spruce forests are not in a typical steady state but continue to undergo structural changes. Aboveground biomass accumulation and net annual growth are not stable but are negative due to the decline in productivity brought about by paludification (Harper et al. 2003; Lecomte et al. 2006b). Instead, biomass accumulates in the forest floor with time (Lecomte et al. 2006b). As in other forests, small-scale disturbances such as windthrow and spruce budworm outbreaks increase throughout stand development but there is an exceptional decline in the oldest forests (Harper et al. 2002, 2003). In these oldest stands, trees grown in more open conditions are less prone to windthrow (Harper et al. 2002). Regeneration of *Picea mariana* in gaps was more common in older black spruce forest (Harper et al. 2005), as described for other old-growth forests.

13.3.2 Old-Growth Mixedwood Boreal Forest

Stand development in mixedwood boreal forest throughout Canada is characterised by the succession from shade-intolerant tree species such as aspen, birch and willow to shade-tolerant species such as balsam fir, white spruce and white cedar (Bergeron 2000; Awada et al. 2004). Tree species diversity is greatest in the intermediate stages of development during which the transition occurs (Fig. 13.3a, Park et al. 2005). There is evidence of more understorey plant species in older mixedwood forests compared to younger forests in Alberta (Timoney and Robinson 1996) but not in Quebec (Fig. 13.3b, De Grandpré et al. 1993; Bartemucci et al. 2006; see also Chap. 6 by Messier et al. this volume).

Trends in deadwood abundance with time are not very conclusive. More snags were found in either intermediate stages (Timoney and Robinson 1996) or in later stages (Awada et al. 2004; Hély et al. 2000; Park et al. 2005); however, trends for which we were able to obtain data are not significant (Fig. 13.3c). Trends that show greater log abundance in younger or intermediate stages are also not significant (Fig. 13.3d, Hély et al. 2000; Park et al. 2005); although Timoney and Robinson (1996) found more abundant logs in later stages of stand development. Data from Bergeron (2000) show more large trees in intermediate-aged stands but more large snags in older stands (Fig. 13.3e). Similar trends were found for structural diversity, with greater tree structural diversity in the intermediate stages and greater snag diversity in older stands (Fig. 13.3f). Tree structural diversity based on crown width was also greatest in intermediate age classes (Paré and Bergeron 1995). However, old-growth balsam fir forests in Newfoundland are uneven-aged with a multi-layered

canopy (McCarthy and Weetman 2006). Fir stands in Quebec's Côte Nord also exhibited increasing tree structural diversity with age (Boucher et al. 2006).

A greater proportion of canopy gaps was found with time since disturbance in Quebec's boreal mixedwood by Kneeshaw and Bergeron (1998) and Park et al. (2005) but not by DeGrandpré et al. (1993; Fig. 13.3g). Bartemucci et al. (2006) found greater canopy light transmission levels in older forests than in younger forests, again indicating more open canopy cover. In terms of other aspects of spatial pattern, understorey patchiness – a typical old-growth attribute – was found in intermediate stages rather than in the oldest forests in boreal mixedwood (De Grandpré et al. 1993). However, Awada et al. (2004) found greater patchiness of white spruce seedlings in older (>100 years) as compared to younger mixedwood forests in Saskatchewan.

Results on processes in old-growth mixedwood forests are varied. Bergeron (2000) found regeneration of dominant trees was greatest in intermediate stands, while Awada et al. (2004) found no trend. Trends of increasing and decreasing tree productivity with time since disturbance in mixedwood forests were not significant (Fig. 13.3h; Hély et al. 2000; Park et al. 2005). Greater deadwood abundance in intermediate or later stages as described above likely indicates increasing mortality in these forests. Understorey productivity decreased steadily during stand development (measured as cover; De Grandpré et al. 1993). Stable tree basal area in later stages of development, indicating a steady-state old-growth forest, was found in the mixedwood by Hély et al. (2000) and Park et al. (2005) but not by Awada et al. (2004) or Paré and Bergeron (1995), who found a decrease in later stages of development similar to that found in black spruce boreal forest. It is also interesting to note that tree basal area decreased even over a relatively short chronosequence from 80 to 110 years in unharvested balsam fir stands in eastern Canada (Sturtevant et al. 1997).

In mixedwood boreal forest, many old-growth attributes were found in the intermediate stage of development that accompanies the change in species composition from mostly deciduous to mostly conifer tree species; these attributes include: greater tree species diversity, understorey plant species richness, more abundant deadwood, more large trees, structural diversity, heterogeneous spatial pattern, regeneration of dominant species and tree basal area. The oldest mixedwood forests were characterised by a few typical old-growth attributes such as more abundant deadwood including large snags, more gaps, patchiness of white spruce seedlings, and tree basal area. Other typical attributes, such as understorey species richness and understorey productivity, were lacking.

Aspen forests can be considered as the early-successional stage of mixedwood boreal forest. However, recent studies have found evidence of self-replacement of aspen and gap dynamics in these forests (Cumming et al. 2000), suggesting that there may be an 'old-growth' aspen forest. We do not intend to resolve this issue here, but instead assess whether the oldest aspen forests contain typical old-growth attributes as compared to younger aspen forests. Although their defining feature – the dominance of a shade-intolerant tree species – contrasts with typical old-growth forests, older aspen forests do contain many typical old-growth attributes. Tree

species diversity is higher as more shade-tolerant species appear during succession (Fig. 13.3a, Lee et al. 1997; Hill et al. 2005); however, the diversity of understorey species was lower in older forests (Timoney and Robinson 1996). Although studies found more snags in either intermediate (Timoney and Robinson 1996; Lee et al. 1997) or later (Lee 1998) stages of development, logs were more abundant in older aspen forests compared to intermediate ages (Timoney and Robinson 1996; Lee et al. 1997). However, at least some of these trends were not significant (Fig. 13.3c,d). Large structural components including trees, snags and logs were all more abundant in older aspen forests (Lee et al. 1997; Lee 1998), and average tree diameter was also larger (Lee 1998). Similarly, measures of greater structural diversity and more heterogeneous spatial pattern were also found in the later stages of stand development including trees of multiple ages and sizes (Lee 1998; Cumming et al. 2000; Namroud et al. 2005), a greater diversity of snags and logs in different decay stages (Lee et al. 1997), a greater proportion of canopy gaps (Cumming et al. 2000; Hill et al. 2005) and greater heterogeneity (Cumming et al. 2000), although the latter was not found by Lee et al. (1997). There was no apparent trend for tree basal area with time since fire (Fig. 13.3h, Hill et al. 2005). Finally, Cumming et al. (2000) found evidence of the process of self-replacement or regeneration of the dominant tree species in older aspen forests. Overall, older aspen forests do seem to be typical of structurally diverse old-growth forests with gap dynamics and self-replacement of the dominant tree species. However, with time, they are likely either to develop into mixedwood stands or to succumb to fire.

13.3.3   Characterisation of Old-Growth Boreal Forests

A summary of the presence of typical old-growth attributes reveals differences among different types of boreal forest (Table 13.2). Black spruce and mixedwood forests each contain less than half of the old-growth attributes commonly listed in the literature. The attributes that do characterise these forests include the dominance of a shade-tolerant species in both forest types; greater structural diversity of deadwood; a heterogeneous spatial pattern and more abundant regeneration in black spruce forests; and more abundant deadwood including large snags and a more open canopy in mixedwood forests. The remaining old-growth attributes were often most abundant in intermediate stages and declined in the later stages of stand development, most likely due to paludification in black spruce forests or a change in species composition in mixedwood forests. The presence of typical old-growth attributes in older aspen forests, but in the intermediate stages of development of mixedwood forests, may be because these aspen forests have not yet undergone succession to shade-tolerant species.

   Certain typical old-growth attributes rarely characterise old-growth boreal forests, while others are more common. Our synthesis (Table 13.2) shows that characteristics such as greater tree species diversity, understorey plant species richness and tree productivity are rarely found in older boreal forests and cannot

Table 13.2 Assessment of typical old growth attributes (as listed in the literature) for different boreal forests: the presence or absence (*Y* yes, *N* no) in each boreal forest type is indicated. The number of studies (or site types for black spruce) with evidence of a characteristic more prominent in older forests compared to younger forests sampled in each study as a proportion of the number of studies who made the comparison is indicated in brackets. The ages of the forests are relative to each study; therefore the results represent general trends. Results are based on visual inspection of the results or statements made in different studies and do not necessarily indicate significance. Aspen forests are treated separately in this table although it should be noted that they are younger than the other forest types and are often considered an earlier stage of development towards mixedwood forests

Old growth attributes[a]	Black spruce[b]	Mixedwood[b]	Aspen[b]
Composition			
Long-lived shade tolerant species[i, iii]	Y (7/7)	Y (3/3)	N (0/1)
Greater tree species diversity[ii, iv]	N (1/7)	N (0/2)	Y (2/2)
Greater richness of understorey vascular plants[ii]	N (0/1)	N (1/3)	N (0/1)
Abundant or large structural elements			
More snags[ii]	N (1/6)	Y (3/4)	N (1/3)
More logs[ii]	(3/6)	Y (2/3)	Y (2/2)
Greater average tree diameter[ii]			Y (1/1)
More large trees[i, ii, iv]	N (2/6)	N (0/1)	Y (2/2)
More large snags[i, ii, iv]	N (2/6)	Y (1/1)	Y (2/2)
More large logs[i, ii, iv]	N (2/6)		
High structural diversity			
Multi-aged[ii, iii, iv]		Y (1/1)	Y (1/1)
Greater diversity of tree sizes[ii] or multilayered canopy[ii, iv]	N (2/7)	(2/4)	Y (2/2)
Greater diversity of snag decay stages and sizes[iii, iv]	Y (4/6)	Y (1/1)	Y (1/1)
Greater diversity of log decay stages and sizes[ii, iii, iv]	Y (6/6)		Y (1/1)
Heterogeneous spatial pattern			
Greater proportion of canopy gaps[ii, iv]	(2/4)	Y (3/4)	Y (2/2)
Larger average tree spacing[ii, iv]		N (0/1)	
Wider range of tree spacing[ii]	Y (1/1)	N (0/1)	
Greater degree of patchiness or heterogeneity[iv]	(1/2)	N (0/1)	(1/2)
Greater understorey patchiness[ii]	Y (1/1)	(1/2)	
Processes			
Greater tree productivity or basal area[ii]	N (2/6)	N (1/4)	N (0/1)
Greater understorey productivity or cover[ii, iv]		(1/2)	
Steady state[ii, iii, iv] as measured by no change in tree basal area	N (1/6)	(2/4)	Y (1/1)
More small-scale disturbances[iii]	N (0/7)		
More regeneration of dominant tree species[iii, iv]	Y (2/3)	N (0/2)	Y (1/1)

[a]References for typical old-growth attributes: *i* Spies and Franklin (1988), *ii* Wells et al. (1998), *iii* Moessler et al. (2003), *iv* Kneeshaw and Burton (1998). The following characteristics were not included: high habitat diversity (*ii*) or structural complexity (*iv*) (structural diversity measures were used instead); compositionally complex (*iv*) (tree species diversity was used instead); broken or deformed tops or boles and root decay (*ii*); pit and mound topography (*iv*); slow growth of trees (*ii*) (not usually measured or compared to other stages of development); and old trees (*i–iv*) (present in all older forests)

[b]References for forest types: *black spruce* Harper et al. (2002, 2003, 2005, 2006), Boucher et al. (2006); *mixedwood* De Grandpré et al. (1993), Paré and Bergeron (1995), Timoney and Robinson (1996), Kneeshaw and Bergeron (1998), Bergeron (2000), Hély et al. (2000), Awada et al. (2004), Park et al. (2005), Bartemucci et al. (2006), Boucher et al. (2006), McCarthy and Weetman (2006); *aspen* Lee et al. (1997), Lee (1998), Timoney and Robinson (1996), Cumming et al. (2000), Hill et al. (2005)

be used as criteria to identify old-growth in boreal forests (cf. Chap. 2 by Wirth et al., this volume). In addition, the old-growth stage of development cannot be considered a stable state, even in the absence of disturbance, since structural changes still take place, e.g. tree basal area decreases still occur over thousands of years in many ecosystems (Wardle et al. 2004). Some typical old-growth attributes that show more promise as criteria for boreal forests include a greater abundance of logs, multi-aged stands, greater structural diversity of deadwood and more open canopy with gap dynamics. However, even these characteristics might not be reliable given longer time spans with no recurrence of fire. Instead, it may be more appropriate to use indices for old-growth such as the cohort basal area proportion (a function of the basal areas of the initial and replacement cohorts, Kneeshaw and Gauthier 2003) to define the old-growth stage, especially for boreal forests. It is important to note that even though old-growth boreal forests may lack some of the typical attributes found in other old-growth forests, they still contain characteristics such as structural diversity that are unique to this stage of development and potentially important to regional biodiversity.

13.4   Implications for Forest Management

At first glance, an even-aged management approach would appear to resemble the natural disturbance regime if timber harvest rotation age approaches that of the natural fire cycle. However, a full even-aged regulation does not produce an age-class distribution similar to that of natural distribution, even for forest rotations that are as long as the fire cycle. Indeed, in an even-aged management context, a forest is referred to as fully regulated when stand age classes are uniformly distributed throughout a territory. Thus, in theory, after one complete rotation, no stands over the rotation age will exist. The same region submitted to forest fires intense enough to generate even-aged stands will, at equilibrium, present a completely different age class distribution of forest stands. Assuming that the probability of burning is independent of stand age, the forest age structure will, again theoretically, resemble a negative exponential curve, with about 37% of forests older than the fire cycle (Johnson and Van Wagner 1985). This means that, for a fire cycle and a forest rotation of similar duration, forest management will not spare any forest that exceeds rotation age whereas fire will maintain over 37% of the forest in older age classes. This difference is fundamental because it implies that full regulation in an even-aged management regime will result in the loss of mature- to old-growth forests. As discussed in the previous section, these intermediate-aged and older forests have unique characteristics that could be essential for the maintenance of biodiversity. Several studies have pointed out the importance of old growth attributes for the maintenance of diversity of many different organisms such as lichens, mosses (Boudreault et al. 2002), (Fenton and Bergeron 2008), birds (Drapeau et al. 2002), fungi (Desponts et al. 2004) and insects (Work et al. 2003; cf. also Chap. 19 by Frank et al., this volume).

Use of rotations of variable length in proportions similar to those observed in the natural fire regime is a possible alternative to fixed rotations (Seymour and Hunter 1999), in order to maintain old-growth forests. However, this approach may be applicable only in ecosystems where species are long-lived and can thus support longer rotations. In boreal forests composed of relatively short-lived species, this approach would probably lead to fibre loss and a decrease in allowable cut. Alternatively, Bergeron et al. (2002) have suggested that silvicultural practices aimed at maintaining structural and compositional characteristics of old-growth in harvested stands could, in boreal regions, guarantee maintenance of habitat diversity while only slightly affecting the allowable cut. It would be possible to treat some stands by clear-cutting followed by seeding or planting (or another even-aged silvicultural system whose outcome resembled the effect of fire), other stands with partial cuts that approach the natural development of intermediate-aged stands, and still other stands with selective harvesting in order to reflect the dynamics of old growth stands (Bergeron et al. 2002).

13.5 Conclusions

Although Canadian boreal forests are controlled by fire, long fire intervals allow for the presence of a significant proportion of old-growth forests. Some of these have been relatively undisturbed for many centuries, even millennia (Cyr et al. 2005). Long fire cycles are not unique to recent historical times but were common during most of the Holocene (Flannigan et al. 2001; Cyr et al. 2009), and old-growth forests can be considered as having been a permanent feature of the Canadian boreal forest for at least the last 10,000 years. Although not studied here, it is very likely that old-growth forests are also very abundant in Eurasian boreal forests, especially in a context where non stand-replacing fires are more common (Gromtsev 2002; Wallenius et al. 2005; Wirth 2005). However, boreal old-growth forests are not devoid of large-scale disturbances such as insects or windthrow (Kneeshaw and Gauthier 2003), and in that respect may stand apart from typical temperate or tropical old-growth forests where small gap dynamics is the typical disturbance regime.

Old forests in the boreal zone possess unique characteristics such as greater structural diversity and gap dynamics not observed in post-fire even-aged cohorts. Other typical old-growth attributes, including higher tree species diversity, greater abundance of larger trees and snags and greater tree basal area, are often found instead in intermediate-aged stands that are still older than the current harvest rotation age. Current forest management practices that use short even-aged rotations do not reproduce the historical age structure, and a decrease in old-growth attributes may threaten biodiversity.

In this context, protecting a proportion of the remaining old-growth in boreal forest is urgently required, but probably insufficient to restore the abundance of old-growth forest in the pre-industrial landscape. Development of silvicultural techniques that maintain or restore old-growth forest compositional, structural and functional characteristics at different scales in the landscape is an important option to explore.

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Chapter 14
Biomass Chronosequences of United States Forests: Implications for Carbon Storage and Forest Management

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14.1 Forest Management and Carbon Sequestration

Forests account for a large fraction of the carbon stored in global soils and vegetation (Dixon et al. 1994). Accordingly, considerable effort has been devoted to understanding the impact of land use and forest management on carbon sequestration, and thus on climate change (Harmon et al. 1990; Lugo and Brown 1992; Heath and Birdsey 1993; Dixon et al. 1994; Houghton et al. 1999; Caspersen et al. 2000; Fang et al. 2001; Pacala et al. 2001; Birdsey et al. 2006). The optimal strategy for forest management aimed at carbon sequestration is controversial. On the one hand, logging diminishes the pool of standing carbon and can result in a large net transfer of carbon to the atmosphere (Harmon et al. 1990; Vitousek 1991; Schulze et al. 2000; Harmon 2001; Harmon and Marks 2002). On the other hand, if the harvested wood has a sufficiently long residence time or is used to offset fossil fuel emissions, repeated harvest and regrowth can effectively sequester carbon (Vitousek 1991; Marland and Marland 1992; Marland and Schlamadinger 1997).

For a given parcel of land, the relative merits of plantation forestry vs old-growth protection or restoration depends, in part, on the late-successional carbon storage trajectory. Classical models of ecosystem development propose that live biomass density (biomass per unit area) increases over time to an asymptote (Kira and Shidei 1967; Odum 1969). In contrast, reviews of biomass dynamics in the forest ecology literature tend to emphasize the variety of patterns that can ensue over the course of succession (Peet 1981, 1992; Shugart 1984). In the context of forest management aimed at carbon sequestration, of particular interest is the possibility that live biomass density may decline late in succession in some ecosystems (Loucks 1970; Bormann and Likens 1979). For example, data in Canada's National Forest Biomass Inventory indicate that biomass declines are common in some types of 'overmature' stands, and these declines are accounted for in the Carbon Budget Model of the Canadian Forest Sector (Kurz and Apps 1999).

The expected trajectory of live biomass density over time does not in itself determine the optimal strategy for carbon sequestration. Additional factors that must be considered include (1) the impacts of management on other forest carbon

pools, particularly soils (Johnson and Curtis 2001) and coarse woody detritus (Harmon 2001; Janisch and Harmon 2002); and (2) the amount of carbon stored under different management scenarios in forests, wood products, landfills, and displaced fossil fuel emissions (e.g., due to biofuel production; Marland and Marland 1992; Marland and Schlamadinger 1997; Liski et al. 2001; Harmon and Marks 2002; Kaipainen et al. 2004). Furthermore, carbon sequestration must be balanced with other management objectives, such as maintaining biodiversity and protecting and restoring old-growth forests (Thomas et al. 1988; Messier and Kneeshaw 1999; Schulze et al. 2002). Nevertheless, were substantial declines in live biomass density expected as forests aged, this would clearly be one factor to consider in devising forest management policies.

Little old-growth forest remains on productive land in the United States (US). In western Washington and Oregon, for example, roughly 20% of the original old-growth remained in the 1980s (Greene 1988; Spies and Franklin 1988), and this fraction has undoubtedly decreased. In the eastern US, less than 1% of the presettlement forest is thought to remain (Davis 1996). Considerable controversy has arisen over the fate of the remaining old-growth in the Pacific Northwest (Thomas et al. 1988), while in the eastern US, there are urgent pleas from conservationists to set aside large tracts of second growth as future old-growth reserves (Zahner 1996). From a carbon sequestration perspective, the attractiveness of protecting or expanding old-growth habitat depends, in part, on the expected late-successional biomass trajectory. The primary goal of this chapter is to quantify these trajectories for different US forest types. We assembled biomass chronosequences for US forest types using data from the US Forest Service's Forest Inventory and Analysis (FIA) program. Where possible, we compared late-successional FIA biomass estimates to old-growth biomass estimates in the literature.

14.2 Mechanisms of Biomass Decline

First, we review mechanisms that could result in late-successional declines in forest biomass, focusing on aboveground live tree biomass (AGB, in per area units). Understanding the effects of these mechanisms on total forest carbon storage would need to consider additional pools (e.g., soils, coarse woody detritus), particularly in cases where declines in live biomass are concurrent with the accumulation of undecomposed dead biomass [see Sect. 14.2.3 and cf. Chaps. 5 (Wirth and Lichstein), 8 (Knohl et al.), 11 (Gleixner et al.) and 21 (Wirth), this volume].

14.2.1 Transition from Even- to Uneven-Aged Stand Structure

Peet (1981) suggested that, depending on the degree of population synchrony in mortality and the time lag between mortality and regeneration, a range of succes-

sional patterns in AGB could occur, including an increase to an asymptote, an increase to a peak followed by a decline to a lower asymptote, or oscillations. A well-known example of how the timing of growth and mortality could cause a late-successional biomass decline involves the 'stand-breakup' hypothesis of Bormann and Likens (1979). Following major disturbance, such as stand-replacing fire, hurricane, or logging, AGB increases as the initially even-aged cohort of trees matures, but may decline as the canopy breaks up (Bormann and Likens 1979). Canopy breakup (i.e., synchronous mortality of a substantial fraction of canopy trees) may occur if the initial cohort is dominated by individuals with similar natural lifespans. In addition, death of large canopy trees may induce a mortality wave if other trees are damaged directly by the falling dead trees, or indirectly by increased wind exposure or insect/disease pressure (Oliver and Larson 1996). Eventually, the landscape may reach a dynamic equilibrium, termed the 'shifting mosaic,' with patches in various stages of development (Bormann and Likens 1979). In the context of AGB declines, the key point is that an even-aged cohort of large trees, characteristic of mature second-growth and plantation forests, can have higher AGB than an uneven-aged old-growth forest. While this scenario is plausible, the transition from an even- to an uneven-aged forest will not necessarily result in an AGB decline. Depending on the growth and mortality rates of surviving trees (which may be released from competition as the even-aged cohort breaks up), as well as the rate of biomass accumulation by younger cohorts, AGB (averaged across the landscape) may increase, decrease, or remain essentially constant during the transition to an old-growth state. At question here is not the validity of the landscape-scale steady-state concept (the 'shifting mosaic'), but whether or not attainment of this steady state typically involves a decline in AGB. In lieu of sufficient data to test their hypothesis directly, Bormann and Likens (1979) presented simulation results from the JABOWA model (Botkin et al. 1972) as evidence in support of their hypothesized AGB decline.

14.2.2 Large Mortality Events

The demographic transitions discussed by Bormann and Likens (1979) and Peet (1981) are generic; i.e., they do not require particular mortality events to trigger AGB declines, but rather view declines as a likely consequence of normal demographic processes. Large mortality events due to wind, fire, or insect outbreaks may also cause late-successional AGB declines. Depending on the severity of disturbance, these events may be viewed as stand-initiating disturbances that reset succession, or as perturbations to the successional trajectory of AGB. Although these disturbances may occur at any time during succession, to the extent that their severity or likelihood of occurrence increases with stand age, it is appropriate to view them as potential mechanisms of late-successional AGB decline. Susceptibility of forest stands to wind damage increases with stand age in some systems (Sprugel and Bormann 1981; Canham and Loucks 1984; Foster 1988), and numerous studies have reported a positive correlation between tree size and vulnerability

to wind (e.g., Greenberg and McNab 1998; Dunham and Cameron 2000; Peterson 2000; Veblen et al. 2001). Susceptibility of some forests to insect attack is also thought to increase with stand age. For example, mature stands of *Abies balsamea* in eastern Canada tend to suffer higher mortality to spruce budworm (*Choristoneura fumiferana*) than younger stands (Maclean 1980). Taylor and MacLean (2005) attributed late-successional wood-volume declines in *Abies balsamea* stands to the combined effects of spruce budworm and wind.

Although wind and insect outbreaks seem reasonable candidates for causes of late-successional AGB decline, the notion that fire could cause such a decline is in many cases problematic. Firstly, stand age may be relatively unimportant compared to weather in determining fire behavior of closed-canopy boreal forests (Bessie and Johnson 1995; Johnson et al. 1998). Secondly, in forests composed of fire-resistant species, susceptibility to fire decreases with tree size and age, and biomass may continue to accumulate for centuries in the presence of recurring surface fires (Wirth et al. 2002). Finally, in some systems (e.g., *Pinus ponderosa* in the southwestern US), dense, crowded stand conditions that encourage crown fire are often attributed to fire suppression, grazing, or logging, rather than natural stand-development (Cooper 1960; Allen et al. 2002; Brown et al. 2004).

14.2.3 Successional Changes in Growth Conditions

Numerous factors may lead to late-successional declines in annual net primary production (NPP) at the stand level (Gower et al. 1996; Ryan et al. 1997). If we express the annual biomass dynamics of a stand as:

$$\Delta \text{biomass} = \text{NPP} - \text{annual losses}$$

where annual losses include litter fall, root turnover, whole-tree mortality, etc., then it is clear that a NPP decline will not necessarily cause a biomass decline. Rather, a biomass decline occurs only if net primary production becomes smaller than the annual losses. Kutsch et al. (Chap. 7, this volume) review the extensive literature on mechanisms of NPP decline and also discuss the relevance of the phenomenon for natural forests. Here, we highlight two scenarios in which successional changes in conditions for growth or regeneration are likely to cause AGB declines.

In boreal forests, the accumulation on the forest floor of insulating moss, lichens, and dead organic matter over the course of succession leads to the development of cool, wet soil conditions ('paludification') with low mineralization rates (Van Cleve and Viereck 1981; Harper et al. 2005). As nutrients accumulate in dead organic matter, there may be insufficient nutrients available to replace AGB losses. In addition to nutrient limitation, development of thick beds of moss or lichen may directly inhibit seedling establishment, thus preventing tree regeneration (Strang 1973; Van Cleve and Viereck 1981). In the absence of fire, which leads

to increased nutrient availabilities and improved regeneration conditions (Van Cleve and Viereck 1981), the endpoint of succession in some boreal forests is a treeless bog (Strang 1973). Although AGB is likely to decline with paludification, total carbon storage may increase as moss, lichens, and dead organic matter accumulate.

Another scenario in which declining growth conditions could result in AGB declines involves species effects on litter quality and nutrient availability. Pastor et al. (1987) suggested that successional replacement of *Betula papyrifera* by *Picea* spp. in boreal North America could result in decreased nitrogen availability (due to poor quality of *Picea* litter) and reduced AGB. Increased understorey light levels and decomposition rates following breakup of the *Picea* canopy could again favor *Betula* regeneration and lead to cyclic succession (Pastor et al. 1987).

14.2.4   Species Effects on Forest Stature

In some systems, early-successional species are replaced later in succession by species of smaller stature. In the US Pacific Northwest, long-lived, early-successional *Pseudotsuga menziesii* (70–80 m height) is eventually replaced (in the absence of major disturbance) by *Tsuga heterophylla* (50–65 m) in coastal forests and *Abies amabilis* (45–55 m) in subalpine forests (Franklin and Hemstrom 1981). In boreal Quebec, late-successional AGB decline was attributed to replacement of *Populus tremuloides* by more shade-tolerant conifers, which are both shorter and more susceptible to insect attack (Pare and Bergeron 1995). Shugart (1984) gives several additional examples of declining forest stature with succession: replacement of *Pinus taeda* by *Quercus falcata* in Arkansas (southeastern US), and replacement of *Eucalyptus regnans* and *Eucalyptus obliqua* (both with a mean height over 90 m) by *Nothofagus-Atherosperma* forest (less than 40 m height) in Tasmania. Species effects on forest stature and AGB trajectories are explored in detail in Wirth and Lichstein (Chap. 5, this volume).

14.3   Aboveground Biomass Chronosequences for US Forests

Clearly, there are a variety of mechanisms that could cause late-successional declines in AGB. However, we are aware of few well-documented examples of this phenomenon in temperate forests. To assess the relevance of late-successional AGB declines for US forest management, we assembled chronosequences of mean AGB for different forest types across the coterminous US (excluding Alaska and Hawaii) using the US Forest Service's Forest Inventory and Analysis (FIA) database. Our main objective was to determine the relative frequency of expected late-successional AGB declines vs increases among US forest types. We adopted

the 'space-for-time' substitution approach (Pickett 1989), i.e., we assembled chronosequences from different-aged stands in different locations. A more direct approach to studying biomass dynamics would be to quantify biomass across time in remeasured plots (e.g., Peet 1981; Debell and Franklin 1987; Taylor and MacLean 2005). However, FIA remeasurement data are not currently available for the entire US. Therefore, we adopted the space-for-time approach, as it enabled us to examine chronosequences for all forested regions of the coterminous US. Because old-growth forests are rare in much of the US, and are therefore unlikely to be well-characterized by the FIA's systematic sampling scheme (one plot per ~2,400 ha), we also searched the literature for AGB estimates from US old-growth forests.

14.3.1   Methods

14.3.1.1   FIA Data

In December 2006, we downloaded all available FIA data for the coterminous US from http://fia.fs.fed.us/; FIA documentation referred to below is available from this site. Roughly half of the data are plot remeasurements, the remainder being initial plot installations. We included both types of plots in our analysis and treated them equally because (1) remeasurement data exist only for some regions; and (2) even for the existing remeasurement data, assembling time series for individual plots is precluded by the plot-labeling system in the data currently available to the public. Accounting for temporal autocorrelation in AGB within remeasured plots would increase our statistical power to detect AGB declines or increases, but the fact that we could not do so (point 2 above) should not bias our results.

14.3.1.2   FIA Sampling and Plot Designs

Beginning in 1999, FIA sampling (i.e., the spatial arrangement of plots and their remeasurement intervals; Bechtold and Scott 2005; Reams et al. 2005) and plot designs have been standardized across the US (USDA 2006). The FIA divides the US into hexagons of ~2,400-ha, with one plot randomly located within each hexagon. Field data are collected on plots located on both public and private lands classified as accessible forest. To be considered 'forest,' an area must be at least 10% stocked with trees, at least 0.4 ha in size, and at least 36.6 m wide. Inaccessible land includes hazardous conditions and private property where access is denied.

Each plot includes four 7.3 m radius subplots: a central subplot and three peripheral subplots whose centers are 18.3 m from the plot center at azimuths 0°, 120°, and 240°. The diameter and status (live, dead, or cut) is recorded for all trees (>12.7 cm diameter) within subplots and for all saplings (2.54–12.7 cm diameter)

within 2.07 m radius microplots (one per subplot). In some parts of the western US, subplot radii are extended to 18 m for large trees (diameter > 53.3, 61, or 76.2 cm, depending on region). Diameter is measured at breast height (1.37 m) or, in the case of multi-trunked western woodland species, at the root collar. Prior to 1999, sampling and plot designs varied by FIA unit (group of counties within a state), with most units adopting a plot design with five or ten variable-radius subplots (i.e., wedge-prism samples) for trees and fixed-radius microplots for saplings.

14.3.1.3 Data Stratification

Each tree or sapling is assigned to a 'condition' whose attributes include stand age, land ownership, soil class (xeric, mesic, or hydric), etc. (USDA 2006). Prior to 1999, each FIA plot was assigned a single condition. Beginning in 1999, a single plot could include multiple conditions, but multiple-condition plots (∼20% of the post-1999 plots; ∼10% of all plots) were excluded from our analysis. Thus, hereafter, we refer to condition attributes as plot attributes. We now describe the plot attributes used to stratify the data.

Forest Type

The FIA uses an algorithm to assign each plot to one of around 150 forest types based on current species composition[1]. In most cases, forest type reflects species composition of the largest trees on a plot, but may reflect species composition of smaller trees if they are very dense, or if there is low stocking density of large trees. We adopt scientific names for each forest type, rather than the English names used by the FIA. Each of the names we present can unambiguously be matched to a forest type in the FIA documentation (Appendix D in USDA 2006).

We split several widespread FIA forest types dominated by species with morphologically distinct varieties (Flora of North America Editorial Committee 1993+): We split the *Pseudotsuga menziesii* type into coastal (var. *menziesii*) and Rocky Mountain (var. *glauca*) varieties. We split the *Pinus contorta* type into coastal (var. *contorta*), Cascades-Sierra Nevada (var. *murrayana*), and Rocky Mountain (var. *latifolia*) varieties. We split the *Pinus ponderosa* type into Cascades-Sierra Nevada (var. *ponderosa*) and Rocky Mountain (var. *scopulorum*) varieties. Because the FIA does not distinguish among the preceding varieties, we reclassified these forest types by comparing plot latitude–longitude to range maps (Flora of North America Editorial Committee 1993+). We also split the *Populus tremuloides* type into eastern and western types based on plot location.

We present AGB chronosequences (mean AGB of FIA plots vs age class) for each forest type separately. Stratifying the data by forest type has the advantage of

[1]http://srsfia2.fs.fed.us/publicweb/statistics_band/stat_documents.htm

minimizing edaphic or other differences across stand ages; i.e., to the extent that species composition reflects the edaphic conditions of a site, we would expect different aged stands of the same forest type to have similar edaphic conditions. Although stratifying by forest type should limit the influence of confounding factors, we note that this strategy is not foolproof. For example, some shade-intolerant species that are replaced during succession by more tolerant species on mesic sites may persist as climax species on drier sites (Horn 1971; Franklin and Hemstrom 1981; Oliver and Larson 1996). To address this concern, we further stratified the data by soil class (see below) within each forest type.

Within each forest type, we pooled FIA data across all US states. Although many forest types are geographically restricted, some occur across large, heterogeneous areas. To determine if aggregation (pooling FIA plots from heterogeneous areas) strongly affected our results, we compared chronosequences derived from pooled data to chronosequences derived from smaller regions (New England, Southeast, upper Midwest, lower Midwest, mid-Atlantic, interior West). These comparisons (not shown) indicated that pooling did not qualitatively change our results.

Stratifying by forest type minimizes successional changes in AGB associated with species turnover (e.g., Sect. 14.2.4). To assess the importance of AGB changes associated with species turnover, we compared chronosequences of typical early-, mid-, and late-successional forest types in several US regions (see Sect. 14.3.2.3, Results, for details).

Soil Class

FIA field crews assign each plot to one of three soil physiographic classes (hereafter, 'soil classes'): xeric (dry), mesic (moderate but adequate moisture), and hydric (excessive moisture). Each of these classes is subdivided into about five subclasses, but this finer classification is available only for post-1999 inventories. Therefore, we used the coarse three-class scheme to stratify data within forest types.

Stand Age

We define stand age as time since the last stand-replacing disturbance (Table 14.1). Because stand age (according to our definition) is not available from the FIA, we used two different proxies for stand age that are available for each FIA plot: mean age of canopy trees (A_μ), and mean diameter at breast height (dbh) of the k largest trees (D_k). (Diameters measured at the root collar were converted to dbh; see Sect. 14.3.1.5.) We restrict our analysis to D_1 (the largest dbh in each plot) and D_2. For each forest-type/soil-class combination with ≥ 250 FIA plots, we assembled three chronosequences, using A_μ, D_1, or D_2 as the time axis defining the age classes. Although A_μ and D_k may depend on species composition, as well as stand age, this should not qualitatively affect our results because chronosequences within forest types, by definition, control for species composition.

Table 14.1 Glossary of abbreviations and terms used in text

Term	Definition
AGB	Aboveground live tree biomass density (Mg ha^{-1}), roughly half of which is corbon
FIA	United States Forest Service's Forest Inventory and Analysis program
Forest type	FIA assigns each plot to a forest type based on current species composition
Stand age	Time since last stand-replacing disturbance
A_μ	Mean age of canopy trees in a stand
D_k	Mean dbh of k largest trees in a stand or FIA plot; D_1 = dbh of largest tree

Below, we discuss the limitations associated with using A_μ and D_k as proxies for stand age. First, we describe the procedure for estimating A_μ (this variable is referred to as 'stand age' in the FIA documentation), which the FIA defines as "the average age of the live trees not overtopped in the predominant stand size-class" (USDA 2005). The FIA estimates A_μ by coring two or three dominant or codominant trees at the point of diameter measurement (breast height for most species) (USDA 2005). Depending on species and region, additional years (typically five or ten) are added to the age of the core to account for early growth (USDA 2005). Field crews have substantial latitude in selecting which trees to core, which – particularly when the predominant size-class is uneven-aged – can result in estimates of A_μ that do not accurately reflect a stand's history (R. Birdsey, personal communication). This should introduce noise into our analysis but should not bias our results.

If AGB peaks and then declines with stand age, then the shape of the relationship between AGB and A_μ or D_1 (or, more generally, D_k) depends on the details of how the decline occurs. First, consider the case where A_μ declines late in succession, as implied by the 'stand-breakup' hypothesis (Sect. 14.2.1), but D_1 continues to increase (Fig. 14.1a). This would occur if at least one canopy tree survived the transition from an even- to an uneven-aged stand structure. In this case, AGB would increase monotonically with A_μ, but would peak and decline with D_1 (Fig. 14.1d). Next, consider the case where A_μ increases with stand age, but D_1 peaks and then declines (Fig. 14.1b). This might occur if tree stature decreased with succession (e.g., due to decreased nutrient availability; Sect. 14.2.3). In this case, AGB would increase monotonically with D_1, but would peak and decline with increasing A_μ (Fig. 14.1e). Finally, consider the case where both A_μ and D_1 peak and then decline with stand age (Fig. 14.1c). This would occur if a synchronized mortality event (e.g., insect outbreak; Sect. 14.2.2) killed all of the large trees in a stand, and would result in an increasing relationship between AGB and both A_μ and D_1 (Fig. 14.1f). Although it would appear, on the surface, that our methods would fail to detect an AGB decline under this scenario, synchronized mortality events often play out over a number of years. For example, although severe spruce budworm attacks may result in whole-canopy mortality, a decade or more may pass before the last individuals succumb (Maclean 1980). Thus, in many stands undergoing a severe mortality event, one or more large trees would still be sampled in inventory plots,
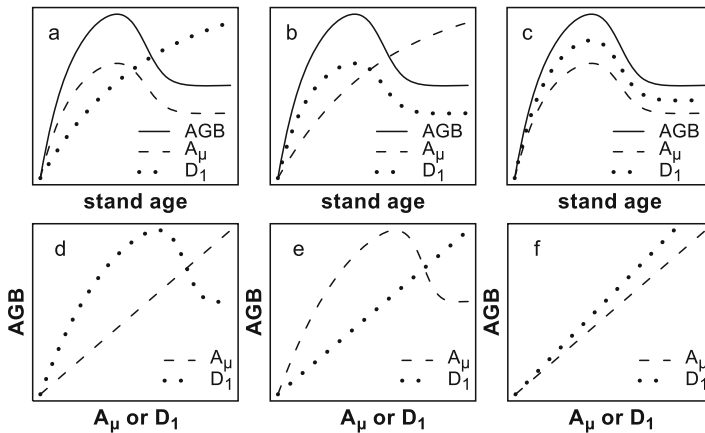
Fig. 14.1 Hypothetical relationships between aboveground live tree biomass (AGB), stand age, mean age of canopy trees in a stand (A_μ), and diameter at breast height (dbh) of largest tree (D_1) (Table 14.1) for three cases (**a–c**) in which AGB peaks and then declines to an asymptote with increasing stand age: **a** at least one canopy tree survives the transition from an even- to an uneven-aged old-growth stand, so that D_1 increases even as A_μ declines; **b** forest stature declines in old stands (e.g., due to paludification), but A_μ continues to increase; **c** both A_μ and D_1 peak and then decline with stand age, as would occur if a synchronous mortality event killed all large trees in a stand. Panels **d–f** show the relationships resulting from (**a–c**) if AGB is plotted against A_μ or D_1 [the stand age proxies available for United States (US) Forest Service's Forest Inventory and Analysis program (FIA) plots]. See Sect. 14.3.1.3 for details. Note that the variables in the figure have different units, so their relative positions on the y-axis are arbitrary

and D_1 would remain a useful proxy for stand age. In many situations, then, the scenario depicted in Fig. 14.1c would reduce our statistical power to detect mean AGB declines, but would not prevent us from detecting declines if sample sizes were large enough.

In summary, if mean AGB declines with stand age, then mean AGB should also decline with A_μ or D_1 in most cases. The primary scenario in which our methods would fail to detect a mean AGB decline is where the decline results from mortality events that kill all large trees in a stand within a short enough time interval so that few stands are undergoing mortality at any given time.

14.3.1.4 Data Filtering

We excluded plots containing multiple FIA conditions (defined above), plots where there was clear evidence of artificial regeneration (e.g., plantations), and plots where any cut trees or saplings were recorded. Cut trees are not recorded on initial plot installations (USDA 2005), and it is likely that data from some of these plots were affected by past selective harvest. For remeasured plots, cut trees are only recorded if harvest occurred between the current and previous plot measurement (USDA 2005); thus, data from remeasured plots may be affected by selective harvest that predated the previous measurement.

14.3.1.5 Biomass Estimation

We estimated total aboveground live biomass (dry weight) for live trees and saplings in the FIA data using diameter-based allometries in Jenkins et al. (2003). To estimate these allometries, Jenkins et al. (2003) compiled biomass allometries from the literature for US tree species, generated pseudo-data from each published equation, and then fit an allometry to pseudo-data pooled within each of ten species groups. Following Jenkins et al. (2003), we used the hardwood biomass allometry of Freedman (1984) for hardwood trees with diameter >70 cm, and – for woodland species whose diameter is measured by the FIA at the root collar – we estimated dbh according to Chojnacky and Rogers (1999). This latter conversion was necessary because the Jenkins et al. (2003) allometries predict biomass from dbh.

AGB of each FIA plot (in Mg ha^{-1}) was estimated as the sum of individual tree and sapling biomasses after appropriate scaling of the individual estimates. This scaling entails dividing each individual estimate by the area on which the tree or sapling is sampled. This area reflects both the FIA plot design (e.g., fixed- vs variable-radius subplots; number of subplots) as well as adjustments for inaccessible land (e.g., if only two of four subplots could be sampled, then the area represented by each tree is doubled). The area sampled by each tree or sapling was calculated from the TPACURR (current trees per acre) field in the FIA SNAPSHOT data (USDA 2006).

14.3.1.6 Old-Growth Literature Data

We searched the published literature for AGB estimates for old-growth forests in the coterminous US. Because old-growth is rare in the eastern US, we also included studies from southeastern Canada. If the same stand was described in more than one study, we cite the one study that provided the most information (species composition, site characteristics, etc.). To be considered old-growth, we did not require that a forest had reached a 'climax' state of relatively stable species composition. Rather, we adopted a broad definition of old growth (see also Chap. 2 by Wirth et al., this volume) including both 'true old-growth' (in which the initial wave of regeneration following major disturbance has entirely disappeared) and 'transition old-growth' (in which relics of the initial regeneration wave still persist) (Oliver and Larson 1996). This broad definition allows for old-growth stands dominated by short-lived, early-successional species (Oliver and Larson 1996).

Many of the studies of old growth in the eastern US are in remnant patches with some history of human disturbance (e.g., selective culling of valuable trees). We included these studies if the stands were described by the original authors as 'old growth,' but we note any known disturbances in our results. We also included stands that, based on the authors' description, we judged to be old-growth, even if the authors did not label them as such. Such cases involved forests recovering from natural disturbance that had attained the typical lifespan of the dominant canopy

species. We excluded AGB estimates from Whittaker (1966) because Busing et al. (1993) concluded that Whittaker (1966) non-randomly selected plots with unusually large trees, and because some of Whittaker's sites were sampled in larger plots by Busing et al. (1993) and Busing (1998). We also excluded the *Pinus ponderosa* study of Hicke et al. (2004) because these authors found that AGB was still rapidly increasing 200 years after fire.

We assigned one or more FIA forest types to each literature study, with multiple types assigned if there was no clear best match. For consistency with the FIA algorithm, we assigned forest types to literature studies based on current species composition. Our assignments differed from those of the original authors if the latter were based on potential climax, rather than current, species composition.

All studies used either locally developed allometries or published allometries to estimate biomass from diameter data. Although these allometries yield different estimates than the Jenkins et al. (2003) allometries that we applied to the FIA data, there should be no systematic bias in comparing our FIA results to the literature data because the Jenkins et al. allometries 'average over' those reported in the literature. Another inconsistency concerning the literature studies involves the minimum size of measured stems. However, since canopy trees comprise the vast majority of AGB, this should have little impact on our results.

14.3.2 Results

14.3.2.1 FIA Chronosequences within Forest Types

Chronosequences of mean AGB vs A_μ for the 79 forest-type/soil-class combinations represented by ≥ 250 FIA plots are shown in Fig. 14.2. The figure and the analyses presented below are restricted to age classes represented by ≥ 10 plots. Standard errors, which indicate our confidence in mean AGB, are small for age classes with many plots, regardless of the variability among plots. We do not present estimates of plot-to-plot variation, because we do not know how much of this variation reflects true heterogeneity among the sampled stands vs sampling errors due to small plot size (i.e., the minimum area sampled for trees is only 0.067 ha per plot under the current FIA plot design).

We tested for late-successional AGB declines/increases as follows: For each of the 79 chronosequences in Fig. 14.2, we performed three two-tailed *t*-tests (one for each time axis: A_μ, D_1, and D_2; see Table 14.1) to determine if mean AGB in the oldest age class was significantly different from the largest mean AGB among all other age classes. Using A_μ as the time axis, there were four late-successional AGB declines and 18 increases out of 79 chronosequences (Table 14.2 and * symbols in Fig. 14.2). Of 79 chronosequences, 6 exhibited a late-successional decline in at least one of the three tests (time axes), whereas 52 chronosequences exhibited an increase in at least one of the three tests (Table 14.2); assuming that in most cases at least one of our time axes is a meaningful proxy for stand age, we can

conclude that late-successional AGB declines are rare among US forest types and that late-successional AGB increases are relatively common across the range of age classes adequately sampled by the FIA. Exactly which chronosequences show significant declines/increases changes somewhat depending on the details of the analysis (e.g., number of age classes; minimum sample size to include an age class), but our main results are robust to such details.

We did not correct for multiple testing (e.g., Bonferroni correction), so the nominal type I error rate (0.05) in the above tests is probably an underestimate. This bias may have resulted in our over-reporting late-successional declines and increases, but should not bias the relative frequency of declines vs increases.

Our estimates of AGB are similar to those from other studies that estimate AGB from FIA data. For example, reported mean AGB estimates from FIA plots in mature eastern US forests range from about 125 to 250 Mg ha^{-1}, depending on forest type and region (Brown et al. 1997; Schroeder et al. 1997; Jenkins et al. 2001). This range includes most of our mean estimates in older age classes in the eastern US (Fig. 14.2).

14.3.2.2 Comparison of Old-Growth Literature and Old FIA Plots

We located old-growth literature AGB estimates for 27/79 cases in Fig. 14.2. Literature values were similar regardless of whether the stands had been subject to selective cutting ('S' symbols in Fig. 14.2) or had no known history of human disturbance ('U' symbols). Therefore, we calculated a single mean literature value

Fig. 14.2 a–e AGB chronosequences for soil-class/forest-type combinations with $n \geq 250$ FIA plots. Means and standard errors are shown for age classes with $n \geq 10$ plots. An *asterisk* above the error bar in the oldest age class indicates that its mean is significantly different from the largest mean of any other age class (Table 14.2). All *y*-axes have a maximum of 500 Mg ha^{-1} except for *Pseudotsuga* and *Tsuga heterophylla* types on mesic soils (panels 61–63). Within each region/soil class, forest types are ordered alphabetically within coniferous and broad-leaved (angiosperm) types. The *histograms* show the age distribution of FIA plots; the bar heights are scaled so that the modal height is equal to the height of the panel frame. The total number of plots is given above each panel. The curves show the mean proportion of AGB in each age class comprised by trees in different dbh classes (see legends at top left): *2.54–50 cm dbh* area below solid curve; *50–70 cm dbh* area between solid and dashed curves; *70–100 cm dbh* area between dashed and dotted curves; *>100 cm dbh* area above dotted curve. Old-growth AGB estimates from the literature are plotted as *S* or *U* at the far right of each panel: *S* indicates stands that have been selectively logged or otherwise disturbed (see Table 14.3 notes), *U* indicates stands with no known history of human disturbance, *triangles* indicate means of literature values. The same literature values are plotted for all soil classes with $n \geq 250$ FIA plots for a given forest type. See footnote v in Table 14.3 for key to literature references. Abbreviations: Ac. rub. *Acer rubrum*; Bet. al. *Betula alleghaniensis*; C-SN Cascades-Sierra Nevada variety; Frax. am./penn. *Fraxinus americana/pennsylvanica*; Jun. *Juniperus*; Liq./Liquidambar *Liquidambar styraciflua*; Lirio./Liriodendron *Liriodendron tulipifera*; Mag. vir. *Magnolia virginiana*; Nys. *Nyssa*; Pin. *Pinus*; Prunus ser. *Prunus serotina*; Pseudotsuga *Pseudotsuga menziesii*; Q. *Quercus*; Ulm. am. *Ulmus americana*
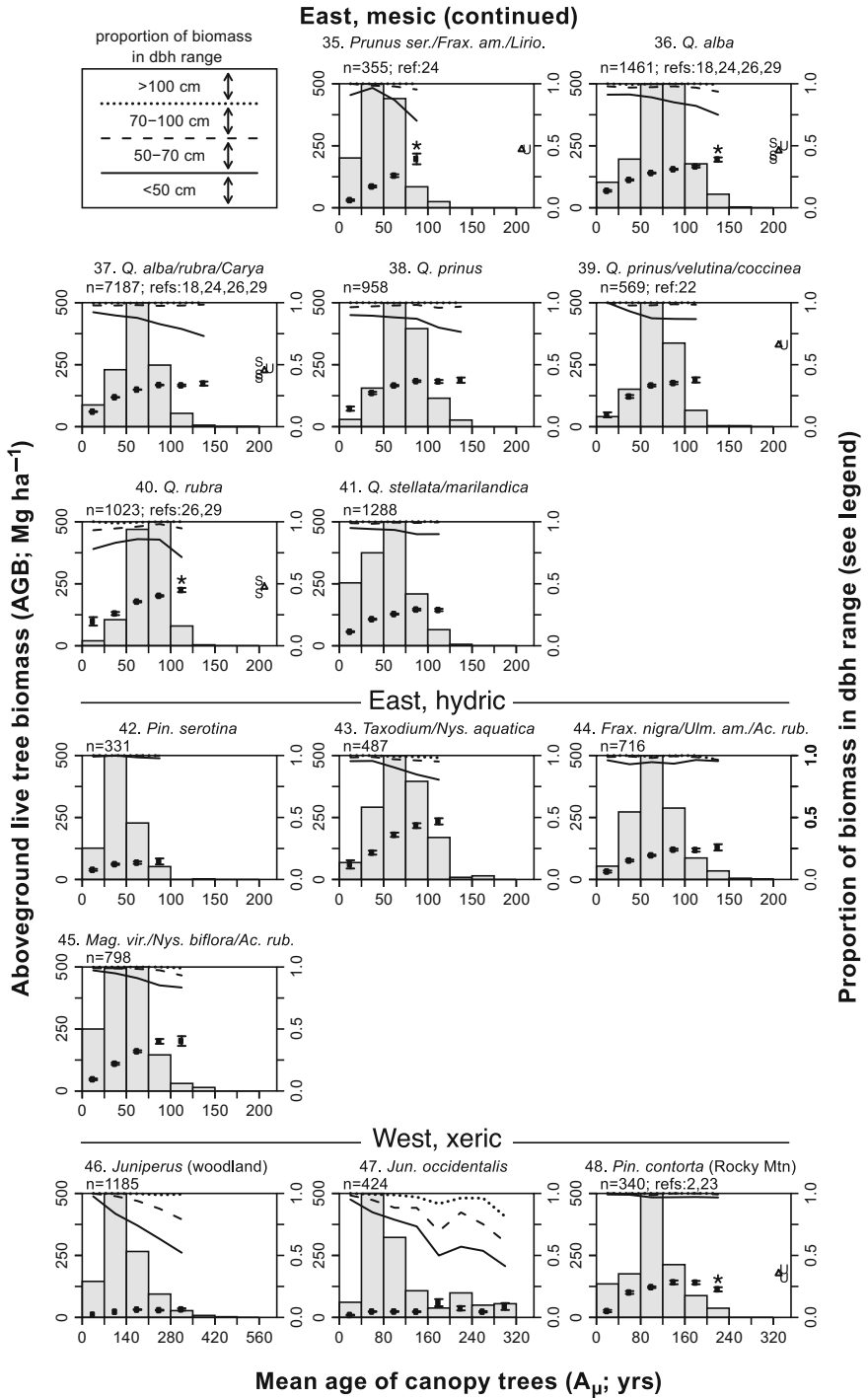
Fig. 14.2a (Continued)

East, mesic (continued)

Aboveground live tree biomass (AGB; Mg ha^{-1})

Proportion of biomass in dbh range (see legend)

Mean age of canopy trees (A$_\mu$; yrs)
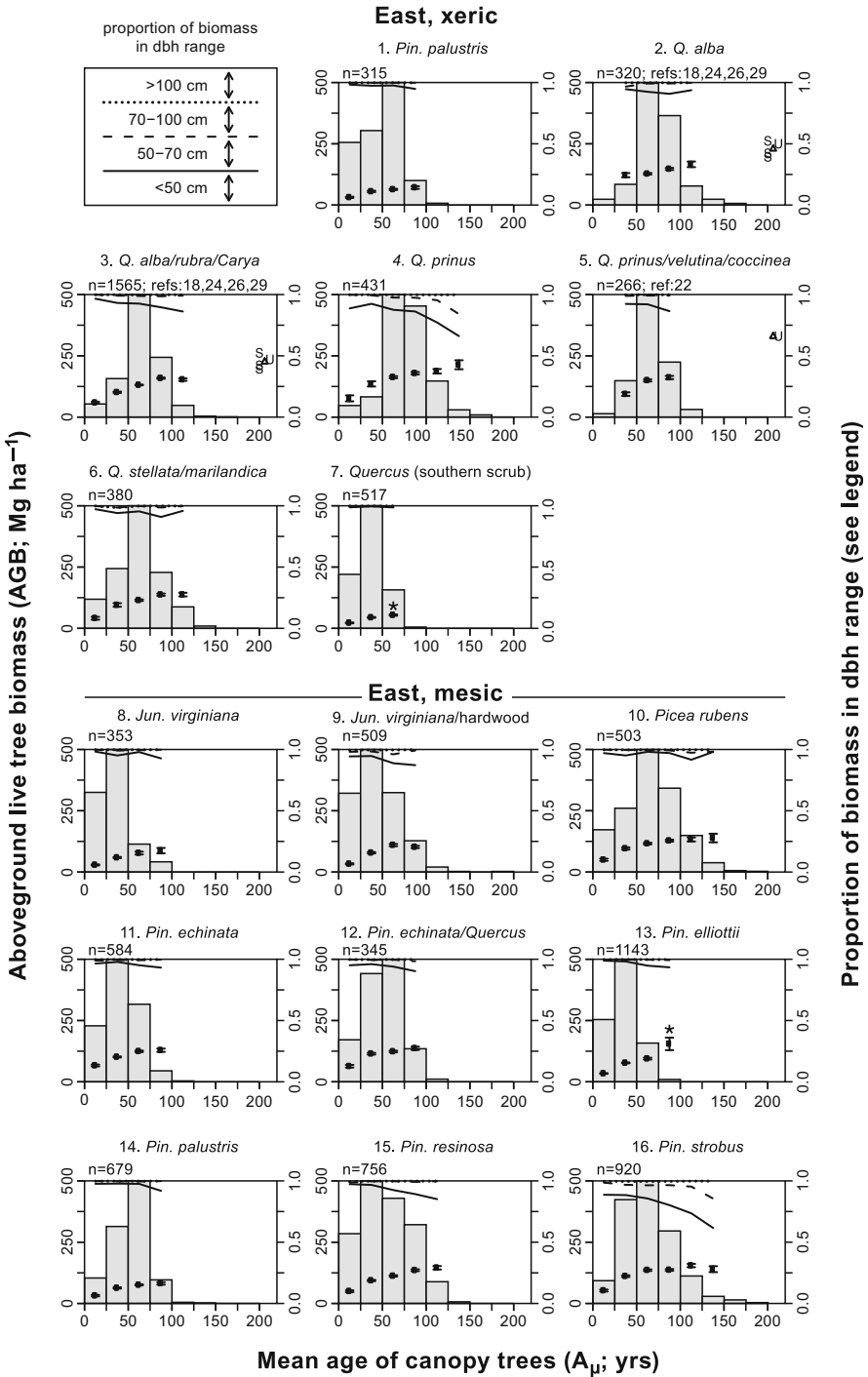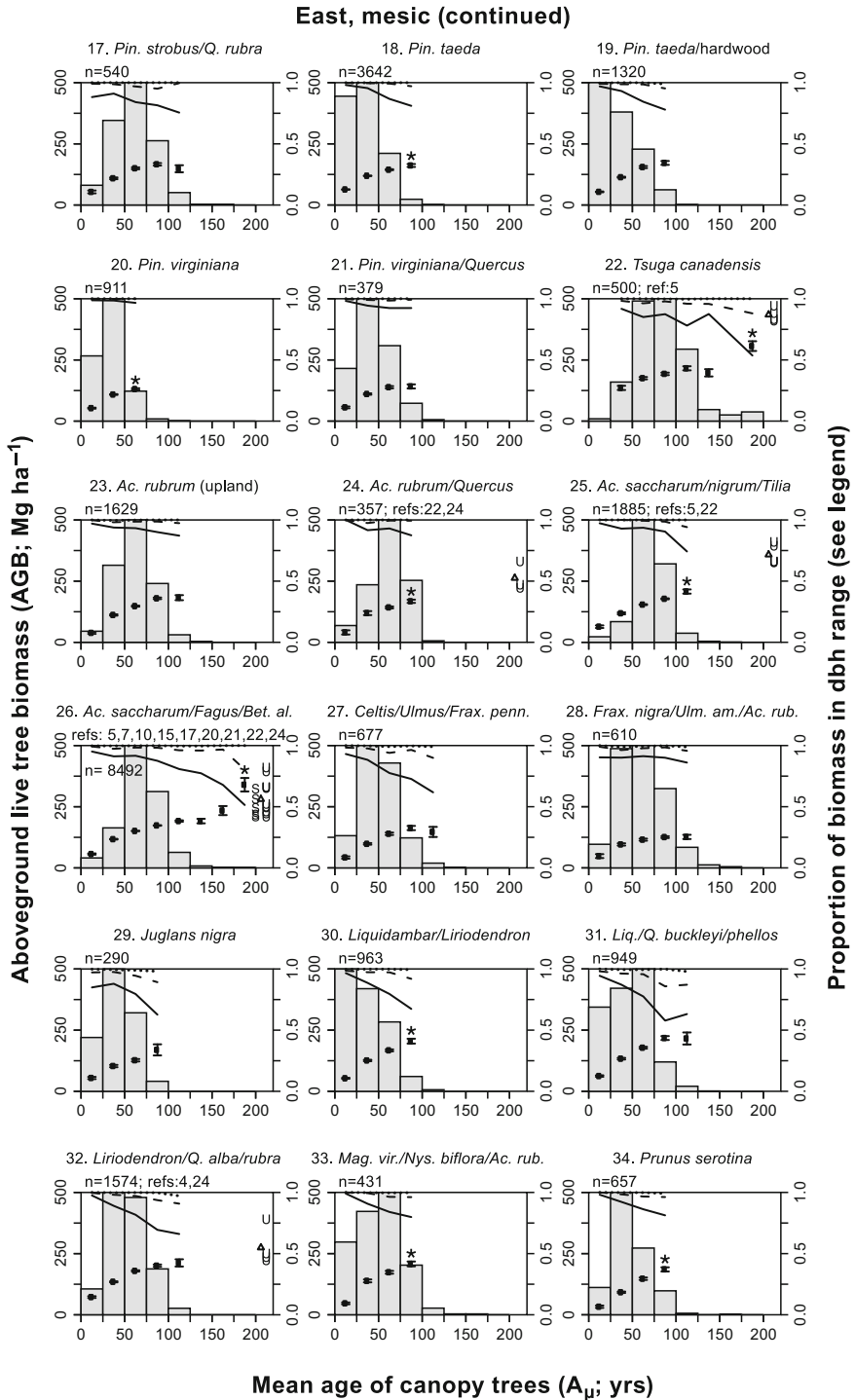
Fig. 14.2b (Continued)

East, mesic (continued)

Fig. 14.2c (Continued)

West, xeric (continued)

Aboveground live tree biomass (AGB; Mg ha⁻¹)

West, mesic

Boreal, xeric

Mean age of canopy trees (A$_\mu$; yrs)

Proportion of biomass in dbh range (see legend)
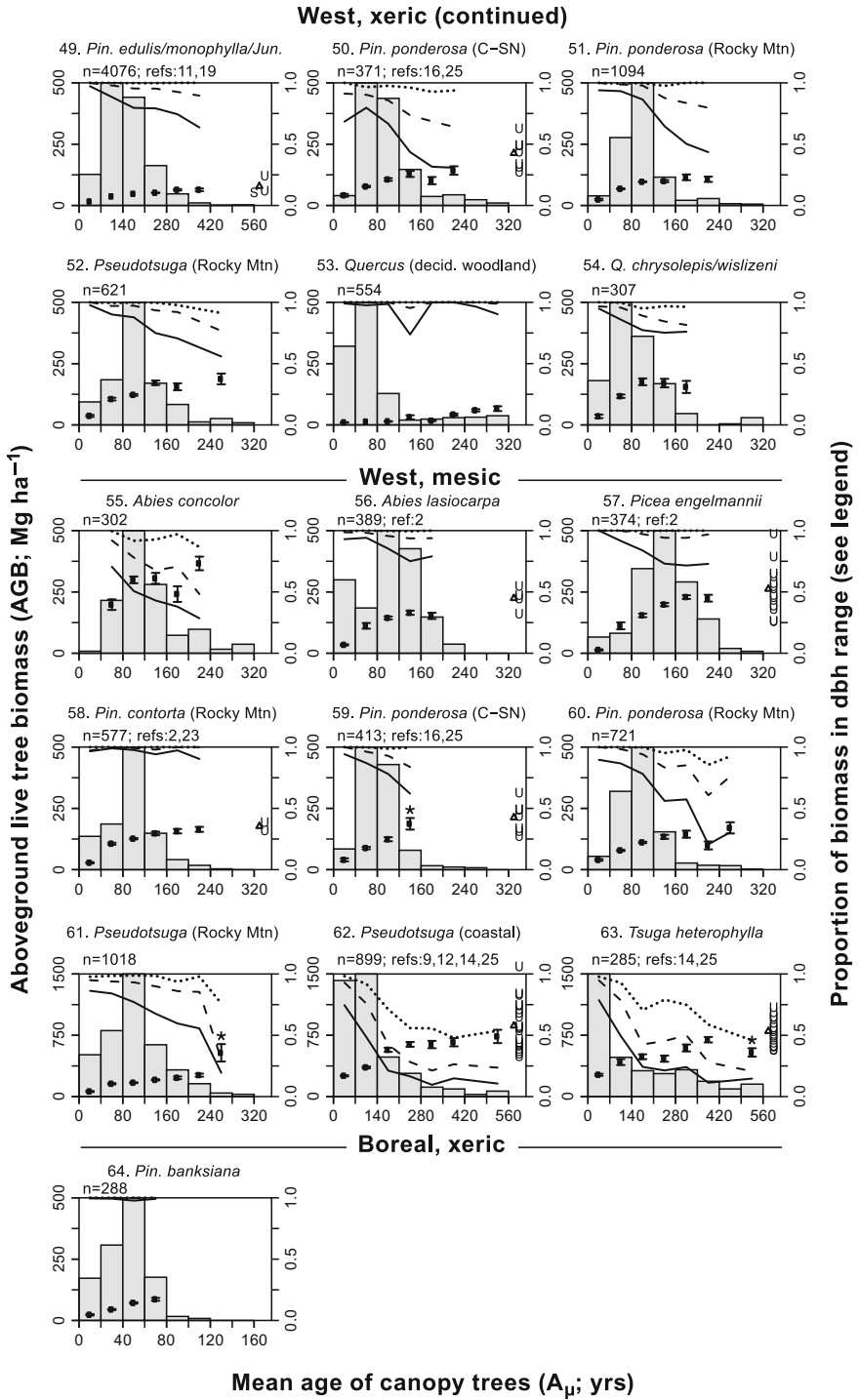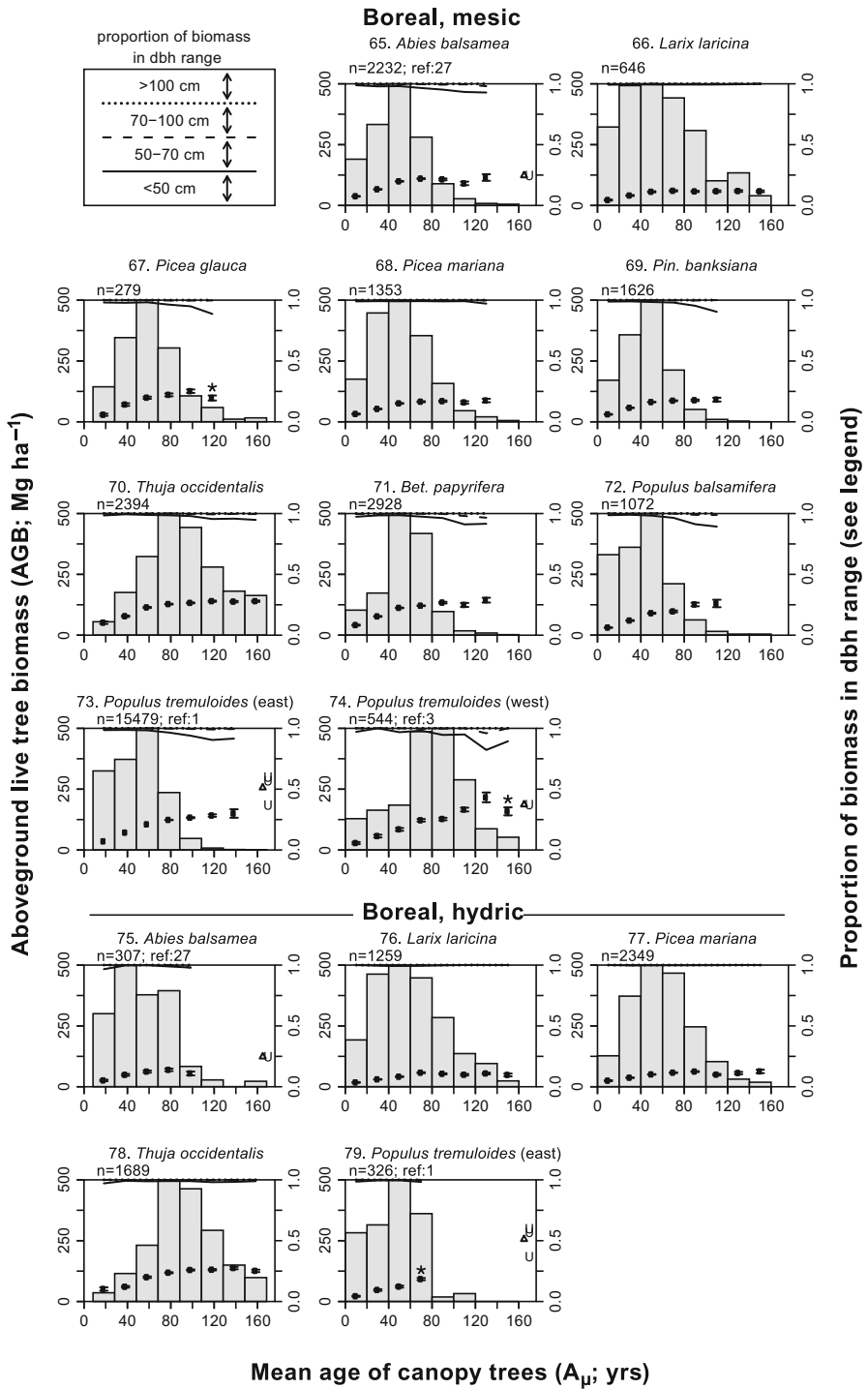
Fig. 14.2d   (Continued)

Fig. 14.2e (Continued)

(triangles in Fig. 14.2) for each of the 27 cases for which literature values were available. Mean literature values were higher than mean AGB in the oldest FIA age class in all but one case (Fig. 14.2, panel 26), and higher than the highest mean AGB of any FIA age class in all but two cases (Fig. 14.2, panels 26 and 74).

Some old-growth AGB estimates from the literature were considerably higher than FIA means, most notably the estimates from the eastern cove forests studied by Busing (1998; upper three literature values in Fig. 14.2, panels 22, 25, and 26) and the exceptional value for *Pseudotsuga* forest (1,591 Mg ha^{-1}; Fig. 14.2, panel 62) from Fujimori et al. (1976). The latter value is an estimate of stem biomass only; the AGB estimate for this stand would be even higher. (All other literature AGB values in Fig. 14.2 were calculated in a way comparable to our FIA estimates.)

For most of the eastern forest types, the contribution of large trees to AGB in the FIA data was small (typically < 5% of AGB due to trees with dbh >70 cm), even for the oldest age classes (see curves in Fig. 14.2 for AGB in different dbh classes). In contrast, Brown et al. (1997) found that trees with dbh >70 cm comprised 20–30% of total AGB in old-growth hardwood stands at different sites in the eastern US. Similarly, Mroz et al. (1985) recorded 12 trees ha^{-1} with dbh >65 cm in two *Acer saccharum* stands in northern Michigan, which would account for roughly 20% AGB in their study. Spetich and Parker (1998) found that trees with dbh >100 cm accounted for 16% of total AGB in an old-growth mixed *Quercus* stand in Indiana. Based on geography, soil, and topography, the above studies are probably representative of old-growth hardwood forests in much of the eastern US. On unusually good sites in the eastern US, large trees may comprise an even greater proportion of AGB. For example, in the southern Appalachian mixed hardwood and *Tsuga canadensis* forests studied by Busing et al. (1993) and Busing (1998), trees with dbh >70 cm and >100 cm comprised about 70% and 25%, respectively, of total AGB. These stands are in moist, topographically sheltered 'coves,' and are of unusual stature among surviving eastern old-growth forests. In contrast, eastern old-growth on poor soils or near the northern or elevational limits of the temperate hardwood zone may have much lower AGB contributions of large trees. For example, Martin and Bailey (1999) found very few trees with dbh >50 cm in a transition northern-hardwood/subalpine-conifer old-growth stand in the White Mountains in New Hampshire. Similarly, Morrison (1990) found that trees with dbh > 50 cm comprised just 14.5% and 6.5% of total AGB in two old-growth *Acer saccharum* stands in northern Ontario.

In contrast to eastern forest types, large trees accounted for a substantial proportion of AGB in the FIA data for some western forest types, particularly those found at low to mid elevations on mesic soils. For example, trees with dbh > 100 cm accounted for roughly half of AGB in the oldest FIA age classes for the coastal *Pseudotsuga menziesii* and *Tsuga heterophylla* types (Fig. 14.2, panels 62 and 63). Trees with dbh > 100 cm are characteristic of old-growth *Pseudotsuga* forests in the Pacific Northwest (Franklin et al. 1981) and accounted for roughly 50–70% of total live stem biomass in five old-growth *Pseudotsuga* communities studied by Grier and Logan (1977).

Table 14.2 Number of FIA chronosequences in which the mean AGB of the oldest age class was significantly different than the largest mean AGB of any other age class (two-tailed t-test; $\alpha = 0.05$). Three tests were performed for each forest type, using A_μ, D_1, or D_2 (Table 14.1) as the time axis defining the age classes. AGB increases with respect to D_1 and D_2 should be viewed with caution, due to the inherent circularity

	Coniferous forest types									Broad-leaved forest types								
	n total[a]	n declines[b]				n increases[c]				n total	n declines				n increases			
		A_μ	D_1	D_2	Any[d]	A_μ	D_1	D_2	Any		A_μ	D_1	D_2	Any	A_μ	D_1	D_2	Any
East																		
Xeric	1	0	0	0	0	0	0	0	0	6	0	0	0	0	1	3	3	6
Mesic	15	0	0	0	0	4	1	3	6	19	0	0	0	0	9	9	8	14
Hydric	2	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0
West																		
Xeric	7	1	0	0	1	0	6	4	6	2	0	0	0	0	0	1	2	2
Mesic	9	1	1	0	2	2	8	6	8	0	–	–	–	–	–	–	–	–
Hydric	0	–	–	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–
Boreal																		
Xeric	1	0	0	0	0	1	0	1	1	0	–	–	–	–	–	–	–	–
Mesic	6	1	0	0	1	0	2	2	2	4	0	0	0	1	0	4	3	4
Hydric	4	0	0	1	1	0	1	1	1	1	1	0	0	0	1	0	1	1
Total	45	3	1	1	5	7	19	18	25	34	1	0	0	1	11	17	17	27

[a]Number of forest types that appear in Fig. 14.2, which includes forest-type/soil-class combinations with ≥ 250 FIA plots

[b]Number of forest types in which mean AGB of oldest age class was significantly less than the largest mean of any age class in a given chronosequence

[c]Number of forest types in which mean AGB of oldest age class was significantly greater than the largest mean of any other age class in a given chronosequence

[d]Number of forest types in which a significant difference was observed in at least one of the three tests (A_μ, D_1, or D_2)

Table 14.3 Literature AGB estimates for old-growth forests in the coterminous US and southeastern Canada

Dominant species (in decreasing order of importance)	AGB (Mg ha^{-1})[a]	Age[b]	Panel numbers[c]	State/province	Reference key[v]
Populus tremuloides	284	55	73, 79	Minnesota	1[d]
Populus tremuloides	299	74	73, 79	Minnesota	
Populus tremuloides	184	64	73, 79	Minnesota	
Picea engelmannii, Abies lasiocarpa	130	400	57	Colorado	2
Picea engelmannii, Abies lasiocarpa	325	400	57	Colorado	
Picea engelmannii, Abies lasiocarpa	217	250	57	Colorado	
Picea engelmannii, Abies lasiocarpa	273	200	57	Colorado	
Picea engelmannii, Abies lasiocarpa	313	200	57	Colorado	
Abies lasiocarpa, Picea engelmannii	274	350	56	Colorado	
Picea engelmannii, Abies lasiocarpa	228	350	57	Colorado	
Picea engelmannii, Abies lasiocarpa	237	250	57	Colorado	
Abies lasiocarpa, Picea engelmannii	161	450	56	Colorado	
Pinus contorta, Picea engelmannii, Abies lasiocarpa	194	200	48, 57, 58	Colorado	
Picea engelmannii, Abies lasiocarpa	132	300	57	Colorado	
Abies lasiocarpa, Picea engelmannii	237	450	56	Colorado	
Picea engelmannii, Abies lasiocarpa	285	450	57	Colorado	
Abies lasiocarpa, Picea engelmannii	223	400	56	Colorado	
Picea engelmannii, Abies lasiocarpa	394	450	57	Colorado	
Picea engelmannii, Abies lasiocarpa	488	400	57	Colorado	
Picea engelmannii, Abies lasiocarpa	264	400	57	Colorado	
Picea engelmannii, Abies lasiocarpa	180	400	57	Colorado	
Populus tremuloides	186	123	74	New Mexico	3[e]
Liriodendron tulipifera, Quercus alba, Quercus velutina	390	340	32	Maryland	4
Liriodendron tulipifera, Quercus alba	430	340	–	Maryland	
Tsuga canadensis, Halesia carolina	416	>400	22	Tennessee	5[f]
Tsuga canadensis, Halesia carolina	441	>400	22	Tennessee	
Tsuga canadensis, Halesia carolina	471	>400	22	Tennessee	

(*continued*)

Table 14.3 (Continued)

Dominant species (in decreasing order of importance)	AGB (Mg ha⁻¹)[a]	Age[b]	Panel numbers[c]	State/province	Reference key[v]
Acer saccharum	394	>400	25, 26	Tennessee	
Halesia carolina, Acer saccharum	329	>400	25, 26	Tennessee	
Halesia carolina, Aesculus octandra, Acer saccharum	326	>400	25, 26	Tennessee	
Tsuga canadensis, Acer rubrum, Halesia carolina	410	>400	22, 25, 26	Tennessee	
Sequoia sempervirens	3,350–4,642	>1,000	–	California	6[g]
Acer saccharum, Acer saccharinum, Fagus grandifolia	218[m,n]	–	26	Ohio	7
Pinus albicaulis	390	640	–	Montana	8[h]
Pinus albicaulis	240	360	–	Montana	
Pinus albicaulis	225	310	–	Montana	
Pinus albicaulis	206	330	–	Montana	
Pseudotsuga menziesii	1,591	>500	62	Oregon	9[i]
Abies procera, Pseudotsuga menziesii	1,687	310	–	Washington	
Acer saccharum, Betula alleghaniensis	261	–	26	New Hampshire	10
Juniperus monosperma, Pinus edulis	53°	350	49	Arizona	11
Pseudotsuga menziesii	665	450	62	Oregon	12
Pseudotsuga menziesii	976	450	62	Oregon	
Pseudotsuga menziesii	492	450	62	Oregon	
Pseudotsuga menziesii	808	450	62	Oregon	
Pseudotsuga menziesii	555	450	62	Oregon	
Abies amabilis	446	180	–	Washington	13
Pseudotsuga menziesii, Tsuga heterophylla	620	500	62, 63	Washington	14
Acer saccharum, Quercus rubra, Fagus grandifolia	230	400	26	Quebec	15
Pinus ponderosa	245	190	50, 59	Oregon	16
Pinus ponderosa	247	251	50, 59	Oregon	
Pinus ponderosa, Calocedrus decurrens	314	316	50, 59	Oregon	
Betula alleghaniensis, Fagus grandifolia, Acer saccharum	209	–	26	New Hampshire	17
Quercus alba, Acer saccharum, Carya glabra	197[m, p]	–	2, 3, 36, 37	Illinois	18
Pinus monophylla, Juniperus osteosperma	60–121	260–320	49	Nevada	19[j]

Species				Location	
Acer saccharum, Betula alleghaniensis	245[q]	≥ 120	26	Ontario	20
Acer saccharum	210[q]	≥ 120	26	Ontario	
Acer saccharum	324[r]	–	26	Michigan	21
Acer saccharum	282[s]	–	26	Michigan	
Fagus grandifolia, Quercus prinus, Acer saccharum	330[m]	–	5, 24, 25, 26, 39	Kentucky	22[k]
Pinus contorta	160	300	48, 58	Colorado	23
Fagus grandifolia, Quercus alba, Acer saccharum	250[m]	–	2, 26, 32, 36	Indiana	24
Fagus grandifolia, Acer spp.	247[m]	–	26	Indiana	
Mixed hardwoods	235[m]	–	3, 24, 32, 35, 37	Indiana	
Fagus grandifolia, Acer spp., Liriodendron tulipifera	222[m]	–	24, 26, 32	Indiana	25
Pseudotsuga menziesii, Acer macrophyllum	584	460	62	Oregon	
Pseudotsuga menziesii, Tsuga heterophylla	649	460	62	Oregon	
Pseudotsuga menziesii, Thuja plicata	848	460	62	Oregon	
Pseudotsuga menziesii, Tsuga heterophylla.	837	460	62	Oregon	
Pseudotsuga menziesii, Tsuga heterophylla	635	450	62	Oregon	
Pseudotsuga menziesii, Tsuga heterophylla	1,244	460	62	Oregon	
Pseudotsuga menziesii, Tsuga heterophylla	1,065	460	62	Oregon	
Pseudotsuga menziesii, Pinus lambertiana	862	460	62	Oregon	
Pseudotsuga menziesii, Pinus lambertiana	524	450	62	Oregon	
Abies procera, Pseudotsuga menziesii	685	450	–	Oregon	
Tsuga heterophylla , Pseudotsuga menziesii	744	450	63	Oregon	
Pseudotsuga menziesii, Tsuga heterophylla	1,261	450	62	Oregon	
Pseudotsuga menziesii, Thuja plicata	1,124	450	62	Oregon	
Pseudotsuga menziesii, Thuja plicata	1,024	450	62	Oregon	
Tsuga heterophylla, Picea sitchensis	820	150	63	Oregon	
Tsuga heterophylla, Picea sitchensis	975	150	63	Oregon	
Tsuga heterophylla, Picea sitchensis	1,030	150	63	Oregon	
Tsuga heterophylla, Picea sitchensis	1,093	150	63	Oregon	
Tsuga heterophylla, Picea sitchensis	900	150	63	Oregon	

(continued)

Table 14.3 (Continued)

Dominant species (in decreasing order of importance)	AGB (Mg ha⁻¹)[a]	Age[b]	Panel numbers[c]	State/province	Reference key[v]
Tsuga heterophylla, Picea sitchensis	798	150	63	Oregon	
Tsuga heterophylla, Picea sitchensis	972	150	63	Oregon	
Tsuga heterophylla, Picea sitchensis	844	150	63	Oregon	
Pinus ponderosa	169	300	50, 59	Oregon	
Pinus ponderosa, Pinus contorta	137	400	50, 59	Oregon	
Pinus ponderosa, Pinus contorta	157	400	50, 59	Oregon	
Pinus ponderosa, Pinus contorta	219	500	50, 59	Oregon	
Tsuga heterophylla, Thuja plicata	569	500	63	Washington	
Abies amabilis, Chamaecyparis nootkatensis	726	300	–	Washington	
Abies amabilis, Thuja plicata	727	700	–	Washington	
Abies amabilis, Tsuga heterophylla	419	750	–	Washington	
Tsuga heterophylla, Pseudotsuga menziesii	721	750	63	Washington	
Abies amabilis, Tsuga heterophylla	1,024	1,000	–	Washington	
Abies amabilis, Tsuga heterophylla	799	1,000	–	Washington	
Abies amabilis, Tsuga heterophylla	800	1,200	–	Washington	
Pseudotsuga menziesii, Tsuga heterophylla	1,113	550	62	Washington	
Pseudotsuga menziesii, Tsuga heterophylla	702	470	62	Washington	
Tsuga heterophylla, Picea sitchensis	610	280	63	Washington	
Tsuga heterophylla, Picea sitchensis	945	280	63	Washington	
Tsuga heterophylla, Picea sitchensis	574	280	63	Washington	
Tsuga heterophylla, Picea sitchensis	843	280	63	Washington	
Tsuga heterophylla	658	230	63	Washington	
Tsuga heterophylla, Picea sitchensis	694	230	63	Washington	
Tsuga heterophylla, Picea sitchensis	766	230	63	Washington	
Quercus rubra, Quercus alba, Quercus macrocarpa	211[t]	–	2, 3, 36, 37, 40	Indiana	26
Abies balsamea	123	60	65, 75	New York	27[l]
Abies amabilis	465	175	–	Washington	28
Acer saccharum, Carya ovata, Quercus velutina	262[m, u]	–	2, 3, 36, 37, 40	Illinois	29

Sequoia sempervirens	732	–	–	California	30
Sequoia sempervirens	1,799	–	–	California	
Sequoia sempervirens	2,980	–	–	California	
Sequoia sempervirens	3,280	–	–	California	
Sequoia sempervirens	3,300	–	–	California	

[a] Numbers are in biomass units, rather than carbon (C). If aboveground C was reported, we converted C to AGB assuming a biomass:C ratio of 2:1

[b] Age is given if reported by authors. Depending on the study, 'age' may refer to mean tree age, maximum tree age, or time since last stand-replacing disturbance

[c] Panel number(s) in Fig. 14.2 in which old-growth AGB estimate appears. Based on reported species composition, each old-growth study was assigned to one or more FIA forest types. No panel number is given in cases where no matching FIA chronosequence was available (<250 FIA plots for the forest type in each soil class)

[d] Stands with age > 50 years and where *Populus tremuloides* comprised > 50% of total AGB are included here: authors state that *P. tremuloides* stands in their study area "attain at least some old-growth characteristics, such as fallen large trees and standing snags, by age 50–80"

[e] Regeneration from 1880 stand-replacing fire

[f] Stand ages reported in Busing et al. (1993)

[g] AGB range reflects different allometric assumptions for same stand

[h] Stands with age > 300 years are included here. Authors report total stand biomass (above- and below-ground) for all stands. We report AGB as 75% of total, based on the reported range across stands (70–80%)

[i] AGB estimate is for stem biomass only

[j] Cited in Grier et al. (1992), who report AGB and age range from Meeuwig (1979)

[k] Three communities identified in 52-ha tract: *Fagus grandifolia* (lower slope), *Acer saccharum/Tilia heterophylla* (middle slope), and *Quercus prinus/Acer rubrum* (upper slope). Brown et al. (1997) estimated mean AGB for the entire tract from the pooled dbh distribution reported by Muller (1982)

[l] We considered this 'wave-regenerated' stand to be old-growth because its age is close to the natural lifespan of *Abies balsamea* in the study area according to the author

[m] Biomass calculated by Brown et al. (1997) by applying standard allometric equations to dbh distribution reported in original paper. All other AGB values were estimated by the original authors using allometric equations

[n–u] Selectively logged or otherwise disturbed stands:

[o] Part of study area (Carmean Woods) selectively logged for large *Quercus* until ~50 years prior to study

[p] Cattle and sheep grazing and small amount of fuel-wood removed

[q] Study area (21 ha) selectively cut until 1898, and 1.2 ha completely cleared in 1800s. No trees cut between and 1898 and time of survey (1964)

[q] A few valuable *Betula alleghaniensis* removed in 1950s

[r] Selective logging of *Ulmus americana* and *Tilia americana* in early 1900s

ˢSelective logging of *Quercus alba* around 1900

ᵗGrazed from mid-1800s to 1917. Up to 50 dead or damaged trees removed from 8-ha tract in 1940s–1950s. Theft of 3–4 *Juglans nigra* in 1960s. Surveyed in 1992

ᵘAbout 100 trees removed from 7-ha tract from 1800s to 1950s. Surveyed in 1967

ᵛ*1* Alban and Perala (1992), *2* Binkley et al. (2003), *3* Binkley et al. (2004), *4* Brown and Parker (1994), *5* Busing (1998), *6* Busing and Fujimori (2005), *7* Cho and Boerner (1991), *8* Forcella and Weaver (1977), *9* Fujimori et al. (1976), *10* Goodale and Aber (2001), *11* Grier et al. (1992), *12* Grier and Logan (1977), *13* Grier et al. (1981), *14* Harmon et al. (2004), *15* Hooper et al. (2001), *16* Law et al. (2003), *17* Martin and Bailey (1999), *18* McClain and Ebinger (1968), *19* Meeuwig (1979), *20* Morrison (1990), *21* Mroz et al. (1985), *22* Muller (1982), *23* Ryan and Waring (1992), *24* Schmelz and Lindsey (1965), *25* Smithwick et al. (2002), *26* Spetich and Parker (1998), *27* Sprugel (1984), *28* Turner and Singer (1976), *29* Weaver and Ashby (1971), *30* Westman and Whittaker (1975)

14.3.2.3 Successional Changes in Biomass Associated with Species Turnover

We assembled FIA AGB chronosequences for early-, mid-, and late-successional forest types on mesic soils within restricted geographic and/or elevation ranges (Fig. 14.3; see figure legend for details of plot filtering). We used A_μ as the time axis to define the age classes; but because the emphasis here is on comparing AGB between, rather than within, chronosequences, our results do not depend strongly on how the age classes are defined. Our assignment of forest types to successional stages follows published accounts (Christensen and Peet 1981; Franklin and Hemstrom 1981; Heinselman 1981; Burns and Honkala 1990; Bergeron and Dansereau 1993; Pacala et al. 1996), but some degree of subjectivity is unavoidable. We included forest types with ≥ 10 plots in at least three different age classes. Some of the included types are represented by fewer than 250 FIA plots and therefore do not appear in Fig. 14.2. If more than four types were available for a given successional class in a region, we present chronosequences only for the four types with the longest available chronosequences; this restriction does not qualitatively affect the results. It is most meaningful to base comparisons among successional stages on the older age classes or on the overall mean across age classes; i.e., it does not make sense to compare AGB in old age classes of early-successional types to young age classes of late-successional types.

Among the seres we examined (Fig. 14.3), the *Pseudotsuga-Tsuga* transition in the Cascade Mountains of the Pacific Northwest provides the strongest evidence for an AGB decline associated with species turnover. In the upper Midwest, the mid-successional temperate forest types of relatively high AGB (*Acer rubrum*, *Quercus rubra*, *Pinus strobus*) are most likely to be replaced by the late-successional temperate types (*Acer saccharum/Fagus/Betula* or *Tsuga canadensis*) with similar AGB, rather than the late-successional boreal types (*Picea glauca*, *Abies balsamea*) with relatively low AGB (Burns and Honkala 1990). In all of the comparisons in Fig. 14.3, it is possible to identify transitions that could result in AGB declines; e.g., *Liquidambar/Liriodendron* to *Quercus/Carya* in the Piedmont, *Quercus rubra* to succeeding types in New England, or *Betula/Populus* to *Picea/Abies* in the upper Midwest. However, with the exception of the *Pseudotsuga-Tsuga* transition, these declines are small, and the overall impression is that species turnover is not associated with substantial AGB declines.

Unlike the FIA chronosequences within forest types (Fig. 14.2, Table 14.2), there was no evidence for late-successional AGB increases across forest types; i.e., except for the *Pseudotsuga-Tsuga* transition, mean and maximum AGB appeared relatively constant across successional stages in the seres we examined (Fig. 14.3).

For most forest types, the chronosequences in Fig. 14.3 are similar to those in Fig. 14.2 (which pools data across all geographic locations), although in some cases, small sample sizes in Fig. 14.3 result in chronosequences with few age classes and large standard errors (e.g., Rocky Mountain *Pseudotsuga*). AGB is somewhat

higher for coastal *Pseudotsuga* in Fig. 14.3 compared to Fig. 14.2 (panel 62), perhaps because the former was restricted to elevations 400–1,200 m, whereas the latter included all elevations (up to 1,866 m). For *Abies lasiocarpa*, the sharper decline in AGB in Fig. 14.3 compared to Fig. 14.2 (panel 56) may reflect sampling errors in the smaller dataset used in Fig. 14.3, violation of the space-for-time substitution assumption in Fig. 14.3 (e.g., if older stands tend to be at higher elevation), or a genuine effect that is masked in Fig. 14.2 by pooling over too large a geographic area.

The coastal *Pseudotsuga-Tsuga* AGB decline from ∼800 to 500 Mg ha^{-1} suggested by the FIA data (Fig. 14.3) is greater than that suggested by the old-growth literature data (Fig. 14.2, panels 62, 63), which have a mean of 878 and 809 Mg ha^{-1} for coastal *Pseudotsuga* and *Tsuga*, respectively. However, all but three of the literature values for *Tsuga* are from coastal *Tsuga/Picea sitchensis* sites (Smithwick et al. 2002). The three old-growth *Tsuga* literature values from the Cascades have a mean AGB of 678 Mg ha^{-1}. This brings the mean decline suggested from the literature (∼200 Mg ha^{-1}) closer in line with that suggested by the FIA data (∼300 Mg ha^{-1}).

14.4 Discussion

14.4.1 Late-Successional AGB Trajectories

Three lines of evidence suggest that, in most US forest types, AGB will stabilize or increase late in succession: (1) in the FIA chronosequences that controlled for successional changes in species composition (Fig. 14.2), late-successional AGB declines were rare, whereas late-successional AGB increases were relatively common (Table 14.2); (2) for a given forest type, old-growth AGB estimates from the literature tend to be higher than AGB in the oldest FIA age classes (Fig. 14.2); and (3) only one of the six regional seres we examined (Fig. 14.3), which account for successional changes in species composition, provides evidence for a substantial late-successional AGB decline. We now examine each of these lines of evidence and discuss the validity of our results.

14.4.1.1 FIA Chronosequences Within Forest Types

FIA data for only six of 79 forest-type/soil-class combinations provided statistical evidence for a late-successional AGB decline (Table 14.2). The true number of declines may be even smaller, because we did not correct for multiple testing (e.g., Bonferroni correction). Mechanisms that could lead to late-successional AGB declines within forest types (i.e., in the absence of major changes in species composition) are reviewed in Sects. 14.2.1–14.2.3. Either these mechanisms are not very important in the US, or our approach masked their effects. We now address three factors that could bias our FIA chronosequence results within forest types:
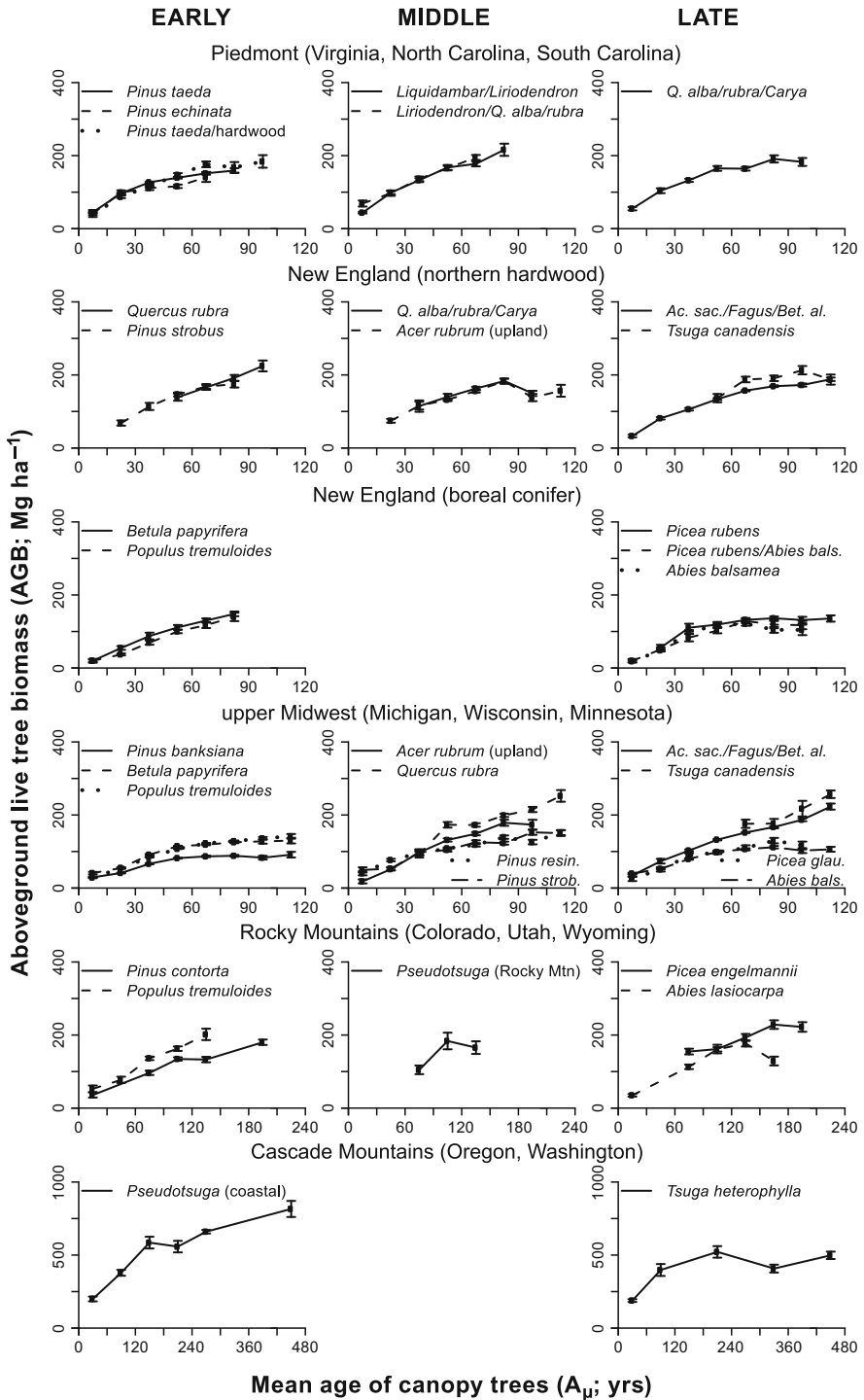
Fig. 14.3

(1) violation of the space-for-time substitution assumption, (2) inadequate proxies for stand age, and (3) limited chronosequence lengths.

Space-for-Time Substitution

The key assumption of the space-for-time substitution approach (Pickett 1989) is that stands that are currently in older age classes are informative about the future condition of stands (in other locations) that are currently in younger age classes. There are many reasons why this assumption might be false. We mention three that seem particularly important. (1) Beginning in the late 1800s, agricultural abandonment followed by forest regrowth would likely have occurred first on the least productive soils (Williams 1989; Birdsey et al. 2006). This would bias the older FIA age classes towards being on poorer sites than the younger age classes, and could potentially bias our results towards detecting 'false' late-successional declines. (2) Unlogged forests tend to be on unproductive and/or inaccessible sites (Stahle 1996), which would again bias the older age classes towards being on poor sites. (3) Since the most productive sites, supporting the most massive forests, would have been logged first, they may now host relatively old second-growth, while the poorest sites (logged later) may now host relatively young second-growth. This would bias the older age classes towards being on the richest sites. We do not know the relative importance of these different factors, but taken together, they seem as likely to bias our results in favor of detecting 'false' AGB declines as to prevent us from detecting 'true' ones.

Stand-Age Proxies

Because stand age (time since the last stand-replacing disturbance) is not available for FIA plots, we used three proxies – A_μ, D_1, and D_2 (Table 14.1) – as the time axes

Fig. 14.3 AGB chronosequences from FIA data for typical early- (*left column*), mid- (*middle column*), and late-successional (*right column*) forest types in several US regions. Only in the Cascade Mountains is there strong evidence for a substantial AGB decline associated with successional changes in species composition. In the upper Midwest, the mid-successional forest types with the highest AGB (*Acer rubrum*, *Quercus rubra*) are likely to be replaced by late-successional types of similar AGB (*Acer saccharum/Fagus grandifolia/Betula alleghaniensis* or *Tsuga canadensis*), rather than the boreal types of lower AGB (*Picea glauca*, *Abies balsamea*). Means and standard errors are shown at the midpoint of each age class with $n \geq 10$ plots. All data are from plots classified as being on mesic soils. 'New England' includes New York, Massachusetts, Connecticut, Rhode Island, Vermont, New Hampshire, and Maine. Data for other regions are restricted to the states indicated in the figure labels. Additional restrictions are as follows: Piedmont plots are east of the Appalachian Mountains; Rocky Mountains plots are at 2,500–3,500 m elevation; Cascade Mountains plots are at 400–1,200 m elevation and 121–123° W longitude. Abbreviations: Abies bals. *A. balsamea*; Abies lasio. *A. lasiocarpa*; Ac. sac. *Acer saccharum*; Bet. al. *Betula alleghaniensis*; Pic. engel. *Picea engelmannii*; Picea glau. *P. glauca*; Pinus resin. *P. resinosa*; Pinus strob. *P. strobus*

for AGB chronosequences within FIA forest types. A_μ is the time axis for the chronosequences presented in Fig. 14.2, whereas all three indexes were used in the analyses presented in Table 14.2 As discussed in Sect. 14.3.1.3 (see Stand Age) in most cases, mean AGB should decline with at least one of these indexes if in fact mean AGB declines with stand age. We acknowledge that there is no real substitute for knowing the true stand ages, but the fact that we detected significant late-successional AGB declines in only six of 79 chronosequences (Table 14.2) suggests that such declines rare in the US.

Chronosequence Lengths

In some forest types, there may be insufficient FIA data in old age classes to quantify late-successional AGB trajectories. This is likely the case, for example, in some of the *Pinus* types in the eastern US (Fig. 14.2, panels 11–20). The proportion of chronosequences showing late-successional AGB declines was lower in the east than in western or boreal regions, regardless of which stand-age proxy was used to define the age classes (Table 14.2). Nevertheless, AGB declines were neither common nor severe in any region. Comparing the three regions in terms of late-successional AGB increases is less straightforward: using A_μ as the stand-age proxy, relatively more increases were observed in the east compared to western or boreal regions (Table 14.2). In contrast, if we take D_1 or D_2 as the stand-age proxy, relatively fewer increases were observed in the east. Because of the circularity in testing for AGB increases using age classes defined by D_1 or D_2, the results based on A_μ are perhaps more credible. In this case, we would conclude that the relatively greater number of AGB increases in the east might be due to limited chronosequence lengths in this region.

   "In summary, the conclusion that late-successional AGB declines are rate in US forests appears to be robust, despite limited chronosequence lenghts in the eastern US. In contrast, this data limitation may have inflated the observed frequency of late-successional AGB increases in the eastern US."

14.4.1.2   Comparison of Literature and FIA Data

We were unable to locate old-growth literature AGB estimates for most forest types, so that literature values were available for comparison with only 27/79 FIA chronosequences (Fig. 14.2). The paucity of old-growth literature estimates reflects at least three factors: (1) Most studies of old-growth structure do not report AGB estimates. We hope that our work will encourage more researchers to include AGB estimates in their published work. If local biomass-allometry equations are not available, generalized equations (e.g., Jenkins et al. 2003) can be used. (2) The concept of old-growth is difficult to apply to forest types dominated by short-lived pioneer species (e.g., *Populus* spp. and some *Pinus* spp.) and to ecosystems where

the expected return time of stand-replacing disturbances (e.g., fire) is shorter than the time required for forests to reach quasi-equilibrium (Johnson et al. 1998). (3) Examples of old-growth are rare or nonexistent for some US forest types, particularly in the eastern US. This reflects the young age of most forests in this region (Fig. 14.2, histograms), as well as the elimination of the conditions needed to create or maintain some old-growth communities. For example, old-growth *Pinus palustris* (Platt et al. 1988, Means 1996) and *Pinus taeda/echinata* (Bragg 2002) forests – which are maintained by frequent, low-intensity fires in the southeastern US – have been mostly replaced by more shade-tolerant hardwoods due to disruption of natural fire-regimes (Means 1996; Gilliam and Platt 1999; Bragg 2004).

Old-growth literature AGB estimates were higher, on average, than mean AGB in the oldest FIA age class in 26/27 cases, and higher than the largest mean AGB of any FIA age class in 25/27 cases (see triangles in Fig. 14.2 for mean literature values). Other studies have also found that AGB estimates from FIA plots tend to be lower than those reported in the literature (Brown et al. 1997; Van Tuyl et al. 2005). One possible explanation for higher AGB in the old-growth literature is that these studies may sample older forests than the oldest FIA age classes, and that AGB tends to increase late in succession. This explanation is consistent with the observation that late-successional AGB increases are common relative to declines in FIA chronosequences (Table 14.2). Another explanation for higher AGB in the literature is sampling. Researchers, particularly those interested in old growth, may introduce sampling biases when selecting study sites; e.g., by (perhaps unintentionally) selecting sites with few gaps and unusually large trees (Busing et al. 1993). In contrast, the FIA is a systematic (unbiased) inventory. Thus, aside from any differences in stand age, FIA plots may be on poorer sites and may be more impacted by both natural and anthropogenic disturbances (e.g., selective logging, edge effects) compared to old growth described in the literature. On the other hand, because unlogged forests tend to be on unproductive sites (Stahle 1996), there could be a poor-site bias in the old-growth literature. In light of the unknown impacts of the above sampling effects, the observation that AGB in the old-growth literature tends to be higher than AGB in the oldest FIA age classes cannot be taken as strong evidence for late-successional AGB increases. However, this observation is at least consistent with our conclusions from the FIA chronosequences that late-successional AGB declines are rare in US forests, whereas increases are relatively common.

Associated with the differences in mean AGB between the old-growth literature and the oldest FIA plots are structural differences, with large trees (e.g., dbh >70 cm) comprising a smaller proportion of total AGB in the FIA compared to the literature, particularly in the eastern US (Sect. 14.3.2.2). The extensive literature review of eastern US old-growth by Tyrrell et al. (1998) does not include biomass estimates, but does include data on size (dbh) distributions that could be compared with FIA data. We expect that such a comparison would show that the density of large trees is higher in the old-growth literature compared to the oldest FIA age classes. As with comparisons of mean AGB, it would be difficult to know if

structural differences between the literature and the FIA are due to differences in stand age or other sampling effects.

14.4.1.3 Impact of Successional Changes in Species Composition

Our results are consistent with previous reports that, in some systems, changes in species composition result in late-successional AGB declines (Franklin and Hemstrom 1981; Shugart 1984; Pastor et al. 1987; Pare and Bergeron 1995). However, our results suggest that in the US, such declines typically represent less than 10% of peak AGB (Fig. 14.3). Among the seres we examined, the largest AGB decline associated with species turnover was in the Cascade Mountains in the Pacific Northwest, where FIA data suggest that a transition from old-growth *Pseudotsuga menziesii* to old-growth *Tsuga heterophylla* would result in a mean AGB decline from ~800 to 500 Mg ha^{-1} (Fig. 14.3). This decline is most likely due to the stature of the dominant species in these forest types (Franklin and Hemstrom 1981; Chap. 5 by Wirth and Lichstein, this volume). AGB estimates from the Cascade Mountains sites in Smithwick et al. (2002) lead to a qualitatively similar result (decline from 878 to 678 Mg ha^{-1}) for an old-growth *Pseudotsuga-Tsuga* transition. It is important to note that the successional transition resulting in this AGB decline of 200–300 Mg ha^{-1} may occur over millennia (Franklin and Hemstrom 1981), a time scale that is not particularly relevant to forest management. In contrast, conversion of an old-growth *Pseudotsuga* landscape to a managed landscape with a 50–100 year rotation length releases ~250–350 Mg C ha^{-1} (equivalent to 500–700 Mg biomass ha^{-1}) into the atmosphere, after accounting for storage in wood products (Harmon et al. 1990; Harmon and Marks 2002). In terms of forest management aimed at C storage in the Pacific Northwest, stand-replacing fires, though infrequent (Franklin and Hemstrom 1981), seem a more relevant concern than the possible loss of biomass over millennial time scales due to species turnover.

Unlike the FIA chronosequences within forest types (Sect. 14.4.1.1), the seres we examined provided no evidence for late-successional AGB increases across forest types (i.e., due to species turnover; Fig. 14.3). Thus, late-successional AGB increases, when they occur, are not expected to depend on late-successional changes in species composition.

14.4.2 Summary and Validity of Results

In summary, our results suggest that substantial late-successional AGB declines are rare in US forests. In contrast, late-successional AGB increases are relatively common, particularly in the eastern US. This may be due to the fact that many 'old' eastern forests are still accruing AGB as they transition from mature second-growth to old-growth. The largest decline we identified involves replacement of

Pseudotsuga menziesii in the Pacific Northwest by a late-successional species, *Tsuga heterophylla*, of smaller stature. Our approach may have underestimated the importance of late-successional AGB declines due to major windthrow or insect outbreaks, because the stand-age proxies available to us for FIA plots would not be meaningful if all large trees in a stand died within a short period of time (Sect. 14.3.1.3, Stand Age). Even so, it is unlikely that this situation is common in US forests, and our conclusion that AGB of most US forests will not, under current conditions, decline with age should be robust. Paludification and other mechanisms involving late-successional nutrient depletion (Sect. 14.2.3) appear to be of minor importance in most of the coterminous US; this is not surprising, since these mechanisms have been described primarily in boreal regions (e.g., Van Cleve and Viereck 1981; Harper et al. 2005). The boreal forests at the northern fringes of the coterminous US may not be representative of those at higher latitudes.

14.4.3   Implications

Among the proposed mechanisms for late-successional AGB declines that we reviewed, the most generic is the demographic transition from an even-aged forest of large trees to an uneven-aged forest of different-sized trees (Bormann and Likens 1979). The AGB chronosequences we present for different US forests types, together with the old-growth AGB estimates we compiled from the literature, suggest that this demographic transition does not typically result in AGB declines in US forests. This finding is consistent with the biome-wide biomass chronosequences that Pregitzer and Euskirchen (2004) assembled from literature data, which show a small live biomass decline in the oldest age class for boreal forests, but an increase in temperate and tropical forests. This suggests that late-successional biomass declines tend to occur in particular environments for particular reasons (e.g., insect outbreaks in boreal forests; MacLean 1980; Bergeron et al. 1995), rather than as an inevitable result of successional dynamics (see also Chap. 5 by Wirth and Lichstein, this volume). While not discounting the possibility that the demographic hypothesis of Bormann and Likens (1979) may be correct in some cases, we note that the evidence originally presented in support of this hypothesis was based not on data, but on the JABOWA forest simulator (Botkin et al. 1972). Other forest simulation models, including FORET (Shugart 1984), FORCLIM (Bugmann 1996), and SORTIE (Pacala et al. 1996), also show mid-successional biomass peaks, followed by a decline to an asymptote. Pacala et al. (1996) attributed the biomass peak in SORTIE to an overly simplistic mortality submodel that failed to cause sufficient self-thinning of large saplings.

   For all forest types, the age distribution of FIA plots in our sample peaked at either early- or mid-successional age classes (Fig. 14.2, histograms). In some boreal and western ecosystems, where natural return times for stand-replacing disturbances are relatively short, the age distributions in Fig. 14.2 may be similar to those expected in unmanaged landscapes. In contrast, in most of the eastern US

and in productive forests of the Pacific Northwest (e.g., Fig. 14.2, panels 62 and 63), the observed age distributions largely reflect landuse history (e.g., extensive clearing followed by agricultural abandonment in the east) and forest management (Williams 1989; Van Tuyl et al. 2005; Birdsey et al. 2006). The age distributions in Fig. 14.2 are not rigorous descriptions of the age distributions of US forest types because we did not correct for inaccessible land or for regional variation in sampling intensity and coverage prior to implementation of the FIA's national standard protocol in 1999. Nevertheless, the age distributions in Fig. 14.2 should be good approximations of the true distributions for most US forest types.

Because landuse and management have shifted the age distribution of US forests on productive sites towards younger age classes, and because our results do not support the notion of widespread late-successional declines in AGB, a substantial amount of additional carbon could probably be stored in US forests if large tracts of second growth were reserved from future harvest. This conclusion is consistent with previous studies of carbon storage in US forests (Heath and Birdsey 1993; Brown et al. 1997; Jenkins et al. 2001; Smithwick et al. 2002). It is well known that recovery of US forests from past landuse plays an important role in the northern hemisphere terrestrial carbon sink (Birdsey et al. 1993; Heath and Birdsey 1993; Houghton et al. 1999; Caspersen et al. 2000; Pacala et al. 2001; Birdsey et al. 2006). Our results suggest that projections of future carbon storage in US forests (e.g., Birdsey et al. 1993, 2006; Heath and Birdsey 1993) can reasonably assume that, in most cases, AGB will stabilize or increase, rather than peak and decline, as succession proceeds. Clearly, this conclusion applies to biomass accumulation in the absence of major disturbance such as stand-replacing fire.

The expected increase in US forest carbon stores under a reduced harvest regime does not translate directly into a prescription for forest management, which must balance socio-economic, carbon sequestration, and biodiversity objectives at different spatial and temporal scales. Forest management aimed at preservation of biodiversity and old-growth habitat must look beyond local and regional landscapes (Messier and Kneeshaw 1999; Berlik and Kittredge 2002); e.g., reduced harvest of US forests may be harmful for global conservation unless US consumption of wood products is also decreased. While recognizing the need to balance the goals of US forest management with those of global conservation, we note that there is so little old growth remaining on productive lands in the US that preserving these remnants would have little impact on available national harvest. Indeed, there is so little old growth left in the eastern US ($< 1\%$) that increasing its current area by an order of magnitude is not incompatible with maintaining or increasing total harvest from US forests.

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Chapter 15
Temperate and Boreal Old-Growth Forests: How do Their Growth Dynamics and Biodiversity Differ from Young Stands and Managed Forests?

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15.1 Introduction

Countries in the northern hemisphere are responsible for the emission of most of the 6.5 Gt carbon (C) produced from fossil fuels annually by humankind. However, it has also been estimated that from 1980 onwards, terrestrial ecosystems have been providing an effective sink for much of this carbon (Schimel et al. 2001; IPCC 2001, 2007). It has been proposed that the net carbon uptake of Europe, North America and Siberia has been as much as 4 Gt C year^{-1} in recent years, with a 0.4 Gt C year^{-1} sink-strength over Europe and a 1.3 Gt C year^{-1} sink-strength over Siberia (Schimel et al. 2001). Between 1980 and 2000 these regions jointly appeared to balance almost 90% of the fossil fuel emissions (1.9 Gt C year^{-1}) of the EU-15 and Russia.

Russian forests, due to their vast extent, appear to play a key role in the global carbon cycle, even though a major part of such forest is unmanaged primary or "old-growth" forest (Shvidenko and Nielsson 1994; TBFRA 2005). Thus, unmanaged forests may be an important component of the northern hemisphere terrestrial carbon sink (Luyssaert et al. 2008). However, the national reporting and accounting of carbon stocks that is submitted to the climate secretariat of the UNFCCC (United Nations Framework Convention on Climate Change), is based on UNFCCC (1992; Art. 2), which states that only anthropogenic interferences with the climate system shall be stabilised. From this it follows that unmanaged systems are not considered under the UNFCCC reporting system (Luyssaert et al. 2008; and see Chap. 20 by Freibauer, this volume), even though they provide an important service to mankind. Moreover, despite being carbon sinks, and thus contributing to stabilising atmospheric CO_2 concentrations, they do not qualify for carbon credits under current international legislation. One biological reason for excluding old-growth forests from reported carbon budgets has been the scientific paradigm that, in old forests, carbon uptake is balanced by respiration (Odum 1969). This view is

supported – but not proven – by a stand-level decline in net primary productivity (NPP) in even-aged mono-specific plantations (Binkley et al. 2002). It appears that these findings have been uncritically transferred to uneven-aged mixed old-growth forests, implying that old-growth forests are redundant in the global carbon cycle. Although this view has been challenged (Carey et al. 2001; Chap. 4 by Kutsch et al. this volume), this assumption highlights the notorious lack of observational or experimental evidence for Odum's equilibrium hypothesis, which can possibly be ascribed to the limited knowledge of unmanaged forests compared to managed systems.

Contrary to Odum's hypothesis, recent data show that untouched, primary and old-growth forest can be an important carbon sink (Luyssaert et al. 2008). At the same time, these forests represent a significant economic resource, yielding a multiplicity of products including environmental services. These services are endangered by intensified development and harvest (IPCC 2001), which often lead to complete or partial destruction of the current carbon stock and sink strength, turning these forests into substantial carbon sources. This has been clearly demonstrated using the deforestation of North America and the Amazon as examples (Houghton et al. 1999, 2000). The degradation of primary forest is now recognised as a significant component in the global carbon cycle, worthy of an international effort to reduce emissions from deforestation and degradation (Decision-/CP.13 2007).

In this chapter, the definition of the Food and Agriculture Organisation of the United Nations (FAO; TBFRA 2005) will be used to describe primary forest, which is "a forest of native species, where there are no clearly visible indications of human activities and ecological processes are not significantly disturbed". This definition includes all successional stages after disturbance (Korpel 1995), as well as "old-growth" forests at the more advanced stages. Thus, the term "primary forest" also includes naturally regenerating stands after large-scale wind-throw, insect outbreaks, fire, or avalanches as long as there was no human interference, e.g. wood extraction. Because the data sources we use in this chapter do not allow us to judge the degree of "old-growthness", in either the successional or structural sense (see Chap. 2 by Wirth et al., this volume), we refer mostly to "primary forest". When we use the term "old-growth", we refer to stands that approach a maximum biomass at high age. This usage of the term is based on plot-scale observations, which may differ according to regional and landscape perspectives. We deliberately avoid the terminology used throughout forestry industry of young, mature and over-mature forests. This is not suitable in our context because "maturity" in this narrow sense refers to the maximum economic value of the harvested wood from the forestry viewpoint. Over-mature forest has lost its timber value, but this could be at a very early age, depending on the product to be sold, and the same stand could become very "valuable" in terms of its biodiversity and its role in the global carbon cycle.

In the following, we discuss to what extent unmanaged primary forests differ from managed forests in terms of C-sequestration and biodiversity, and to what extent they may also be similar.

15.2   Global Distribution of Temperate and Boreal Forests

Temperate forests (Fig. 15.1) occur between 40° and 60° latitude in both the northern and southern hemisphere. Temperate climate is characterised by a strong seasonality (Chapin et al. 2002; Sitte et al. 2005) with mean summer temperatures in the range of 18–20°C and mean winter temperatures around 3–5°C. Forests occur when annual precipitation is sufficient to support tree growth, which is usually above 600 mm. This definition of temperate forests includes the coastal coniferous forests of the Pacific Northwest. Towards the tropics of Cancer and Capricorn there is a transition from temperate to Mediterranean and subtropical evergreen forests. Towards the northern polar circle, temperate forests turn into boreal forests, largely dominated by coniferous species extending beyond about 50° up to 71° N (Hatangar, Russia). In boreal forests, the winter is dominated by polar and the summer by temperate air masses, producing very cold winters (<-60°C temperature minima) and warm summers (>30°C temperature maxima). The temperature regime and the high latitude result in a short growing season of about 3 months with over 20 h of daylight per day. Precipitation ranges between 300 and more than 1,000 mm, depending on the distance to the nearest ocean.

The FAO assessment of temperate and boreal forest resources (TBFRA 2005) distinguishes between primary forest and various types of forest that are modified by man. The global forest area is estimated at 3.9×10^9 ha, of which one-third (1.3×10^9 ha) is still considered primary forest. About 45% of this primary forest is located in the northern hemisphere (0.57×10^9 ha), of which more than 90% is
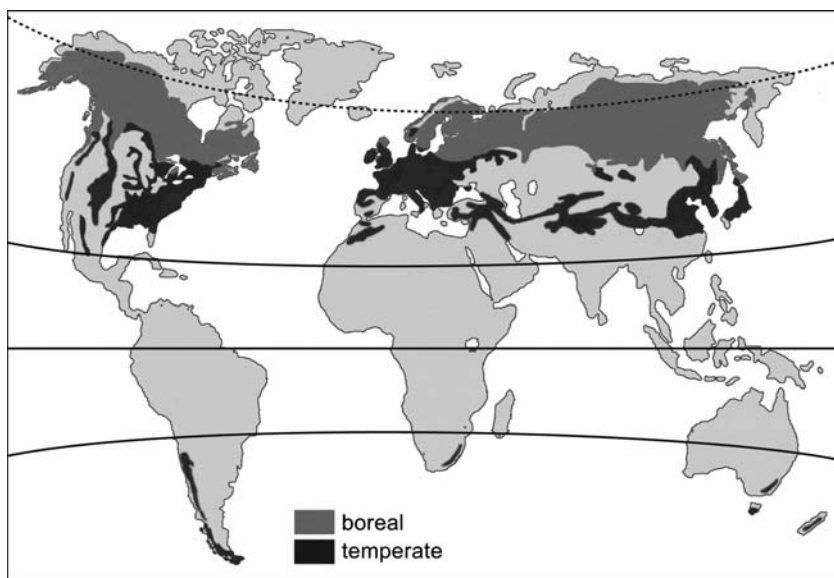
Fig. 15.1 Global distribution of temperate and boreal forests (after Sitte et al. 2005)

boreal forest in Russia, the United States and Canada. It is important to recognise that the primary forests of the northern hemisphere account for about 15% of the global forest area. The TBFRA report does not distinguish between boreal and temperate forest, therefore both regions are discussed jointly in the following.

15.3 Productivity of Temperate and Boreal Forests

Our analysis is based on a database of eddy-flux sites (Luyssaert et al. 2007) including managed and unmanaged stands. Additionally, old-growth forest sites in Europe and in North America were included (Korpel 1995; Van Tuyl et al. 2005). "Stand age" refers to the age of emergent trees of the main canopy, which is different from an average stand age (see Chap. 14 by Lichstein et al., this volume). The database includes a total of 513 forest sites where flux towers have been established. Selecting both boreal and temperate sites (Table 15.1), there are 152 sites where net ecosystem productivity has been measured. An additional 67 old-growth sites were taken from the literature, when biomass, NPP and stand density had been published. Not all sites reported this information in full. Thus, the number of sites varies for different aspects of this study.

We found that biomass accumulates with age, and that accumulation continues even in stands with 800-year-old canopy trees (Fig. 15.2a; see also Luyssaert et al. 2008). This pattern of biomass accumulation holds for broadleaf and coniferous stands as well as for temperate and boreal forests. The response was irrespective of management. The variation in biomass accumulation for a given age is large, especially in the temperate zone, where some forest species have much higher growth rates than others (e.g. *Populus* vs *Quercus*, or *Pseudotsuga* vs *Thuja*). Also large variations exist within a species according to site quality (yield class). In contrast to managed forests, most natural forests are uneven aged. Thus, an 800-year-old canopy may contain a second or third canopy layer of younger trees, but

Table 15.1 Number of sites for which data were available to analyse the relationships of age and density to biomass, net primary productivity (NPP) and net ecosystem productivity (NEP)

	Age			Density		
	Biomass	NPP	NEP	Biomass	NPP	NEP
Boreal	72	83	27	65	45	22
Temperate	147	120	102	108	105	73
Deciduous	84	64	40	50	46	21
Mixed	5	11	6	5	1	4
Evergreen	135	129	91	123	104	75
Managed	94	58	63	60	44	37
Unmanaged	30	36	19	20	15	12
No information	92	80	62	90	83	39
Recently disturbed	3	23	8	3	1	7
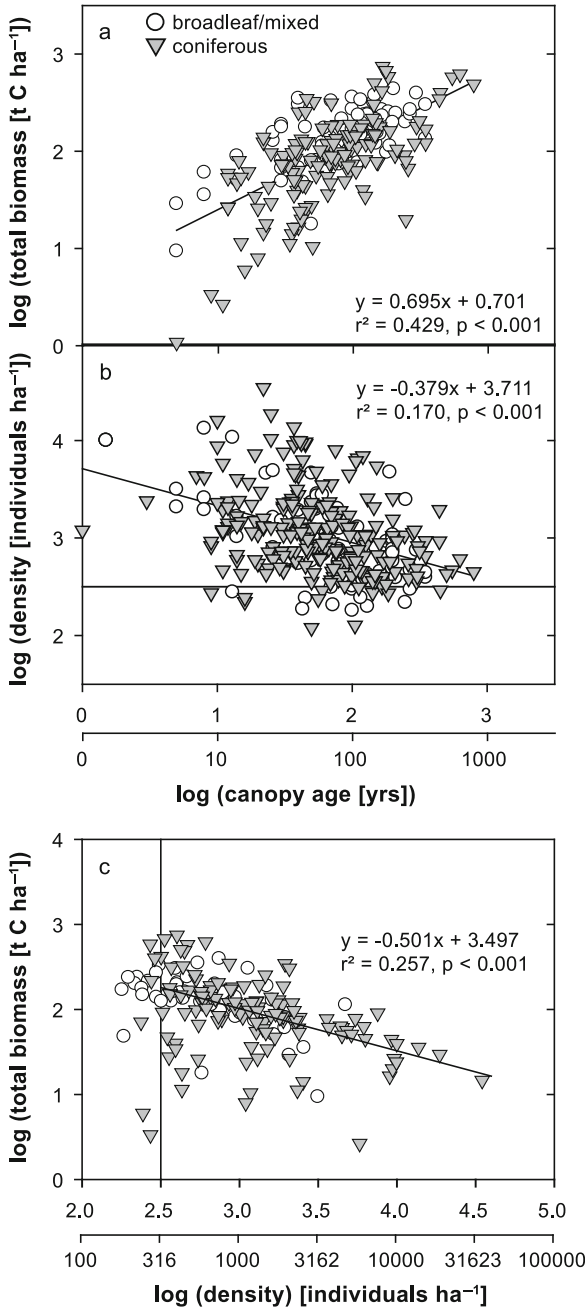
Fig. 15.2 a Total biomass accumulation and **b** stand density in temperate and boreal forests as related to the age of the emergent trees of the main canopy. The data show that low stand density is not restricted to old-growth forests, but can be found in all age classes. The *horizontal line* in **b** indicates the cut-off point in the self-thinning line where the crowns of the remaining canopy no

the processes at the stand level are still dominated by the old canopy. Carbon accumulation in aboveground biomass between age 100 and 300 years is about 0.3 t C ha^{-1} year^{-1}. Based on the areal extent of primary forest in the northern hemisphere, these unmanaged forests may accumulate about 0.4 Gt C year^{-1} in their aboveground woody biomass (not even accounting for changes in soil carbon). Thus, they represent a major fraction of the total northern hemisphere sink.

When relating biomass to density, it emerges that all stands follow a process of density-driven mortality, which is described by the thinning rule (Yoda et al. 1963). Some trees continue to dominate and get bigger at the expense of subdominant trees, which die. The slope of the biomass-density relationship as observed in this study is close to the theoretical self-thinning line of 0.5 that was developed for monocultures (Fig. 15.2c). Biomasses below this self-thinning line represent forests where the canopy is not fully closed due to management, stand disturbances, or stands of multiple canopy layers (Schulze et al. 2005a, p 405).

With increasing age, stand density decreases exponentially (Fig. 15.2b). If calamities occur, old forests may reach densities where the projected crown area of canopy trees no longer covers the ground area, and biomass falls below the self-thinning line (vertical line in Fig. 15.2c; horizontal line in Fig. 15.2b). With sufficient regeneration in the understorey, these stands will recover and reach the self-thinning line again at higher stand density. Thus, the variation in density is huge, depending on species, site conditions and canopy structure. However, there is no significant difference between boreal and temperate, or between broadleaf and coniferous forest.

The interpretation of the biomass-age relationship of Fig. 15.2a is complex. Based on the same dataset we investigated some of the component processes (Fig. 15.3). It emerges that biomass per living tree increases almost linearly over time, as is known from growth curves of large individual plants (Hunt 1982). The net growth rate per tree was constant up to an age of 850 years (0.5 kg C tree^{-1} year^{-1}). However, at the stand level, a large number of trees died in thickets of regeneration. This mortality results in removal of living into dead biomass at a constant rate of 0.3 kg C tree^{-1} year^{-1}. Thus, total tree biomass growth was 0.8 kg C tree^{-1} year^{-1} up to age 800 years. Mortality accounts for 37% of total productivity. The growth rate per total biomass decreased from 0.2 t C t C^{-1} year^{-1} at age 1 year to 0.001 t C t C^{-1}year^{-1} at age 850 years due to increasing biomass. The growth analysis shows that growth of the remaining trees accumulates 63% of total productivity. The effect of mortality of individual trees may be different for broadleaves and conifers. Broadleaved trees are better able to extend branches laterally

Fig. 15.2 (continued) longer cover the ground area. **c** Self-thinning shown as the relationship between the logarithm of aboveground biomass and the logarithm of stand density (redrawn from Luyssaert et al. 2008). The *vertical line* was placed visually to indicate the cut-off at which the number of individuals becomes too small to cover the area. The *regression line* indicates the self-thinning line according to Yoda et al. (1963). In all panels *circles* denote broadleaf and mixed forest, while *triangles* denote coniferous forests
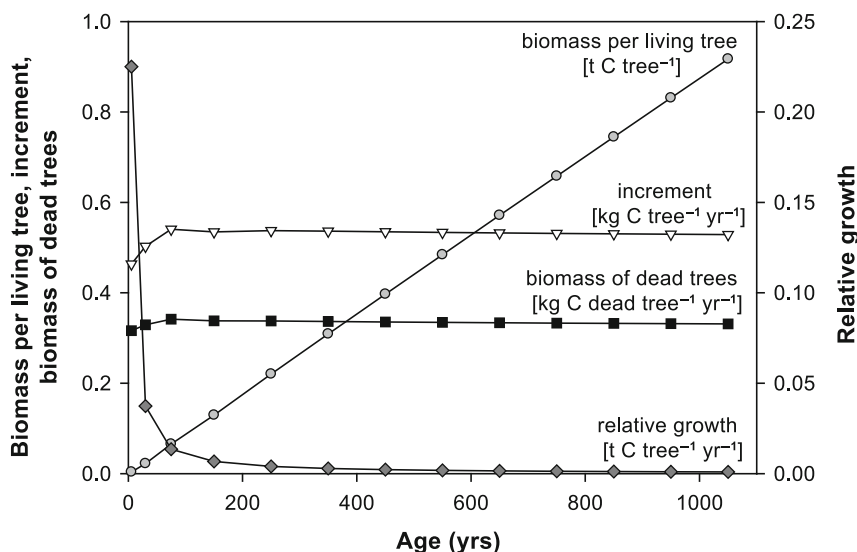
Fig. 15.3 Tree biomass and growth, tree mortality, and relative growth rates as related to stand age. The curves were calculated from the biomass and density relations shown in Fig. 15.2

and close gaps, while the lateral growth of branches in conifers is limited and gaps may remain open. This is shown in Fig. 15.2c as the critical stand density at which the biomass accumulation becomes saturated – probably in the range of 200–300 trees/ha for broadleaved trees (crown diameter of 6–8 m), and 500–1,000 tree/ha for conifers (crown diameter 3–6 m). The inventory-based data of Lichstein et al. (Chap. 14, this volume) demonstrate such an asymptote in biomass with increasing age, especially in stands with multiple canopy layers. It should be emphasised that the decline in biomass at low densities is neither age-dependent nor density-dependent but rather the result of calamities that cause size-independent mortality.

In unmanaged forests, a decrease in stand density, or gaps due to the loss of a major canopy tree, results in a new generation of trees, which sustains stand density. The process of re-generation may be closely linked to stand density to the extent that stand biomass may continue to increase even during replacement of the main canopy, as shown for fire successions of *Larix* and evergreen conifers in Siberia (Schulze et al. 2009; see also Fig. 15.8). At this point it becomes important that we selected sites where flux measurements were available. Reichstein et al. (2007) showed that ecosystem respiration is linked closely to stand photosynthesis (Reichstein et al. 2007), and Luyssaert et al. (2008) demonstrated that the ratio of heterotrophic respiration R_h and NPP was constant with age, reaching a value of 0.6 to 0.7. Thus, ecosystem respiration is driven by assimilation. This was confirmed experimentally by large-scale girdling experiments (Hoegberg et al. 2001), where ecosystem respiration dropped to 30% of the initial value. Knohl et al. (Chap. 8, this volume) also confirm that NPP and net ecosystem productivity do not decrease significantly with age. The ecosystem carbon-balance cannot reach zero or be
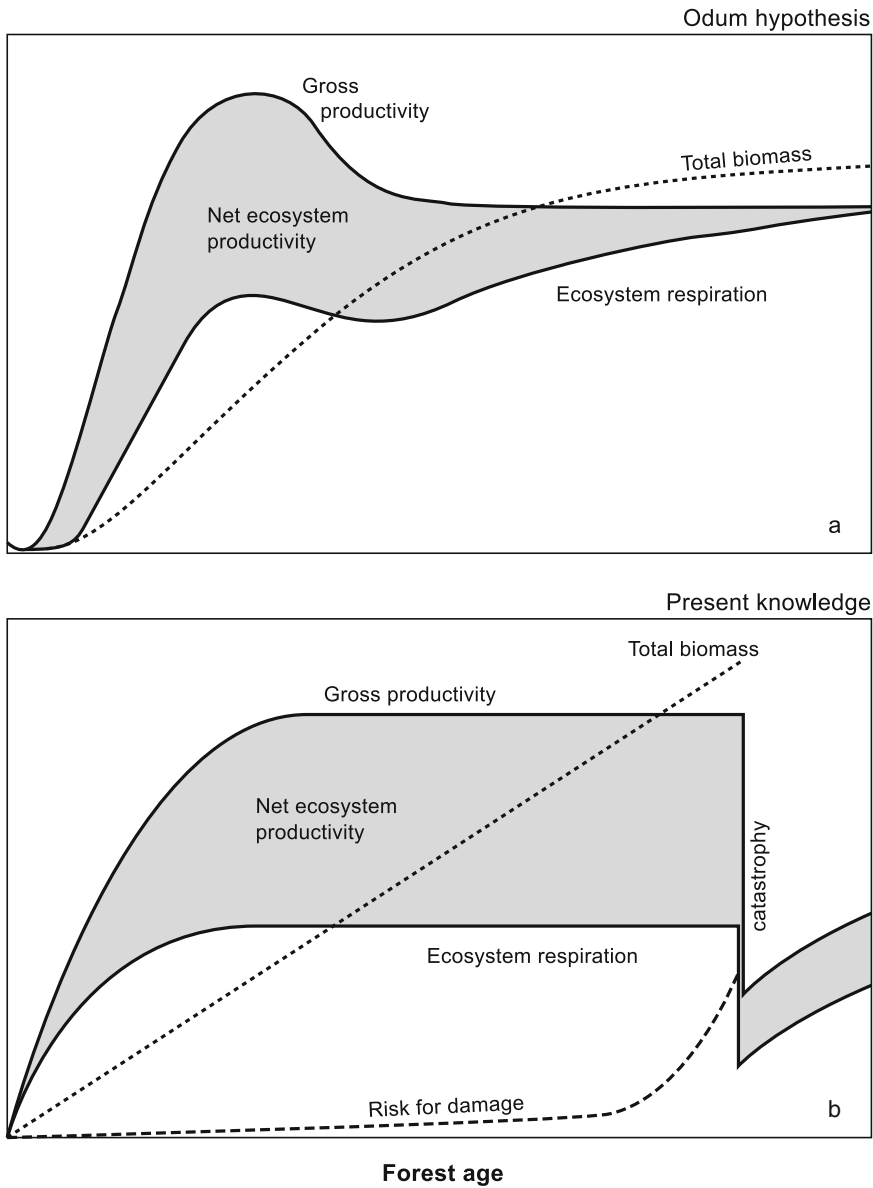
Fig. 15.4 a Schematic presentation of gross primary productivity, ecosystem respiration, net primary productivity and stand biomass as a function of forest age according to Kira and Shidei (1967) and Odum (1969, redrawn from Carey et al. 2001). **b** Proposed age dependency of gross primary production, ecosystem respiration, net primary productivity, total biomass and the risk for damage

negative, except for transitional periods of times – mainly after catastrophic events. The accumulation of carbon in soils, coarse woody detritus and charcoal since glaciation of the boreal forest in Siberia is a visible sign that an equilibrium between assimilation and respiration has not been reached also at larger scale (Ciais et al. 2005).

The age-independent ratio of R_h/NPP as shown by Luyssaert et al. (2008) is the most convincing demonstration that the Odum-paradigm of a zero carbon balance in old-growth forests must be rejected. Figure 15.4 depicts the main idea of Odum (1969), namely that gross primary productivity reaches a maximum at a young age and levels off with further growth, while ecosystem respiration continues to increase due to the increased biomass. At high age, ecosystem respiration approaches gross primary production, and it is at this point that Odum (1969) assumed that the carbon balance of the system approaches zero. At late age, total biomass remains constant, i.e. growth balances the production of litter. At present knowledge, gross primary production is constant over time, dependent only on available radiation and leaf angle (Schulze et al. 2005a). Since respiration depends on available carbohydrates and not on biomass (which in trees is mainly dead wood), the carbon balance remains positive and constant. Stand biomass continues to increase with age. However, there is an additional process, namely the risk of damage, which increases exponentially with biomass. This leads to catastrophes (windbreak, fire), which can be partially or totally stand replacing. However, ecosystem respiration will also decrease, unless accumulated resources are open to decay (e.g. woody detritus after windbreak). Otherwise the system will continue to grow and recover. After all, in contrast to the organisation in animals, trees are open systems, which enables them to restore growth even after severe damage.

The self-thinning rule suggests that mortality is a function of the growth rate. In fast-growing species (e.g. Douglas fir), the critical stand density of canopy opening is reached faster (and at an earlier age) than in slow-growing species (e.g. red cedar). Thus, only inherently slow-growing species, or sites supporting only low yield classes, will reach a high biomass, and the status of "old-growth" forest, at a later age (Schulze et al. 2009).

Based on Fig. 15.3, forest density and growth rates appear to be more important than age in explaining stand biomass. Forest stands may accumulate biomass for centuries, and in this process they will lose individual trees by self-thinning mortality or disturbances (windbreak, fungal disease, or lightning) or by management. The net effect can be an accumulation of biomass until a critical threshold of biomass or density is reached. Is there a maximum biomass or carbon density? It seems that forests can accumulate biomass to levels of up to 800 t C ha^{-1}, which is about 3,200 m^3 wood ha^{-1}, depending on the species. In Fig. 15.3, stands reaching this biomass were *Pseudotsuga* stands at an age below 200 years and *Thuja* stands at an age beyond 600 years. Obviously, at some point in time, depending on species, the system appears to become mechanically unstable (Quine and Gardiner 2006), and individual components of the forest, or even the entire forest, may collapse due to external forces, mainly wind (Fig. 15.2c, vertical line), which initiates a new succession. The effect of wind increases with exposed crown area, and with the
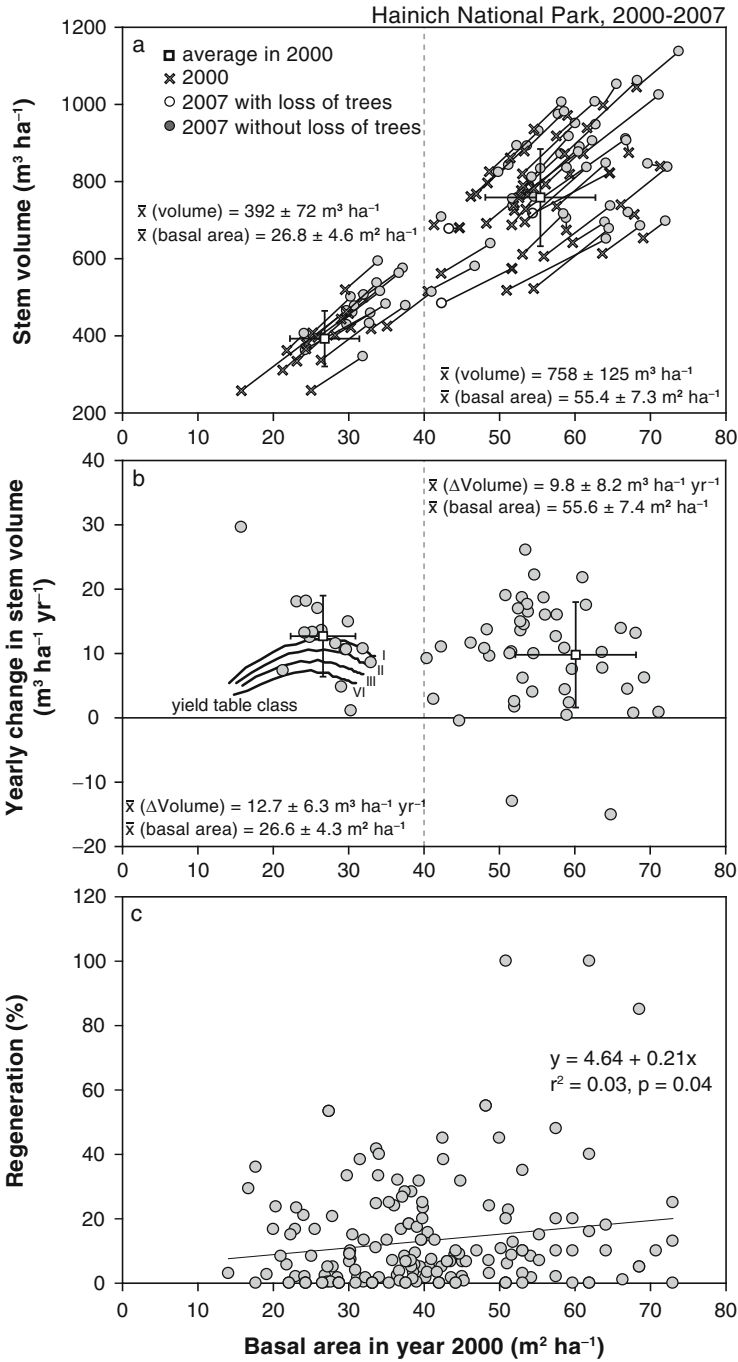
Fig. 15.5 **a** Stem volume as related to basal area on several plots of a repeated inventory of the Hainich National Park, Germany. The inventories were made in the years 2000 and 2007. **b** Annual change in stem volume between 2000 and 2007 as related to basal area in 2000. Negative

distance between trees, i.e. with decreasing stand density (Quine and Gardiner 2007). In addition, old trees become increasingly affected by fungal heart-wood rot (Schulze et al. 2009), which in turn decreases their stability and their strength to withstand strong wind. Consequently, the decline in stand density is related not to age, but results from species-specific structural attributes, disease, or management.

An inventory study of the Hainich National Park (NP) in Germany is given as an example of the biomass dynamics in an old-growth beech forest (*Fagus sylvatica*). Stand volume and basal area are linearly related, which implies that stand height is almost constant (Fig. 15.5; Hessenmoeller et al. 2009). Within the time of two consecutive surveys, stand volume and basal area increased at all inventory spots, except at those where a tree had collapsed. This happened on 3 out of 63 plots (5% of plots) within 7 years. Plots where such loss occurred had reached neither the highest stand volume nor the largest basal area. Although plot biomass decreased in these cases, it never became zero, and we can assume that these plots will again accumulate biomass in the future. Plot history of growth and losses revealed that the variation of biomass increased with basal area. The net growth rate of woody biomass in the old-growth stand was the same as the growth rates of 150-year-old beech trees according to the yield tables (Fig. 15.5b, curved lines). However, the total stand volume of the old growth stand was higher by a factor of 2 than that presented in the relevant yield tables. On average, the net increment in woody biomass (which is woody NPP minus biomass losses) was $9.3 \pm 0.6 \, \mathrm{m^3 \, ha^{-1} \, year^{-1}}$.

In the case of Hainich NP, when a single tree collapsed or was felled by wind, the neighbouring canopies remained undamaged. Uprooting and wind throw of individual trees resulted in relatively small gaps that were soon colonised by new regeneration. The instability of the stand, and the magnitude of fungal attacks, increased with basal area (S. Kahl, personal communication). Regeneration was high even in stands with high age and high basal area (Fig. 15.5c). The whole process of regeneration initiated by the collapse of individual trees resembles the earlier hypothesis of Watt (1947) that, in terms of their spatial extent, the successional stages in a plant community resemble at any given time a dynamic mosaic of patches.

Large-scale disturbances and stand destruction can occur at any time and at any place. A stand needs to be shielded for centuries from these events in order to turn into an old-growth stand. Since biomass accumulation and collapse are highly asymmetric with respect to the time it takes for destruction and recovery, and even though extreme climatic events are stochastic, the probability that a disturbance is caused is higher in stands with high aboveground biomass. As a consequence, old stands are rarer than young stands, even in an unmanaged landscape (see

Fig. 15.5 (continued) numbers indicate the loss of a major canopy tree. The small parabolic curves show the yearly increment in stem volume of different yield classes according to yield tables. It is interesting to note that yield tables cover only the lower end of basal areas that are found in the unmanaged forest, and that unmanaged forest stands reach higher annual wood increment rates than predicted by yield tables. **c** Regeneration in 2007 as related to basal area (after Hessenmoeller et al. 2009)
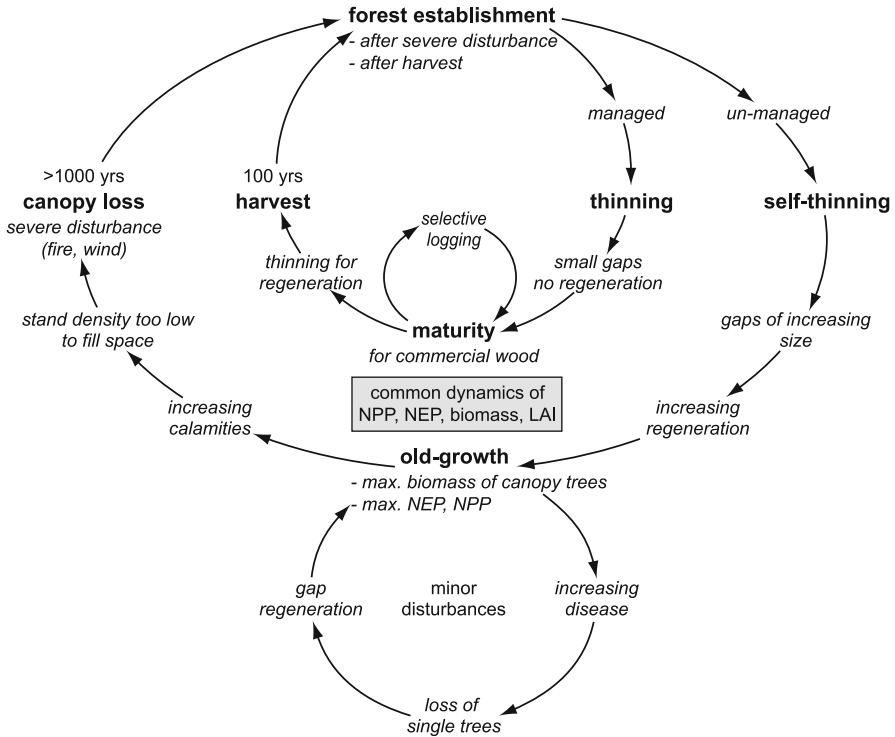
Fig. 15.6 Conceptual scheme of processes that affect biomass and turnover in managed and unmanaged forests

below; Mollicone et al. 2002; Chap. 2 by Wirth et al., this volume). At the landscape level, there is a mosaic of forests characterised by different times having elapsed since the last stand-replacing disturbance. Nevertheless, these differently aged forests follow the same relationship trend between biomass and age (Fig. 15.2a).

We may conclude that old-growth forests do not differ from younger stands with respect to their productivity at similar yield class and, on average, they maintain the capacity for carbon sequestration due to gap regeneration. The processes that determine stand biomass in managed and unmanaged forests are summarised in Fig. 15.6. Following disturbance, managed and unmanaged forests develop very similarly. In managed forests, thinning by forestry reduces stand density, but gaps are kept small to avoid regeneration. The managed forest reaches "maturity" whenever a commercial yield of timber is reached. Maturity could be reached at age 30 years for firewood and at age 100 for saw-wood timber. Thereafter, depending on species, the stand is harvested, or regenerated below an increasingly open canopy. A permanent canopy cover is also possible in forests that are managed by selective cutting. In unmanaged forests, self-thinning reduces stand density initially but, with increasing dimensions of trees, gaps may become large enough to initiate
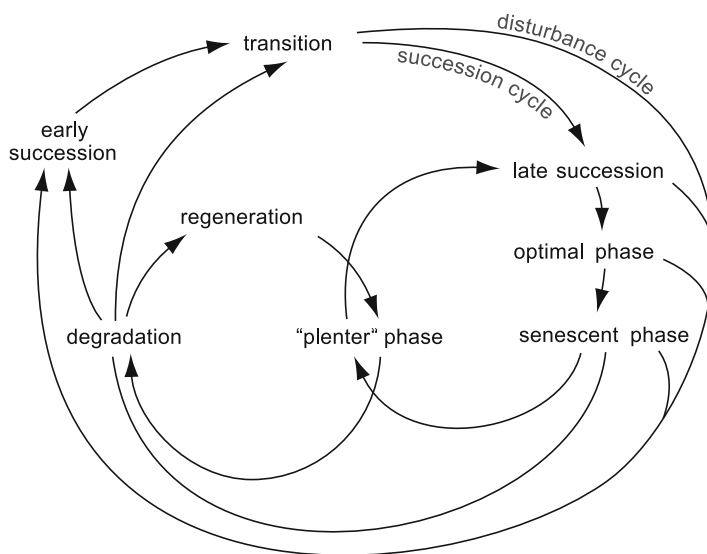
Fig. 15.7 Stages of natural forest succession in primary forests without and with disturbances (after Scherzinger 1996)

regeneration. The stand reaches an "old-growth" stage when the maximum biomass of the canopy is reached. At that stage, there is increased risk that single canopy trees collapse due to increasing attack of heartwood by fungi, and due to increased load for wind. Single-tree-collapse results in gaps that are closed by regeneration. However, increasing calamities may also open the canopy and induce further risk of mortality by wind or by fire, which may lead to total canopy loss also in primary forests. This results in new forest establishment as in managed forests. Thus, managed and unmanaged forests have similarities in their dynamics. The main difference is the total time required for turnover, and the end-product. Managed forests produce commercial wood for products, while unmanaged forests contribute coarse woody detritus to the carbon pool in soils.

15.4   Disturbance and Forest Succession at the Regional Scale

According to Scherzinger (1996), the successional cycle distinguishes between early and successional stages, which contain an optimal phase and a senescent phase, and which then returns to the successional stage. However, this idealised cycle may not exist in nature. Various kinds of disturbances appear to drive forest succession at different spatial scales. Disturbance can be an immediate destructive process at any one of these stages (Fig. 15.7). In fact, regeneration and senescence may become a continuous parallel process that may result in old-growth forests of heterogeneous spatial structure. Disturbances may be natural or anthropogenic, and
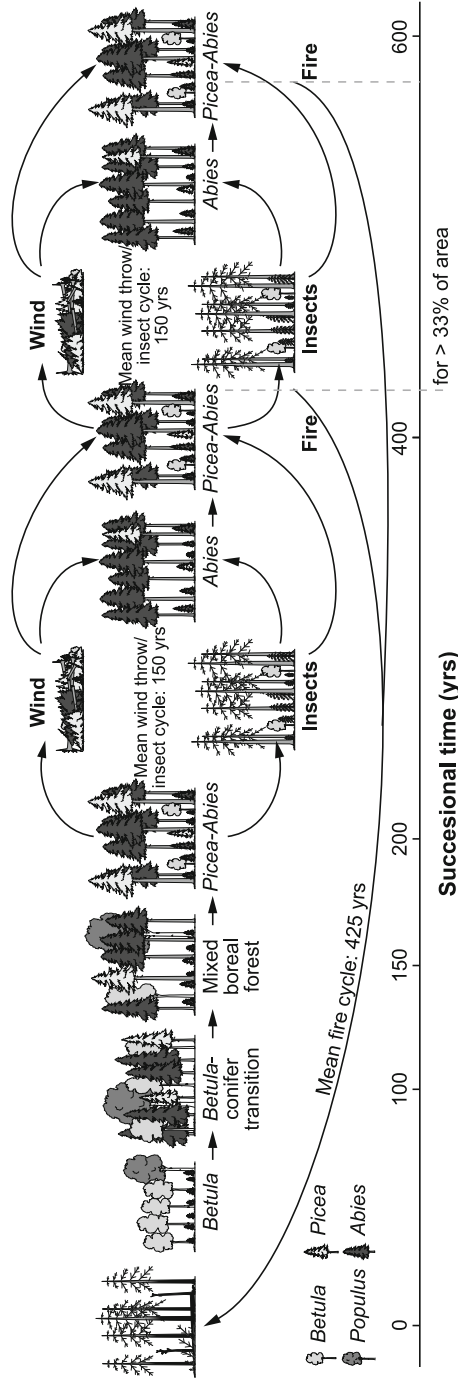
Fig. 15.8 Succession in a *Picea*- and *Abies*-dominated dark Taiga of central Siberia (Schulze et al. 2005b)
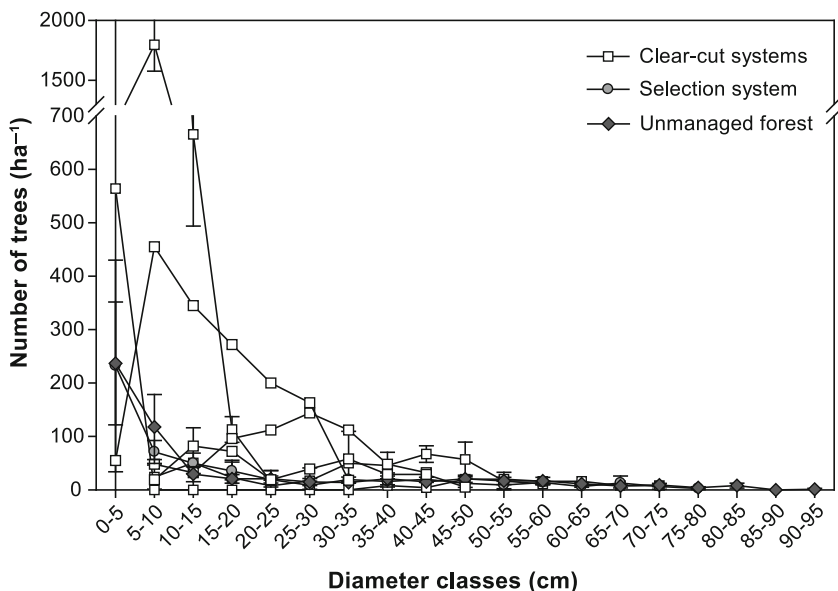
Fig. 15.9 Number of trees belonging to different breast height diameter classes in forests of different management. The unmanaged forest and the selection system contain all diameter classes within the same stand at almost equal numbers. In contrast, the shelterwood system exhibits cohorts of diameter classes in individual stands. Thus, each age class has a specific diameter distribution, and a strong decrease in overall stand density. *Unmanaged* Hainich National Park, Germany; *selection cutting* Langula district in the Hainich area; *clear-cut* Leinefelde age class management

some natural disturbances, especially fires and insect outbreaks, have been shown to have an anthropogenic background (e.g. Mollicone et al. 2006).

In contrast to the disturbance cycle in temperate forests, which is dominated by fungal attack and wind (see Hainich NP case study above), the boreal primary forest is characterised by a stand-replacing fire, which may result in regeneration of deciduous forest as shown for the example of the Siberian dark taiga (Fig. 15.8). The dark taiga differs from the "light" taiga, which is dominated by pine or larch, mainly with respect to re-occurring ground fires which do not exist in the dark taiga where deep branching crowns always lead to stand-replacing crown fires (Chap. 2 by Wirth et al., this volume). In the dark taiga, fire succession starts with birch and poplar forest, which collapse without regeneration because these species require mineral soil and high light for germination. Conifers, which germinate on organic soils and in the shade of the deciduous early fire succession, take eventually over in the canopy (Schulze et al. 2005b). The conifers then form multi-aged and multi-species stands that are disturbed mainly by wind and by insect attacks on both a single tree basis and at the scale of whole stands or even at a regional level. When the forest is disturbed by wind or insects it does not return to the fire successional phase with deciduous species but regenerates with conifers. The life cycle of the

different coniferous species determines the species composition. If fire is absent for a long time, old-growth boreal forests may develop. Thus, primary boreal forests can idle between old stands and coniferous succession after insect attack or wind-throw for centuries until a fire again starts a fire succession. The fire return time can be estimated based on the extent of deciduous stands in the region (Mollicone et al. 2002). Fires may be initiated by lightening in the absence of humans. For central Siberia, this mean fire cycle was estimated to be 425 years (Schulze et al. 2005b). The fire successional stages cover about 67% of the landscape, 33% is covered by insect-windthrow succession. Thus, old-growth forest (>200 years) would cover only about 0.1% of the area (see also Chap. 13 by Bergeron et al., this volume). However, since fire frequency has increased due to human impact (Mollicone et al. 2006), the area of old-growth forest is likely to have decreased.

15.5 Effects of Management

Management interferes with natural succession through the extraction of wood on an individual tree basis (selective harvest) or on a stand basis (thinning and clear-cut). We did not observe differences in the diameter distribution (Fig. 15.9) between the unmanaged old-growth forest in Hainich NP and nearby managed forests under a selective harvesting regime (Mund and Schulze 2006). Under both management systems, regeneration is a continuous process and requires only a relatively small number of seedlings to maintain productivity. Cohorts of shade-tolerant seedlings develop to a second or even third canopy below the main canopy, which consists of a few large and old trees. Deciduous trees growing in the shade generally loose their apical dominance, and are barely able to grow into the main canopy after gap formation. Regeneration of the main canopy generally originates from seedlings (or coppices) that germinated after gap formation, and which exhibit high apical growth. This is different in coniferous stands, where regenerating trees do not lose their apical dominance in the shade, and are ready to take advantage of an opening in the canopy (Schulze et al. 2005a). In unmanaged forest, upon death, old trees contribute to the coarse woody detritus pool. In contrast, under selective harvesting, old trees are harvested and used economically (Wirth et al. 2004). The aboveground biomass was 20% higher (497 ± 16 m^3 ha^{-1}) in the unmanaged Hainich NP forest than in selectively harvested forest (409 ± 21 m^3 ha^{-1}) (D. Hessenmoeller, personal communication; Erteld et al. 2005).

  In contrast, in forests that are based on thinning and final clear-cuts, the density of regeneration is much higher than under selective cutting. In beech forest, the "clear-cut" follows the principles of a shelter-wood, where the early stage of regeneration takes place under the protection of the old stand at reduced stand density. Clear-cut of the remaining canopy trees follows regeneration (Fig. 15.9). In this management system regeneration leads to a surplus of individuals that are extracted through thinning and used economically. Thinning aims at a stand density below the self-thinning line (Kramer 1988, p 186). Thus, tree densities just before

a

Saw wood extraction

① Forest pasture
few *Larix* trees, grass cover

② Degradation by overstocking

200-400 years

⑪ Forest grazing

150-200 years

100-150 years

③a Land slides ③b Mechanical disturbances ③c Afforestation ⑳ Deforestation

⑩ Mixed tall forest

No forest grazing

⑨ Selection forest

Picea abies

④ Pole stand of Larix
Picea abies
Pinus cembra

㉑ Hay meadow

Abandonment
Picea abies
Pinus cembra

⑧ Saw wood Extraction

⑥ Tall forest of Larix

Decreased stand density

㉒ Successional forest

⑦ Litter raking

⑤ Saw wood ④a Extraction of fence poles

b

Diameter (cm) vs Tree age (yrs)

○ Stem base
● Breast height

Fig. 15.10 a Succession and land use of *Larix* forests. The *numbers* refer to specific properties in the study region where these stages can be observed. b Diameter of trees as related to tree age during the course of a successional cycle (after Schulze et al. 2007)

the clear-cut are lower than those observed under selective cutting. The average woody biomass over the whole rotation period (340 m^3 ha^{-1}, highest yield class of beech with a 150-year rotation period, Schober 1995) is about 30% lower than that in unmanaged forest. Economically, the loss in biomass is outweighed by the economic value of large amounts of wood of uniform quality.

The interaction between natural disturbance and management can result in a wide variety of successional stages and land uses. To illustrate these complex interactions, the example of Alpine larch forests is shown in Fig. 15.10. European larch (*Larix decidua*) is an early successional species, which can regenerate only on mineral soil and under high light (Schulze et al. 2007). Old *Larix* forest form pastoral woodlands with single large trees on meadow-like grazing land. These forests do not regenerate unless overgrazing results in the exposure of mineral soil
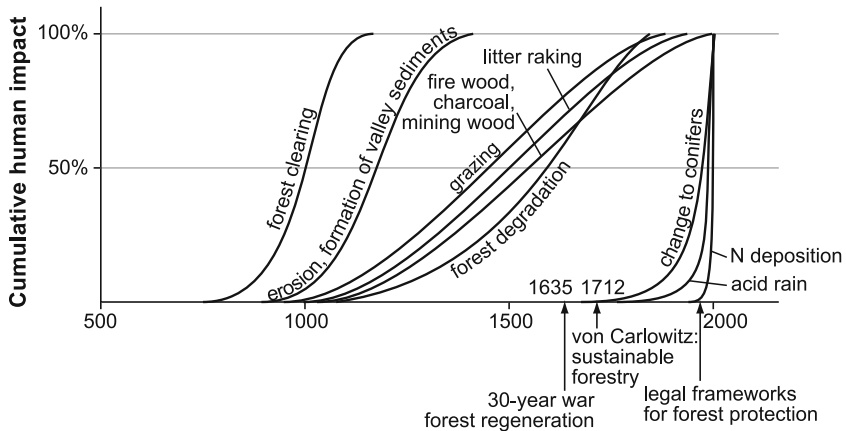
Fig. 15.11 Anthropogenic effects on forest ecosystems over time in Europe (after WBGU 1997). The *y*-axis scales the relative effect of each type of disturbance during the time it was operating, e.g. forest clearing terminated about in the year 1200. The change towards conifers started after 1700 and has probably reached its peak in present times

or causes land-slides enabling larch to regenerate. This successional larch forest type is then followed by successional species such as Norway spruce (*Picea abies*) and Swiss Stone pine (*Pinus cembra*). At the pole stage (Fig. 15.10a), individual pine and spruce will be thinned for fence poles. After thinning, the stand grows into a tall forest, where larch, spruce and pine continue to be selectively harvested for saw timber. Without management, these forests would turn into spruce/pine forest; however, selective harvest further reduces the number of evergreen trees, opens the canopy and allows grasses to colonise the herb layer. In this phase, the forest becomes attractive for grazing, which again increases the risk of overgrazing or land-slides, which in turn could initiate a new successional cycle starting with *Larix*. The full regeneration cycle has a length of 200–400 years. During this successional cycle, individual *Larix* trees exhibit no sign of age-related decline, but rather show an exponential growth rate (Fig. 5.10b) because they experience an increasing amount of available light, and probably gain from manure input from grazing.

15.6   Forest Management and Forest Protection in Europe

In large parts of Europe, the forests are shaped by almost 1,000 years of interaction between management and other anthropogenic disturbances (Fig. 15.11). In the earliest phase of management, forest clearing was the main activity. This period was followed by periods of erosion, grazing, and litter raking. Forest degradation reached its height in the seventeenth century due to over-use for firewood and the production of charcoal, and supplies for continuing wars. The devastation of European forests resulted in the establishment of legal frameworks for sustainable
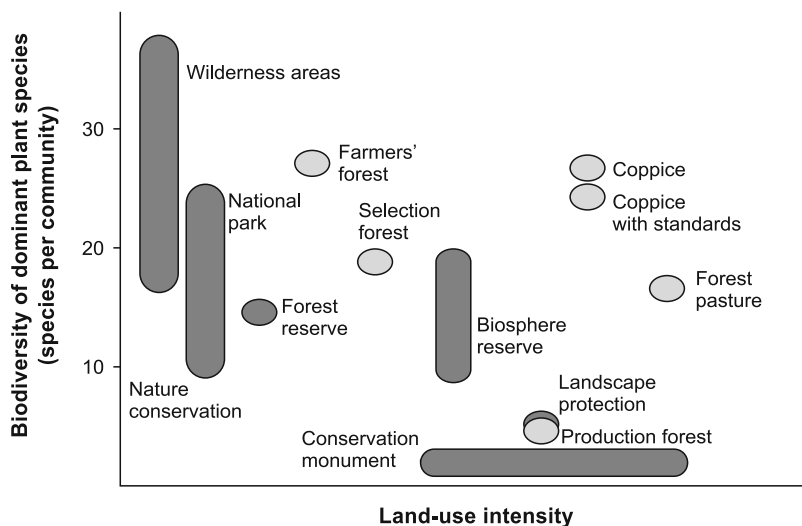
Fig. 15.12 Plant biodiversity of forest systems as related to management-intensity in central Europe. *Dark grey symbols* Forest types under nature conservation: *Wilderness areas* regions without management in historic times (only remnants exist, e.g. Rotwald in Austria); *Natural Parks* presently under nature conservation but usually had been managed in historic times - the range in plant diversity depends on geological conditions; *Forest reserves* single stands of small scale; *Biosphere reserves* larger entities but maintain some human management; *Landscape protection area* full agriculture and forest management but restricted industrial development; *Conservation monuments* single individuals in a region where land-use intensity may be very high (e.g. 1,000-year-old lime tree in a village). *Light grey symbols* Different management systems in forestry: *Farmers' forests* small plots with the high tree diversity needed to operate a farm in historic times. In former times each farm tool was made of a different wood. Trees, such as oak, were in part planted; *Selection forest* a management system where individual tall trees are harvested according to market value; *Coppice forest* provides mainly firewood in a 30-year rotation period; *coppice with standards* contains an upper canopy of tall trees for construction wood, mainly oak; *Forest pasture* open forest canopy with ground cover of grasses for grazing; *Production forest* an age-class forest. Each of the forest systems will have a range in its diversity and in its land-use intensity. However, at present no data exist to quantify this range

forest use, and the shift from broad-leaved forest into more productive conifers. However, the fingerprint of earlier forest degradation is still recognisable in the decreased amount of soil carbon and cationic nutrients such as potassium, calcium and magnesium depending on the management history (Wirth et al. 2004). The industrial revolution and the accompanying massive use of fossil fuels resulted in acid deposition and further soil acidification. Wide-spread nitrogen deposition, however, accelerated growth (Mund et al. 2002). All these changes affected forests independent of age – some of them also independent of management.

The main objectives of forestry are the supply timber and fibre for various uses in society, although forests, by virtue of their existence, exhibit a multi-functionality ranging from recreation to water supply. The sustainability of forests is ensured by various production systems, which can range from coppicing to selective logging systems. In managed forests, the production system is protected against

Table 15.2 Species diversity in the Hainich National Park, Germany (National Park Administration Hainich, 2007)

Species group	Total species number	Number on Red-List in Germany	% Red-List species total
Mammals	46 (14 bats)	20	43
Birds	179 (107 nesting)	54	30
Reptiles	5	3	60
Amphibia	12	8	66
Insects			
Ephemeroptera, Odonta, Plecoptera, Satatoria, Heterotera	168	28	17
Coleoptera	1,903 (1,307 in wood)	401	21
Hymenoptera, Formicidae, Trichoptera	260	56	21
Lepidoptera	705	59	8
Diptera	657	19	3
Araneae	221	19	8
Diplopoda	24	–	–
Gastropoda	82	–	–
Total fauna	4,262	–	–
Cormophyta	802	47 (+31 lost species)	6
Bryophyta	220	14	6
Lichens	134	41	30
Fungi	1,548	203	13
Total flora + fungi	2,704	–	–

catastrophic events such as pathogen attack, fire and wind. In some cases, the protection of forest productivity conflicts with the aims of environmental protection, which are to ensure the existence of certain plant and animal species, and the occurrence of natural processes such as fungal attacks, fires and blow downs (Scherzinger 1996). Thus, certain ecosystem types are protected by states to a varying degree in order to maintain natural biogeochemical cycles and biodiversity. Conservation in forests can range from the protection of individual trees as natural monuments, via preservation of landscape arrangements up to small scale forest reserves (>600 stands in Germany covering 1–100 ha in area), and National Parks. Europe has over 60 National Parks, located mainly in Northern and Eastern Europe. The average size is 204 km^2, but none of these areas represent truly pristine primary forests. The situation is similar in eastern North America (Chap. 14 by Lichstein et al., this volume) where less than 1% of the pre-settlement forest is thought to remain. In Europe, these forests are mostly on land that is difficult to manage. However, this land has also been affected by people, mainly following times of war and through air pollution. Nowadays, most of these forests do not have large carnivores, and therefore grazing by reindeer or deer (mostly roe and red deer) determines succession.

The biodiversity of protected areas is often impressive (Table 15.2). For example, a total of 2,704 plant and fungal species and 4,262 vertebrates and invertebrates have been identified in the Hainich NP (National Park Hainich 2006). However, the comparison of managed and protected systems with respect to biodiversity is difficult, because flora and fauna has not been studied with same intensity at managed sites. The main difference between managed and unmanaged systems would be the amount of coarse woody detritus, which hosts a number of specialised fungi and insects. However, managed forests where the management follows a sustainable-use certification also require a certain amount of standing dead biomass and coarse woody detritus. In contrast to the species pool, which is dependent on dead wood, clear-cut forests contain stages in their development where the soil is not covered by a canopy, and a diverse flora and fauna, which is not present under the continuous cover of an unmanaged forest, may exist for a short time. In addition, a comparison of species numbers is valid only when forest with different management systems but similar soil and climatic conditions are compared. Total plant species number increased with the mean of the N- and R-value (site quality indicators according to Ellenberg 1993) of the plant community in beech forests from about 10 plant species on acid soils up to about 100 plant species on calcareous soils (Schulze et al. 1996). Because managed sites in Central Europe may contain more variation in light conditions during succession than a closed canopy old-growth forest [but cf. Chaps. 6 (Messier) and 8 (Harmon), this volume, for other forest ecosystems], managed systems may even carry a higher species diversity than unmanaged systems. For example, Ellenberg (1993) determined the number of the most abundant plant species in primary forests of beech with 20 plant species, forest pasture had 27 species, coppice forest (30 year rotation period) and "coppice forest with standards" had 29 species, and managed age class forest had 18 species. Figure 15.12 shows an "expert view" of the relationship between plant biodiversity and land-use intensity for beech forests, and it is suggested that there are managed systems that can be very diverse (but these may not be the most productive or valuable in terms of timber), and that some of the conservation systems are not very effective in term of species diversity. Consequently, mere species richness seems not necessarily to be an attribute of "old-growth forest", and the effects of management are also related to the scale of the operation at the landscape level.

15.7 Conclusions

Based on our dataset, forests may accumulate woody biomass at an almost constant rate for centuries. There is little evidence in support of an age-related decline in productivity. Instead, self thinning and management lead to a loss of individual trees to an extent that the remaining trees are eventually no longer able to cover the available ground surface, thus leading to a decline in productivity per unit area. This threshold may be reached earlier in fast-growing than in slow-growing species. It

is enhanced by management because trees may lose their economic value with increasing dimensions due to fungal heart-wood rot.

Old forests are similar with respect to carbon-accumulation than young forests at the same yield class and of the same species. However, due to the accumulated mass per area, and the increased spread of fungal heart-wood rot, old forests become unstable and collapse due to external forces, mainly wind. Since accumulation and collapse are highly asymmetric with respect to time, and old forests become more vulnerable to stochastic events because of their size, it follows that old stands are rarer than young stands. Also, unmanaged forests contain a mosaic of age structures at the landscape level.

Forest structure and management rather than stand age determine NPP; therefore, there is no clear distinction in productivity between primary and managed forest, except that managed forests are generally harvested at an age below 100 years.

Although unmanaged forests sustain natural processes, biodiversity – expressed as species richness – is not necessarily higher in unmanaged compared to managed forests. This, however, may be a matter of scale.

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Chapter 16
Old-Growth Temperate Rainforests of South America: Conservation, Plant–Animal Interactions, and Baseline Biogeochemical Processes

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16.1 Introduction

Defining old-growth forests (Chap. 2 by Wirth et al., this volume) must consider both technical and cultural issues. For instance, the term 'old-growth forest' was entirely absent from the most recent survey of Chilean vegetation conducted by the National Forest Service (CONAF-CONAMA-BIRF 1999), where the forestry-related term 'adult' (synonym of tall, >15 m height) forest was used instead to indicate a harvestable unit of land. Moreover, the deriding term 'over-mature' is sometimes used to refer to old-growth stands with a predominance of large, non-harvestable trees (Chap. 2 by Wirth et al., this volume). This bias towards a tree-centred, commercial view of forests suggests that, culturally, we remain unaware of the ecological differences among successional forest stages and of the specific attributes of old-growth forests. Greater public appreciation of the ecological, social and economic values of old-growth forests will depend on our ability to communicate scientific understanding of these diminishing ecosystems.

Based on current knowledge of temperate forests in southwestern South America (e.g. Donoso 1993; Armesto et al. 1996a; Veblen et al. 1996; Neira et al. 2002), we propose here a definition of old-growth forest that combines both structural and compositional (based on species and functional groups) properties of forest stands. The old-growth condition is usually restricted to ecosystems that have not been subjected to recurrent and massive human impact (Chap. 2 by Wirth et al., this volume). Considering the entire range of human impacts, from changes in the concentration of elements in the atmosphere to the extraction of individual trees, it is however unlikely that any forest is completely free of human impact. Therefore, we will consider as 'old-growth' any tract of natural forest with a minimum extent so as to integrate a core area where edge effects are minimal, and which maintains a complex vertical structure dominated by large (old) shade-tolerant trees with emergent pioneers, with a species composition that has not been significantly modified (by recurrent human impact or other large disturbance at least during the past two centuries). Structural and compositional attributes are taken as

indicators of the continuity of biological interactions that sustain biodiversity and ecosystem functions within the ecosystem.

Andean and coastal forests in Chile differ greatly in their probabilities of ever reaching the old-growth stage because of the prevalence of stand-devastating events in Andean forests (Veblen and Ashton 1978; Veblen et al. 1981; Armesto et al. 1996a). Volcanism, earthquake-caused landslides and mudflows have historically been present in Andean forests, so that few areas can recover fast enough for pioneer trees to reach their maximum longevity and eventually be excluded by slow growing, shade-tolerant tree species (Veblen et al. 1996). In turn, coastal forests at comparable elevations differ greatly in tree species composition, as fast-growing, relatively shade-intolerant pioneers may be completely lacking and shade-tolerant species dominate. This is exemplified by the absence of *Nothofagus* trees from most coastal forests at low elevations (<400 m), between 41° and 43° S (Veblen et al. 1981, 1996; Armesto and Figueroa 1987; Armesto et al. 1996a). The canopy of such forests is dominated by shade-tolerant trees such as *Aextoxicon punctatum*, *Laureliopsis philippiana*, *Caldcluvia paniculata*, and several Myrtaceae species (Armesto et al. 1996a). In some cases the semi-tolerant *Eucryphia cordifolia* is a dominant canopy tree (Gutiérrez et al. 2008). Further south and at higher elevations (>400 m) on the coastal range, dominance is shared between the shade-tolerant *Podocarpus nubigena* and the semi-tolerant *Nothofagus nitida* (Innes 1992; Gutiérrez et al. 2004). Accordingly, the old-growth condition in coastal forests is indicated by the frequent presence of large, canopy emergent trees together with patchy regeneration, intense gap-phase dynamics, and a tree species composition completely or largely lacking pioneers (Armesto et al. 1996a; Gutiérrez et al. 2004). The presence of numerous trees over 200 years old characterises stands with an old-growth structure and composition (Aravena et al. 2002). In the literature, the lack of regeneration of shade-intolerant pioneers is often considered a characteristic of late-successional stands (Oliver and Larson 1996). However, in Chilean old-growth stands in coastal areas, juveniles of light-demanding species may form dense patches under canopy openings known as 'sapling banks' (Aravena et al. 2002).

Using this framework, we provide here an overview of the ecological knowledge of temperate old-growth forests in southwestern South America, particularly evergreen rainforests in south-central Chile. We offer a characterisation of these ecosystems focused on three main questions: (1) what is their current status and what are the major threats, and prospects for conservation?; (2) what is the importance of old-growth forest structure and species composition for plant–animal mutualistic interactions (e.g. pollination, seed dispersal), and how do these interactions in turn shape and maintain the structure and function of temperate old-growth forests?; and (3) what are the main features characterising nutrient fluxes in southern temperate forests, and how are they expected to change in response to management? We discuss how old-growth temperate forests functionally resemble or differ from forests that have been disrupted by logging and air-pollution in Chile or in the northern hemisphere. Our analysis identifies key aspects of forest functioning that may have management and policy implications, and

stimulates further research to understand the ecological and social relevance of old-growth forests.

16.2 Conservation Status, Values and Threats

Along the southwestern margin of South America (Fig. 16.1), a narrow band of temperate rainforests, reaching 55° S, is one of the last wilderness frontiers on the planet (Mittermeier et al. 2003), and the largest area of temperate forests remaining
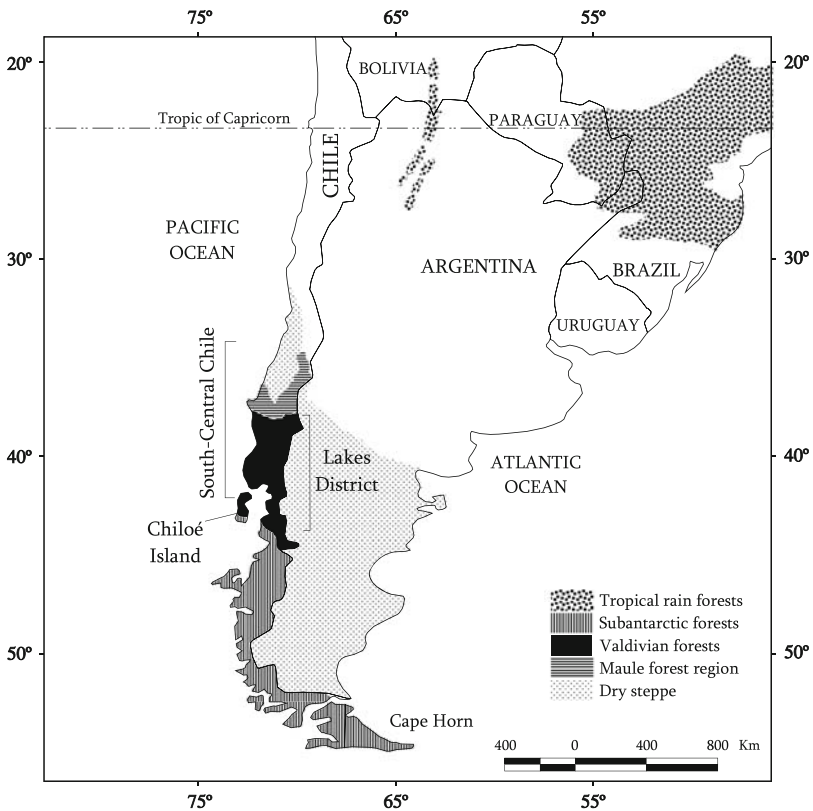
Fig. 16.1 Map of temperate rainforests of southern South America, including deciduous-dominated forests in the Maule region (*horizontal stippling*), and evergreen Valdivian (*black shading*) and Sub Antarctic (*dark grey*) rain forests; the eastern limit of rainforests is the Andes and the dry steppe border in Argentina, and the northern limit is the Mediterranean-climate region in south-central Chile. Southern temperate rainforests are isolated from tropical rainforests (in southern Brazil and in the Andean Yungas of southern Bolivia and north-western Argentina) by extensive semiarid lands and deserts (*light shading* in the map)

in the southern hemisphere. Floristic richness of these rainforests is the highest among evergreen temperate rainforests worldwide (Arroyo et al. 1996). Temperate rainforests of southern South America are inhabited by a host of endemic species, including many monotypic genera of plants and animals (Armesto et al. 1996a, 1998), with close relatives in the southern continents (Australia, New Zealand) and the Sub Antarctic islands (Villagrán and Hinojosa 1997). The long history of geographic isolation from other rainforests within South America (Armesto et al. 1998) enhanced local endemism and the conservation of relict taxa (Hinojosa et al. 2006); at the same time it made this remote "island" of temperate rain forest highly susceptible to land-cover change, species invasions and local species extinction (Armesto et al. 1996a, 2001). The high concentration of endemism in a relatively narrow territory has given this region a unique global conservation value (Olson and Dinerstein 1998; Myers et al. 2000).

16.2.1   Main Threats

Today, significant remnants of old-growth forest continue to disappear in southern Chile despite compelling arguments for their protection (Armesto et al. 1998; Smith-Ramírez et al. 2005a). During the last decades of the twentieth century, rapid expansion of monoculture-based forestry (Lara and Veblen 1993; Armesto et al. 2001), new access roads, and land-use changes associated with agriculture, have all led to increasing loss and fragmentation of the native-forest cover in southern South America (Echeverría et al. 2007). South-central Chile has been the target of much agricultural, industrial and urban development since the nineteenth century. Consequently, the proportion of old forest cover left at different latitudes along the western margin of South America (Fig. 16.2) varies from as little as 1% at 35° S, in the transition between the Mediterranean and temperate climate regions (Maule Region), to about 32% in the Valdivian rain forest region, at 40° S.

Substantial tracts of intact old-growth forests at low elevations are still found on the Coastal Range of the Lake District (39–42° S), particularly west of the city of Osorno and on Chiloé Island (Smith-Ramírez 2004). These largely pristine areas occupying the oceanic slopes of the coastal mountains have been estimated at roughly 500,000 ha (Smith-Ramírez 2004). Old-growth ecosystems are entirely lacking in the central valley between the coastal and Andean ranges, where human settlements and industrial activities are concentrated (Armesto et al. 1998). Some types of old-growth forest have nearly disappeared, including the last stands of the ancient *Nothofagus alessandrii* on the coastal range of Maule Region (Bustamante and Castor 1998), and the last few remnants of *Peumus boldus* and swamp forests in the Valdivian region (Smith-Ramírez et al. 2005a).

The three major continuing trends leading to the loss of remnant old-growth forest cover in southwestern South America (Fig. 16.4) are:

(1) Expansion of plantation-based forestry using exotic tree species (mainly *Pinus radiata* and *Eucalyptus* spp.). This trend, which started in the 1970s in
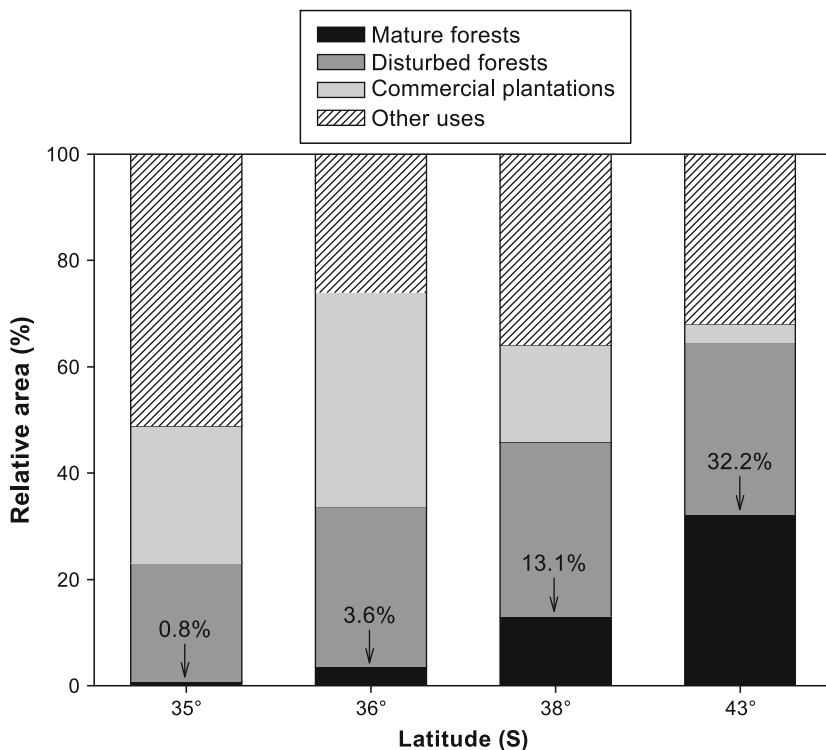
Fig. 16.2 Different land-cover types present today in each region between Maule (35° S), the northern limit of temperate forests, and Chiloé (43°S) in the southern limit of the Lakes District. *Bars* represent the originally forested land before human settlement in each administrative region of Chile from north to south along the western margin of South America. The mean latitude of each administrative region is shown on the horizontal axis. Different shading in the bars represents estimates of the area presently covered by old-growth (mature) forest, successional or degraded (disturbed) forest, and forestry plantations of exotic tree species (mainly *Pinus radiata* and *Eucalyptus* sp.). Cover of old-growth forest habitat was inferred by adding the 'adult forest' category and stunted timberline forests in the most recent survey of Chilean vegetation CONAF-CONAMA-BIRF (1999), and hence it is likely to be an overestimate. *Other uses* Farming, grazing pastures and urban settlements

south-central Chile (35–40° S), increased exponentially during the last two decades of the twentieth century, and in the last 10 years has expanded into Chiloé Island and the mainland south of Chiloé (Fig. 16.1). Forestry plantations are likely to continue their expansion in the coming decade at the expense of native forest; first, because several paper mills requiring large volumes of chips for cellulose production have recently entered into operation and, secondly, productivity of existing plantations is likely to decline due to pathogen attack and losses of soil fertility after several rotations (Armesto et al. 2001).

(2) Selective and stand-scale logging and extraction of timber, firewood and woodchips from native trees (Fig. 16.4). The woodchip industry has fluctuated

Fig. 16.3 Extension of
protected areas (thousands of
hectares) containing old-
growth forest in the Chilean
Coastal Range and Andean
public Parks and Reserves at
the heart of the Valdivian
forest region (40–43° S). A
single National Park on
Chiloé Island represents
much of the government
protected land in the coastal
range (*dark shading*)
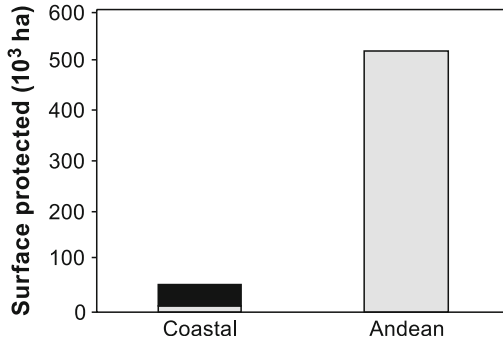
in recent decades due to international market prices (Informe País 2002), but harvesting large trees for woodchips remains a significant driver, especially in accessible rural areas. On the other hand, firewood remains the main source of energy for rural and urban settlements in south-central Chile and stands out as the main degrading activity for native forests (Informe País 2002). In Chiloé Island, a major source of firewood is the tree *Tepualia stipularis* (Myrtaceae), which has excellent caloric properties (Hall and White 1998). However, because of its pros- trate growth habit and numerous stems, which serve as habitat for a high species richness of vascular and non-vascular epiphytes on creeping stems (Muñoz et al. 2003; J. Larraín, personal communication), the loss of old-growth *Tepualia* stands may represent a significant loss of biodiversity.

(3) Forest fires, predominantly as a result of human activities, such as land clearing and opening of forests for timber extraction, represent a major threat to remnant native forests and protected areas in southern South America. For example, fires whose origins were outside parks burned extensive areas of old-growth forests in 1998 in Nahuel Huapi National Park (41° S, Argentina) and in 2002 in Malleco National Reserve (38° S, Chile); these were the first two protected areas created in southern South America (Primack et al. 2001). In Chilean coastal and lowland temperate rainforests, wildfire has been historically infrequent in the absence of humans, but fire frequency and intensity have increased greatly during the twentieth century, becoming a major factor in the decline of coastal old-growth forests (Smith-Ramírez 2004). Only high altitude Andean and coastal forests dominated by the conifers *Araucaria araucana* and *Fitzroya cupressoides* appear to be more resilient to repeated fire disturbance, mainly because of the thick bark of these trees, which allows them to survive ground fires. Wildfires, both natural and human- driven, may have occurred more frequently in these forests during the Holocene (Gonzalez et al. 2005; Armesto et al. 1995) and presumably, because both conifers have a millennial lifespan, they were able to survive a fire regime of low frequency prior to human settlement. Presently, because of human set fires, thousands of hectares of conifer forests on the coastal range have been burned.

16.2.2 Values

The loss of old-growth forests has a high opportunity cost, from the point of view of ecotourism, aesthetics, human health, and priceless natural capital, as suggested by indigenous knowledge of medicinal, craft and other non-timber values of biodiversity (Smith-Ramírez 1996). In addition, late-successional or old-growth stands can provide reference or baseline data on ecological processes (Frelich et al. 2005) that can help us understand the disruptive consequences of ecosystem management, air and water pollution, and land-cover change. South American temperate forests offer a unique opportunity to learn about the functional integrity of ancient ecosystems in a region of the planet that still remains largely unpolluted (Hedin et al. 1995), thus providing valuable clues as to the pre-industrial condition of temperate forests (see below).

Although structurally and compositionally, old-growth coastal forests differ greatly from frequently disturbed Andean forests (Veblen et al. 1996), frequent human impacts are imposing a dominant disturbance regime that enhances the dominance of pioneer trees and promotes the loss of plant and animal species associated with late-successional stages. Anthropogenic disturbance regimes may lead to a loss of spatial heterogeneity and floristic homogenisation of forests as a result of the widespread use of logging and fire. As shown in other forested areas of the world (e.g. Kohm and Franklin 1997; Fuller et al. 1998), regional loss of old-growth forest cover as a consequence of intensive logging and short rotations may cause the loss of numerous species of plants and animals that depend on specific old-growth forest habitats, leading to ecological homogenisation on a regional scale. Key structural features, coupled with complex vertical heterogeneity and tree species composition of old-growth forest stands in Chiloé Island (Gutiérrez et al. 2009), suggest that they can provide specialised habitats for plants and animals as they do in other temperate regions (see Chap. 19 by Frank et al., this volume). Key structural attributes, such as emergent canopy trees, snags, logs, tree-fall gaps, and dense bamboo cover, provide habitat for several endemic species of birds and mammals (Reid et al. 2004; Díaz et al. 2005; Jaña-Prado et al. 2007). Bird species such as the Magellanic woodpecker (*Campephilus magellanicus*), black-throated huet-huet (*Pteroptochos tarnii*) and ochre-flanked tapaculo (*Eugralla paradoxa*) are present regionally only where old-growth forest habitat remains (Table 16.1).

Recent studies have shown that logs on the forest floor function as important microsites for the regeneration of many tree species (Lusk 1995; Christie and Armesto 2003). Hence, the loss of structural components of forests over extensive areas of the landscape, due to logging practices or the use of fire, may impair the regeneration potential of tree species. Some tree species (e.g. *Dasyphyllum diacanthoides* and *Myrceugenia chrysocarpa*) occur only in old-growth stands in Chiloé Island (Gutiérrez et al. 2009). Likewise, trees in old-growth forest patches in rural areas of Chiloé Island have a specialised moss flora, which is richer in endemics than second-growth forests or shrublands (J. Larraín, unpublished data).

Table 16.1 Ratio of forest bird abundance in old-growth and secondary temperate rainforests in the Valdivian eco-region of Chile. *OG* Species that are almost entirely restricted to old-growth forests; *OG/SF* abundance ratio between old-growth stands and secondary forest stands, calculated using data from Rozzi et al. (1996)

Species	Common name	Abundance ratio OG/SF
Campephilus magellanicus[*]	Magellanic woodpecker	OG
Sephanoides galeritus	Green-back, fire crowned	2–4
Anairetes parulus	Tufted tit-tyrant	<1
Elaenia albiceps	White-crested Elaenia	1
*Columba araucana**	Chilean pigeon	2–4
*Tachycineta meyeni**	Chilean swallow	<1
*Pteroptochos tarnii**	Black-throated huet-huet	OG
*Scelorchilos rubecula**	Chucao tapaculo	>10
*Eugralla paradoxa**	Ochre-flanked tapaculo	OG
Scytalopus magellanicus	Magellanic tapaculo	mainly OG
*Sylviorthorhynchus desmursii**	Des Murs' wiretail	1–8

[*]Endemic to south-temperate rainforest

Table 16.2 Comparison of total mass of logs and snags in temperate old-growth forests (age over 300 years) of Chile and North America. Modified from Carmona et al. (2002). *US* United States

Forest type and region	Mean mass of logs (Mg/ha)	Range	Mean mass of snags (Mg/ha)	Range	Reference
Conifer (Pacific Northwest, US)	63	54–73	54	41–63	Spies et al. 1988
Deciduous (Eastern US)	25	16–38	11	–	Harmon et al. 1986
Evergreen broad-leaved (Chiloé Island, Chile)	47	31–65	126	13–249	Carmona et al. 2002

The global decline of old-growth forest is especially relevant for the carbon storage properties of regional ecosystems (Harmon et al. 1990; Carmona et al. 2002; Chap. 8 by Harmon, this volume). The slow decomposition rate of large volume snags and logs, especially in old-growth temperate rainforests (Table 16.2), determines a carbon storage capacity that can be several times greater than that of second-growth forests. Long tree life spans (Table 16.3) and slow growth rates can also contribute to carbon storage properties of temperate forests (Harmon et al. 1986). Although fast-growing plantations or young successional forests can accumulate carbon faster in early stages of stand development, managed ecosystems may have limited long-term storage value because of short logging cycles (Harmon et al. 1990). Accordingly, the decline of old-growth forest cover can drastically reduce carbon storage in the landscape, and their replacement by plantations, pastures and shrublands can additionally affect carbon cycling if these new species have higher carbon-to-nitrogen ratios than native trees. This is

Table 16.3 Life spans of some dominant tree species of Chilean temperate old-growth forests

| Species	Life span (years)	Reference
Aextoxicon punctatum	480	Pollman & Veblen (2004)
Eucryphia cordifolia	650	Pollman & Veblen (2004)
Nothofagus pumilio	400	Rebertus and Veblen 1993
Saxegothaea conspicua[a]	750	Lusk (1996)
Nothofagus alpina	600	Pollman 2005
Weinmannia trichosperma	700	Lusk 1999
Austrocedrus chilensis[a]	1,000	Veblen et al. 1996 in Armesto et al. 1996a
Pilgerodendron uviferum[a]	1,000	Szeicz et al. 2000
Araucaria araucana[a]	1,300	Montaldo 1974
Fitzroya cupressoides[a]	3,500	Lara and Villalba 1993

[a]Conifers

because higher carbon-to-nitrogen ratios are associated with higher litter decomposition rates and different susceptibility to fire (Vitousek et al. 1986; Pérez et al. 2004).

16.2.3 Conservation Prospects

Rapidly shrinking old-growth forest landscapes, especially in small creeks at low elevations (<500 m) and in coastal areas, are the main targets for protection (Smith-Ramírez 2004; Smith-Ramírez et al. 2005a). Moreover, significant areas of public parks and reserves are almost entirely lacking on the Chilean costal range (Fig. 16.3). Ecologists have long since noted this important conservation gap (Simonetti and Armesto 1991; Armesto et al. 1992; Muñoz et al. 1996; Armesto et al. 1998; Pauchard and Villarroel 2002; Smith-Ramírez 2004). Improving the representation of coastal and lowland forests in the Chilean Public System of Protected Areas is difficult because most land is privately owned and in high demand for urban and industrial use. However, much old-growth forest still remains in these areas (Smith-Ramírez 2004), which can be protected through agreements with private landowners.

In recent years, partly in response to advice from the scientific community (Muñoz et al. 1996; Smith-Ramírez and Armesto 2002), some private conservation initiatives have contributed to reducing this gap. Ibarra-Vidal et al. (2005) summarised private conservation efforts at the northern limit of temperate rainforests, which include nearly 60,000 ha of the last old-growth forest remnants in Nahuelbuta Range, which are now completely surrounded by forestry plantations. The World Wildlife Fund and The Nature Conservancy have jointly purchased about 60,000 ha in the Coastal Range of Valdivia, including some remnant old-growth forest stands, as well as secondary and degraded coastal forest, to create a coastal reserve. Indigenous communities in the area of San Juan de la Costa,
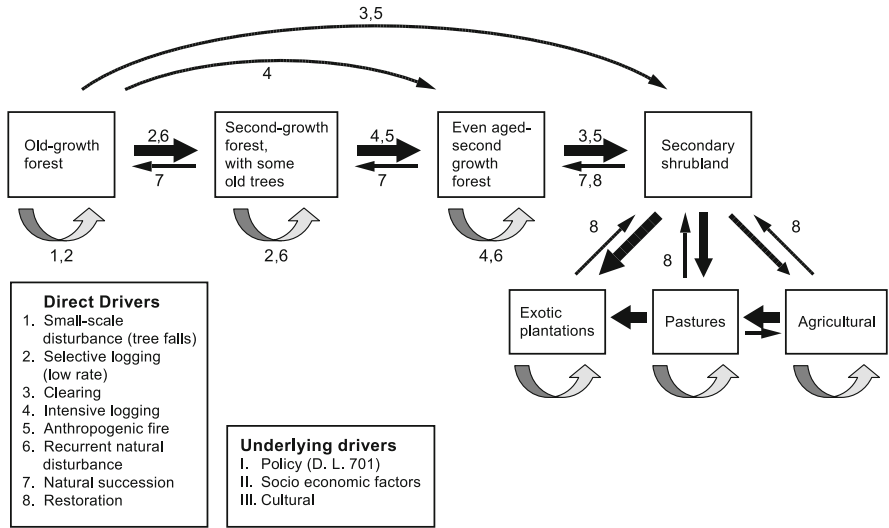
Fig. 16.4 Main transitions among stages (*boxes*) and major drivers associated with the loss or maintenance of old-growth forest cover in south-central Chile. The main direct drivers for each transition are shown by the numbers *1* to *8*. The width of the *arrows* indicates the relative probabilities of each transition. Direct drivers, when anthropogenic, are driven by underlying policy, socio-economic and cultural drivers (*inset*). These are the most relevant drivers for the transitions from native vegetation to agro-forestry uses. A remarkable example of a policy driver is the Chilean law (D.L. 701) from 1974 that subsidised forestry plantations, and hence prevented the successful recovery of native shrublands, promoting their replacement by commercial forestry plantations. A more recent socio-economic factor is the building of new cellulose plants requiring the expansion of present forestry plantations to provide wood chips

Osorno (39° S) are committed to the protection of 700 ha of undisturbed coastal forests and 705 ha of coastal areas adjacent to these forests within Mapulahual Ethnic Park (C. Smith-Ramírez, unpublished report). The Mapulahual Ethnic Park is part of an area of 50,000 ha of indigenous land including much old-growth forests in the coastal range of Osorno. Two large private reserves now protect large tracts of evergreen rainforest, some of it in pristine condition, in the mainland across from Chiloé Island: Pumalin (317,000 ha) and Huinay (34,000 ha). Tantauco Park in southern Chiloé Island protects 118,000 ha of North Patagonian old-growth forest and some remnant *Pilgerodendron uviferum* stands. In addition, some private forestry companies have set aside remnant old-growth forest areas for conservation accumulating several thousand hectares (D. Alarcón, personal communication). However, the present lack of Government incentives and the still uncertain legal status of private reserves in Chile cast some doubts about the feasibility of the long-term conservation goals of these large private investments.

The southern portion of the temperate rainforest region (Fig. 16.1) from Chiloé Island to Cape Horn (43–55° S), including the Sub Antarctic (or subpolar) Magellanic rainforest eco-region (49–56° S), conserves some of the largest remnants of

continuous old-growth forest in temperate regions worldwide (Neira et al. 2002; Silander 2000). It hosts the highest diversity of mosses in the South American temperate forest biome (Rozzi et al. 2008), contains the largest mass of continental ice in the southern hemisphere besides Antarctica (Cassasa et al. 2000), and has the world's lowest human population density within temperate regions (Mittermeier et al. 2003). This remote territory includes the largest public parks and reserves in Chile; most of them, however, lacking proper infrastructure and land-care personnel (Rozzi et al. 2004). The Sub Antarctic region is now the target of major industrial development projects, including hydroelectric power dams, new access roads, and expanding salmon farming (R. Rozzi et al., unpublished data). As stewards of one the last wilderness frontiers of the planet, there is a need for organisations to establish broad partnerships, integrating public and private interests and scientific knowledge, in order to ensure the long-term protection of cultural, economic, and ecological values of the region. A step forward was the recent creation of the Cape Horn Biosphere Reserve (2005), protecting 48,843 km^2 of nearly pristine land at the austral tip of South America. It is the only Chilean biosphere reserve that comprises terrestrial (19,172 km^2) and marine ecosystems (29,670 km^2), and is currently the largest in the southern cone of southern South America, i.e. Uruguay, Argentina, and Chile (Rozzi et al. 2006). The connectivity of conservation efforts from Cape Horn to Chiloé Island, through the Sub Antarctic archipelagoes (Fig. 16.1), remains an important challenge for the future.

The establishment of Cape Horn Biosphere Reserve, as a public-private partnership, with its long-term goals defined by an open process of discussion among stakeholders, government authorities and scientists (Rozzi et al. 2006), provides an inter-institutional model for the integration of private and public conservation efforts with the social and economic welfare of local inhabitants. The Chilean National Forest Service (CONAF) is attempting to replicate this model to create a binational Chilean–Argentinean biosphere reserve in the Valdivian rainforest region, and a World Heritage Area including North Patagonia and the northern area of the Sub Antarctic Magellanic rainforests. The biosphere reserve approach can generate a broad discussion of the socio-economic benefits, values, and logistic problems associated with the preservation of old-growth forests. We propose that it be applied also to remnant forest areas in south-central Chile.

16.3 Plant–Animal Interactions

The high importance of plant–animal mutualisms in South American temperate forests is striking because of their paucity in other temperate forests (Aizen and Ezcurra 1998). The majority of plant species in southern temperate rainforests requires interaction with animal pollinators and/or vertebrate dispersal agents to ensure their natural recruitment (Armesto et al. 1987, 1996b; Armesto and Rozzi 1989; Willson 1991; Willson et al. 1996, Aizen and Ezcurra 1998; Aizen et al. 2002, Smith-Ramírez et al. 2005b). Temperate rainforests of southern South America are

characterised by an unusually high proportion of fleshy fruited species among trees, shrubs, vines and epiphytes; i.e. 70% of the woody flora (Armesto and Rozzi 1989). This proportion of fleshy fruited plant species is higher than that reported for many northern hemisphere temperate forests, and is similar to some wet tropical forests (Armesto and Rozzi 1989; Willson 1991).

As old-growth forest cover shrinks in the regional landscape, mutualistic species are likely to decline and critical biological interactions may cease to function. Preliminary evidence suggests that some species, such as the Chilean pigeon (*Columba araucana*), which may play a role in the dispersal of many fleshy fruited species (Armesto et al. 1987), is present in greater abundance in old-growth forest habitats (Table 16.1). Even some regionally common birds such as the fire-crowned hummingbird (*Sephanoides sephaniodes*) (Armesto et al. 1996b) are several times more abundant in late-successional forest habitats than in younger forests (Table 16.1). Two other passerine bird species, *Elaenia albiceps* and *Turdus falklandii*, which are the main seed dispersers in the Chiloé flora (Armesto et al. 1996b; Amico and Aizen 2005), are more resilient to landscape changes. *Elaenia albiceps* uses a wide variety of foraging sites and habitats, including fragmented old-growth forests, secondary forests and shrublands (e.g. Willson et al. 1994; Armesto et al. 2005), while *Turdus falklandii* is more abundant in second-growth forests and pastures. These behavioural patterns result in a resilient interaction between these avian frugivores and their dispersed plants (Aizen et al. 2002), implying that conversion of old-growth forest cover into secondary forest may not significantly alter the abundance and functional role of the main seed dispersers. In contrast, forest fragmentation and nest predation on forest edges has negative effects on the local abundance of understorey birds with limited flight abilities (Willson et al. 1994; De Santo et al. 2002; Willson 2004; Sieving et al. 1996; Díaz et al. 2005). However, the role of these birds, which have a generalist diet, on the dispersal of forest plants, is still only poorly known (Correa et al. 1990). In addition to avian frugivores, two mammal species, a marsupial (*Dromiciops gliroides*) and a fox (*Lycalopex fulvipes*), and one reptile species (the lizard *Liolaemus pictus*) have been reported to eat the fruit and disperse the seeds of several species of trees, shrubs and vines (Armesto et al. 1987; Willson et al. 1996). In all of these cases we lack information about potential changes in species abundance derived from the expansion of second-growth forests that may affect species interactions. For example, forest exploitation changes the demographic pattern of *D. gliroides*, reducing population recruitment, which may affect its role as a seed disperser.

For fleshy fruited epiphytes in particular (e.g. *Luzuriaga* spp., *Fascicularia bicolor*, Gesneriaceae spp.) and probably for some tree climbers (e.g. *Philesia magellanica*, *Lapageria rosea*, *Lardizabala biternata*, *Boquila trifoliolata*, *Berberidopsis corallina*, and *Cissus striata*) of southern temperate rainforests, avian frugivores and the only arboreal mammal, *Dromiciops gliroides*, may be the main seed vectors, because recruitment of these species is enhanced when propagules are dispersed between tree canopies (F. Salinas, personal communication). An example of such specialised plant–frugivore interaction is the directed dispersal of seeds of the hemiparasitic mistletoe *Tristerix corymbosus* by the arboreal marsupial *Dromiciops gliroides* in southern rainforests (Amico and Aizen 2000). Recently, Rodríguez-Cabal and Aizen (2007) have shown that local extinction of *Dromiciops*

from small forest fragments was associated with the complete disruption of mistletoe dispersal.

Similarly, along the latitudinal gradient from south-central Chile to Cape Horn, 61–80% of the rain forest taxa have biotic pollination syndromes (J. Armesto, unpublished data). An important pollination syndrome in the rain forest flora of western South America is ornithophily, including hummingbird and passerine pollination (Smith-Ramírez 1993; Aizen and Vásquez 2006). In Chiloé Island, 14 out of 42 woody species have red tubular flowers pollinated by hummingbirds (Smith-Ramírez 1993; Aizen et al. 2002). Just one hummingbird species, the green-back fire-crowned *Sephanoides sephaniodes*, is the principal pollinator of the entire plant assemblage (Smith-Ramírez 1993; Armesto et al. 1996b; Aizen et al. 2002), though passerines have been reported to pollinate the red flowers of the Proteaceae tree *Embothrium coccineum* in Chiloé (Smith-Ramírez and Armesto 1998). In old-growth stands, the emergent tree *Eucryphia cordifolia* may be a pivotal resource for pollinators, because of its profuse and massive flowering, which attracts more than 100 species of insect flower visitors (Smith-Ramírez et al. 2005b). Moreover, the pollinators of emergent *Eucryphia cordifolia* trees in old-growth forests are not the same as in secondary forests (C. Smith-Ramírez, unpublished data). The rapid and massive loss of old-growth lowland forests, containing large *Eucryphia cordifolia* trees (Gutierrez et al. 2008), due to logging and forest clearing in recent decades, may disrupt the rich pollinator assemblage of *Eucryphia cordifolia*. It is likely that such disruption of pollinator assemblages may impair the reproduction of a larger number of tree species, which are exogamous and dependent on pollinators for seed set (Smith-Ramírez et al. 2005b).

The low number of species of avian seed dispersers and pollen vectors recorded in temperate rainforests of southwestern South America supports the idea that the high plant diversity of these rainforests depends on a rather poor assemblage of animal mutualists (Armesto et al. 1996b; Amico and Aizen 2005). Conversely, the high number of insect pollinators (Smith-Ramírez et al. 2005b; Devoto et al. 2005) supports the idea that the high insect diversity in old-growth temperate rainforests of southwestern South America depends on a comparatively poor assemblage of plant mutualists. Accordingly, some species could function as critical links for maintaining the network of interactions in these forest ecosystems. Consequently, the non-random loss of species of animal or plant mutualists could have cascade effects on a larger assemblage of interacting species (Armesto et al. 1996b; Willson et al. 1996; Aizen et al. 2002; Amico and Aizen 2005).

Large old trees, snags, logs, understorey cover and epiphytes, which are more frequent components of old-growth forests (Gutierrez et al. 2009) , may be critical habitat components for the maintenance of mutualistic animal species, by providing nesting sites, refuges from predators, and enhanced food availability (Tews et al. 2004). Old trees, snags and logs are the habitat for many invertebrates and cavity nesting birds and mammals (Newton 1994; Willson et al. 1994). It is likely, therefore, that the expansion of young forests at the expense of old forests will alter the distribution and heterogeneity of habitats and resources in the landscape, with consequences for avian behaviour and flight patterns, which in turn may affect seed dispersal and pollination interactions.

The network of mutualistic interactions that we observe in old-growth forests of southern South America is the result of ancient ecological relationships among animal and plant species of Gondwanan origin (Aizen and Ezcurra 1998; Amico and Aizen 2000). Current land-use patterns, forest fragmentation, habitat degradation, air and water pollution, and introduction of species, including aggressive exotic mutualists (e.g. *Bombus ruderatus, Apis mellifera*, Morales and Aizen 2006; *Vespula germanica* and the tree *Eucalyptus globulus*, Smith-Ramírez et al. 2005b), expose forest species to ecological scenarios without precedent in their evolutionary history. This situation may lead to the re-organisation of mutualistic networks incorporating exotic species. Understanding the consequences of such biotic changes can be achieved only by comparison of species interactions to reference old-growth forests. As an example, one of the major changes driven by the expansion of pastures has been the increase in abundance of *Apis mellifera*, which accounts for up to 95% of visits to *Eucryphia cordifolia* trees in patches of rural habitat. While in secondary forests, this bee species accounts for 15–50% of flower visits, honeybees were entirely absent from old-growth stands within a nearby national park (C. Smith-Ramírez et al., unpublished data), where indigenous pollinators increased in species richness and abundance.

16.4   Biogeochemistry

In classic biogeochemical theory, nutrients are accumulated during early succession to reach a steady-state condition in late-successional ecosystems, where most nutrients are recycled internally and trees cease to grow. Accordingly, old-growth forests should exhibit negligible net gain of inorganic forms of nitrogen and phosphorous, as nutrient losses equal inputs from geologic and atmospheric sources (Hedin et al. 1995). This is a relevant characteristic as it suggests that nutrient dynamics in old-growth forests are inherently different from those of younger forests in that old-growth stands have lost their capacity to absorb additional inorganic nutrient inputs, and hence are "leaky" with regard to nutrient inputs. In classic succession theory, no reference is made to fluxes of dissolved organic nutrients in air, water and soil. The Cordillera de Piuchué Ecosystem Study (CPES) was a pioneer project developed to study old-growth evergreen, montane temperate forests in the unpolluted coastal range of Chiloé island (42°S), southern Chile. This project, together with other studies in lowland old-growth forests, has contributed to the current body of knowledge of biogeochemical processes of temperate rainforests in southwestern South America (Hedin et al. 1995; Pérez et al. 1998, 2003a; Perakis and Hedin 2001, 2002; Carmona et al. 2002; Perakis et al. 2005). According to these studies, southern old-growth forests show strong retention of added inorganic nitrogen (N) contrary to predictions of classic biogeochemical theory, and in turn leak large amounts of dissolved organic nitrogen to stream waters. Consequently, late-successional forests are leaky for organic forms of nitrogen, but inorganic forms of nitrogen are strongly retained by soils, microbes and plants (Perakis and Hedin 2001, 2002).

In contrast to southern hemisphere temperate forests, biogeochemical cycles over most of the northern hemisphere have been influenced greatly by human activities, especially as a consequence of chronic nitrogen deposition (Aber et al. 1998; Holland et al. 1999). This anthropogenic "fertilisation" has greatly altered the nutrient steady state. Thus, during the last decade, the study of biogeochemical cycles in unpolluted, old-growth forests of southern Chile has become especially relevant as a baseline that may be characterised as the "unpolluted nitrogen cycle" (Perakis and Hedin 2002). Other sources of atmospheric nitrogen, such as forest fires, are also of limited importance in coastal locations because of the westerly winds derived from over the Pacific Ocean. Our knowledge of the unpolluted nitrogen cycle is extremely fragmentary in comparison to studies of the "polluted nitrogen cycles" of many northern hemisphere temperate forests. In the following sections, we briefly summarise the main biogeochemical characteristics that distinguish temperate old-growth forests of southern South America (Fig. 16.5).

16.4.1 Relevant Features of the Nitrogen Cycle in Unpolluted South American Forests

Element fluxes in old-growth temperate forests in western South America are characterised by the dominance of dissolved organic nitrogen in both atmospheric inputs and hydrologic outputs from forested watersheds (Hedin et al. 1995; Perakis and Hedin 2002; Weathers et al. 2000; Galloway and Cowling 2002). The presence of dissolved organic nitrogen in rain and fog likely derives from an oceanic source (Weathers et al. 2000); however, this is still unconfirmed. Such patterns differ markedly from most temperate forests in the northern hemisphere, where both atmospheric inputs and hydrologic outputs are strongly dominated by dissolved inorganic forms of nitrogen (Bormann and Likens 1979; Johnson 1992; Hedin and Campos 1991).

In southern Chilean ecosystems, where wet deposition of nitrate and ammonium are several orders of magnitude lower than in northern hemisphere forests (Hedin et al. 1991), two major sources of nitrogen for organisms during forest succession become relevant: biological nitrogen fixation and the recycling of organic matter via litterfall to the forest floor. Soil microorganisms mineralise the more labile fraction of soil organic matter to ammonium and nitrate (Pérez et al. 1998), both of which are readily absorbed by plants and/or microbes. According to succession theory, inorganic nitrogen in excess of growth requirements of these organisms may be lost via denitrification (gaseous nitrogen loss) or leaching. However, there is little evidence of either gaseous or hydrologic losses of ammonium or nitrate from late-successional forests (Pérez et al. 2003a). Nitrate and ammonium are found at very low concentrations in forest streams (Hedin et al. 1995), even after experimental addition of these nutrients to forest soils (Perakis and Hedin 2002), indicating strong biotic retention of inorganic nitrogen within the ecosystem (Perakis and Hedin 2001). In contrast, dissolved organic nitrogen accounted for
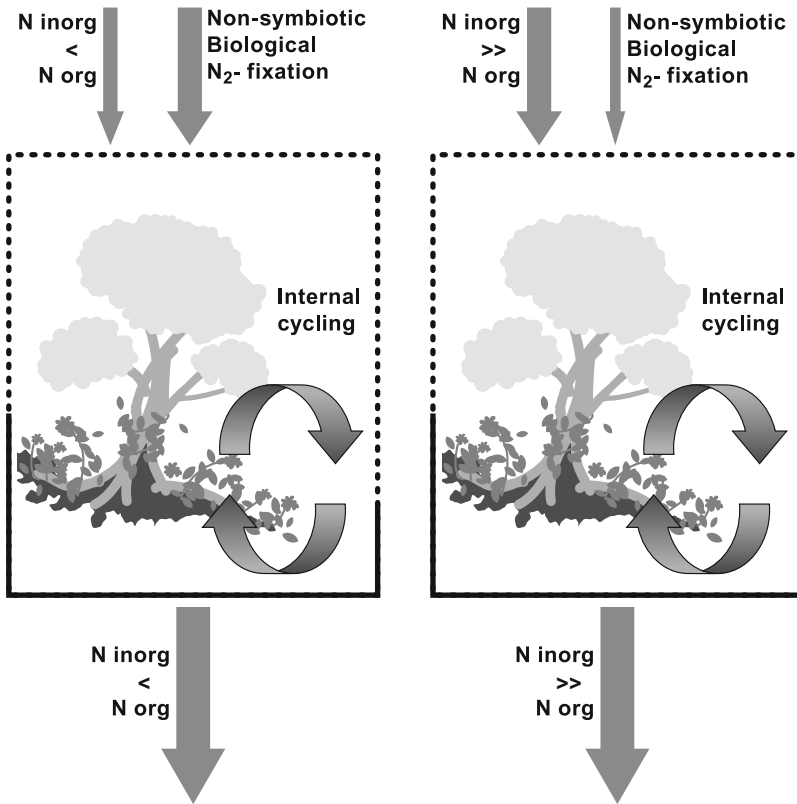
Fig. 16.5 Schematic diagram of the nitrogen cycle in unpolluted southern Chilean old-growth (*left panel*) forests compared to North American temperate forests (*right panel*), which are subjected to higher nitrogen deposition derived from anthropogenic sources. *Arrow* widths indicate the relative magnitude of nutrient fluxes. *N inorg* Inorganic nitrogen, *N org* organic nitrogen. Organic forms (dissolved and particulate) are more important in the outputs from forested watersheds in Chile than in North America. Inputs and outputs in most North American forest are dominated by inorganic nitrogen. Inputs in Chilean forests are also dominated by organic over inorganic forms of nitrogen. Notice that nitrogen fixation increases in relative importance in southern forests relative to atmospheric inputs

up to 95% of total nitrogen in CPES streams versus ca. 8% in streams draining forested watersheds of the northern hemisphere (Hedin et al. 1995, Perakis and Hedin 2002). This comparison strongly suggests that northern hemisphere old-growth forests have lower accumulation of dissolved organic forms of nitrogen and have limited capacity to retain soil nitrate. The reason for such differences in the retention of different forms of nitrogen in forest soils remains unclear.

Recent studies in Chilean temperate rainforests (Carmona et al. 2002; Pérez et al. 2004, 2003a) have highlighted the functional importance of recalcitrant and massive soil compartments, such as dead wood biomass and the litter layer (Oi horizon), both associated with the activity of free-living (non-symbiotic)

nitrogen fixers. Nitrogen input via non-symbiotic nitrogen fixation has been estimated in the range of 0.2–2.3 Kg N ha^{-1} year^{-1} (Pérez et al. 2003a, 2004). Furthermore, the contribution of symbiotic nitrogen fixation cannot be ruled out in these forests, because several lichen and hornwort species have symbiotic associations with cyanobacterial diazotrophs (J. Duckett, personal communication), a process that deserves further study.

Internal fluxes of nitrogen in CPES forests indicate low rates of soil net nitrogen mineralisation, accompanied by high gross nitrogen mineralisation rates (Pérez et al. 1998; Perakis et al. 2005) and strong retention of both ammonium and nitrate within the ecosystem (Perakis and Hedin 2001). In addition, Vann et al. (2002) observed that the high amount of nitrogen accumulated in the live biomass of coastal montane forests, in association with low inorganic nitrogen production in these soils, suggests high nitrogen use efficiency. This is further supported by the high leaf C/N ratios of canopy trees and high retranslocation from senescent leaves to living tissues (Pérez et al. 2003b; Aravena et al. 2002). Another important finding is that slow decomposition and high accumulation of organic matter in old-growth forest soils tends to enhance soil cation exchange capacity (Pérez et al. 1998, 2003a), thus contributing to enhanced ammonium retention (Perakis and Hedin 2001).

Current knowledge of biogeochemical cycles in Chilean old-growth forests is restricted largely to nitrogen dynamics (Hedin et al 1995; Pérez et al. 1998; Perakis et al. 2005), because nitrogen is considered the principal nutrient limiting plant growth in boreal temperate forests, whereas phosphorus (P) limits plant growth in tropical rainforests (Aber and Melillo 1991). Nevertheless, exploration of phosphorus limitation in evergreen temperate rainforests in New Zealand and Hawaii has shown that phosphorus becomes limiting when high rainfall and low disturbance promote leaching losses of phosphorus (Wardle et al. 2004). Accordingly, old-growth forests in southern temperate areas of southwestern South America could potentially be phosphorus- as well as nitrogen-limited in late stages of succession. Despite the fact that annual precipitation in CPES forests exceeds 3,000 mm, phosphorus limitation has not been reported (Thomas et al. 1999; Vann et al. 2002). While high N to P ratios of leaves in CPES forests (mean N:P = 18.6 ± 1.3, Vann et al. 2002) are indicative of potential phosphorus limitation (Wardle et al. 2004), Thomas et al. (1999) considered soil phosphorus concentrations in CPES forests to be sufficient for plant growth. The evidence is still inconclusive and further research on plant growth responses to phosphorus addition in unpolluted old-growth South American temperate forests are necessary.

16.4.2   Human Impact on Biogeochemistry of Southern Forests

Human activities have fragmented and reduced the area of land covered by old-growth forests. Remnant patches are now surrounded by secondary forests, shrublands, and anthropogenic prairies, which are subjected to logging, fire and grazing. Rural landscapes offer an opportunity to assess nutrient dynamics under mixed land

use, including remnant forest stands. Forest fires and logging may disrupt the tightly closed nitrogen cycle that characterises old-growth forests, decreasing soil nitrogen retention capacity while increasing soil nitrogen availability, thus enhancing ecosystem nitrogen losses, mainly via decomposition and leaching (Pérez et al. 2004; C. Pérez, unpublished data). In addition, higher nitrogen availability in disturbed forests can decrease phosphorus availability, leading to an increase in N:P ratios and changed species composition (A. Gaxiola et al., unpublished data). Nevertheless, recent studies comparing soil nitrogen processes between secondary and old-growth lowland forests in Chiloé Island have shown minimal differences in nitrogen and carbon storage, nitrogen availability and mineralisation (Pérez et al. 2004). Such results suggest a strong resilience of old-growth ecosystem processes to moderate human impacts (Aravena et al. 2002). However, recurrent human disturbances, such as increased fire frequency, chronic nitrogen deposition, and short logging cycles are likely to affect the potential recovery of forests and, in some cases, lead to alternative stable states that require active restoration (Fig. 16.4). We have documented the long-lasting effects of forest canopy removal, from logging or fire, on the hydrologic cycle, which lead to a raised water table and inhibition of tree establishment (Díaz et al. 2007).

16.5   Conclusions

Old-growth forests play significant roles in maintaining global biodiversity, retaining essential nutrients, storing carbon for long periods of time, and providing aesthetic and spiritual values to society. They certainly cannot be disregarded as 'over-mature' stands of decaying trees. Mature forest cover must be nationally inventoried and monitored as valuable natural capital. Human impact over the past two centuries in south-central Chile has led to homogenisation of stand structures and landscape patterns through the conversion of old-growth forests into degraded secondary forests, followed by the expansion of pastures and forestry plantations. Old-growth forests have declined to less than 1% of the land in the northern limit of the temperate forest distribution in south-central Chile.

To prevent the demise of the last remnants of old-growth forests, we recommend that intensive logging practices for timber, woodchips and firewood extraction should be concentrated in the extensive degraded secondary forests in south-central Chile (Echeverria et al. 2007). Some small-scale selective logging practices in old-growth forest remnants may not affect their function as habitat for animal species and may represent an environmentally friendly management option in rural landscapes. On the other hand, some frequent forms of disturbance could be highly disruptive of plant–animal mutualisms in forests, as predicted in the case of the eradication of large old trees of *Eucryphia cordifolia*, a tree sustaining one of the richest pollinator assemblages in lowland temperate forests. Conservation of rapidly declining old-growth remnants in south-central Chile must be guided by a discussion process among a broad stakeholder base, considering both ecological

and socio-economic values among other land uses. In addition, long-term ecological research and education programs, in combination with approaches such as the development of biosphere reserves and networks of biological stations, are critical to effectively integrate ecological understanding, decision making and general public conservation attitudes (Rozzi et al. 2008).

Ongoing studies of biogeochemical processes show a strong resilience of old forests to moderate impacts but alteration of recovery processes under recurrent impacts (Fig. 16.4). Strong inorganic nutrient retention in old-growth forests is not consistent with the predictions of current succession theory and contrasts with the leaky condition of northern hemisphere ecosystems in areas of high nitrogen deposition. In addition, high annual precipitation in Chilean forests can result in a rapid loss of available phosphorous, a process that could differ from northern hemisphere forests where phosphorous limitation is rather negligible. Knowledge of nutrient cycling in unpolluted southern forests can contribute to advancing our understanding of the consequences of global change, particularly the long-term effects of enhanced nitrogen deposition in forest soils.

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Chapter 17
Tropical Rain Forests as Old-Growth Forests

John Grace and Patrick Meir

17.1 Introduction

In the context of this book, we may begin by making the general observation that many rain forests are *par excellence* old growth forests. They have the diagnostic characteristics mentioned in the companion chapter (Chap. 2 by Wirth et al., this volume), including mixed ages and species, and large amounts of standing and downed deadwood in all stages of decay. Some authors use the term 'virgin' to describe them, but generally they are not at all virgin, having been colonised by indigenous people in former times using slash and burn agriculture and undergone re-growth for several hundreds of years (Clark 1996). This is known from artefacts and charcoal found in the soil (Gomez-Pompa et al. 1987). We also recognise 'old growth secondary forest', which may have remarkably high biomass and much of the general appearance of undisturbed forest but lacks some of the biodiversity and the old and dead trees (Brown and Lugo 1990).

The status of tropical rain forests is widely discussed in the literature. These forests occupy some 12% of the terrestrial surface; they contain 55% of the biomass; they are thought to hold over half of the global biodiversity. They occupy the warm and wet regions of the Earth, occurring where the temperature of the coldest month is at least 18°C, and where every month has 100 mm of rain or more. One can argue to some extent with these figures, as the definition of tropical rain forest is not hard and fast (see for example, Richards 1952; Clark 1996; Whitmore 1998). We may adopt one of the first definitions (Schimper 1898):

> Evergreen, hygrophilous in character, at least 30 m tall and usually much more, rich in thick-stemmed lianas and in woody as well as herbaceous epiphytes.

Tropical rain forests are disappearing at a rate that is also generally disputed, but which is somewhere between 0.4 and 0.6% per year, corresponding to 4–6 millions of hectares per year (Achard et al. 2002; and Chap. 18 by Achard et al., this volume). Political awareness of their real value as a resource and as a global environmental service is now higher than ever before, and there are signs that steps may be taken to reduce deforestation rates (see Chap. 20 by Freibauer, this

volume), although this requires international initiatives, which will take some time. We will return to this aspect later.

The aim of this chapter is to comment on the structure and function of the rain forest canopy, inasmuch as it influences, and generally interacts with, the global climate.

17.2   Structure

Numerous authors have commented on the vertical stratification of rain forest canopies, asserting that a distinguishing feature of rain forests is that the canopy forms strata or storeys. The earliest author to put forward this point of view may have been von Humbolt (1808); later the concept was championed in the English-speaking world by Richards (1952), whilst elsewhere there was a focus on the diversity of individual tree architecture (Hallé et al. 1978). The evidence for stratification comes from profile-drawings, in which a high degree of subjectivity may have influenced the result. When attempts have been made to describe the distribution of leaf area in an objective way, either by felling trees and cutting them into segments corresponding to different heights (Kira 1978, McWilliam et al. 1993), by photographic survey inside the canopy using suspension-wires (Koike and Syahbuddin 1993) or from a tower with photography (Meir et al. 2000) or state-of-the-art canopy sensors (Dominguez et al. 2005), the canopy does not show the discontinuities that one might expect from the stratification paradigm (Fig. 17.1). In fact, it is similar to that found in other forests, differing only in scale: the rain forest is taller than most temperate forests and the canopies of the tallest trees are broader. There is, however, vertical stratification in another sense. Recognisably different life forms are present at different heights, and they occupy different levels within the continuum. The tall-growing emergent species are sparse and often have the discoid individual canopies that give rain forest its characteristic appearance; underneath these is the main canopy made up of trees with lianas and epiphytes [Richards (1952) recognised two of these layers], beneath that we have a conspicuous understorey or ground layer of palms, seedlings, saplings and herbs. The light climate at ground level is complex, but this applies equally to all old-growth forests (Montgomery and Chazdon 2001; see also Chap. 6 by Messier et al., this volume). In all of these, the radiation is different from normal daylight in the following: spectral distribution, planes of polarisation, directional distribution, temporal patterns and, most importantly, it has a much diminished flux density, typically only a few percent of daylight.

Several claims are commonly made of rain forest canopies from a theoretical point of view. One is that the discoid emergent trees create a special light climate, with sun-flecks at a different angular elevation to that of temperate forests (Terborgh 1985); another is that tropical forests can support twice the leaf area of temperate forests (Leigh 1975). After several decades of research, neither of these assertions have much observational support. Leaf area index (LAI) has usually been measured indirectly by optical means, and this introduces uncertainty into its determination

Fig. 17.1 Vertical distribution of leaf area density for five rain forests: *1* Mbalmayo, Cameroon (△); *2* Reserva Jaru, Rondonia, Brazil (●); *3* Cuieiras, Brazil (▾); *4* Embrapa, Brazil (○); and *5* Pasoh, Malaysia (■). Cases *1–3* are determined optically by Meir et al. (2000); *4* and *5* are obtained by destructive harvesting and are from McWilliam et al. (1993) and Kira (1978), respectively
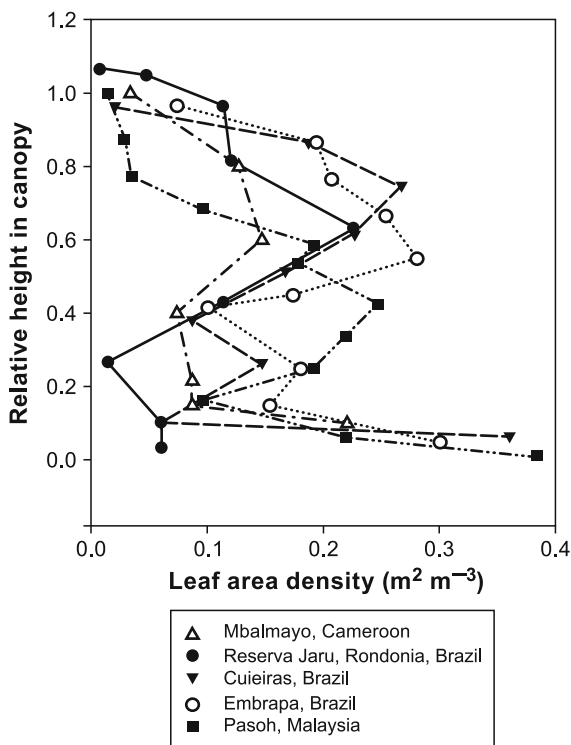
because leaves are clumped together instead of being random and, moreover, optical methods do not usually distinguish leaves from stems and branches. Where it has been measured destructively (Kira 1978; McWilliam et al. 1993), the LAI is in the range 5.0–7.5. It is clear that deciduous forests in the temperate parts of the world also have leaf area indices in this range, although they can often be lower, and certainly do become lower in old-growth as a result of trees falling (Eriksson et al. 2005). Another misrepresentation of rain forests is that they hold extremely large and very old trees; in fact the trees are not usually extremely old, although a few of them are indeed very large. Chambers et al. (1998) made determinations of age of emergent trees using ^{14}C measurements in rain forest at Manaus, Brazil, and discovered a few slow-growing trees over 1,000 years old; however, most were fast-growing and younger (Fig. 17.2).

How then is the structure of the rain forest canopy really different from the temperate deciduous canopy? Here we identify two aspects. The first is that the canopies of individual trees are often tied together with lianas. This means that when one large tree is blown down, other trees are damaged and sometimes uprooted too, leading to a more complex disturbance regime, and a larger scale of spatial variation than in other canopies, which probably has led to a rather different selection pressure on seedlings. Earlier authors commented on the regeneration niche of rain forests, and the way that tree species may have become specialists for
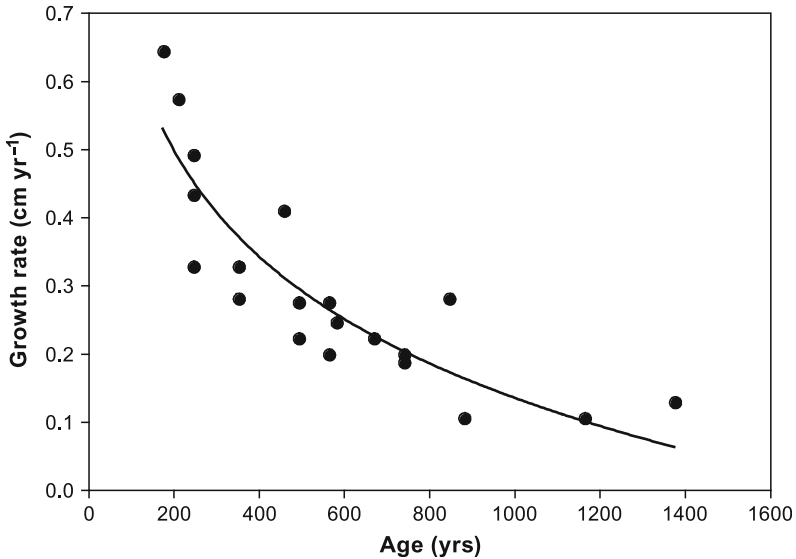
Fig. 17.2 The average long-term growth rates in diameter of large emergent trees from a forest near Manaus, Brazil. Growth rates were obtained by dividing the diameter of the stem by the age of the tree. The age was determined by radiocarbon dating. Data from Chambers et al. (1998)

particular types of gaps (Denslow 1980), although ecophysiological investigations do not generally support such a high degree of categorisation as has sometimes been claimed (Brown and Whitmore 1992). The second aspect is that the vertical pattern of LAI is large, i.e. the leaf area is spread over a height of up to 50–60 m. One aspect of this is that there are large volumes of air in between leaves and branches. This has implications not only for microclimate but also for habitats, especially of flying animals. It also has some interesting implications for storage of heat and gases that mean that the lower part of the canopy is relatively decoupled from the atmosphere and may become considerably rich in carbon dioxide and other gases that emanate from the soil. It may be the diversity of microclimates resulting from the immense structural heterogeneity that contributes to the great richness of non-tree plant species, epiphytes in particular (Gentry and Dodson 1987). An example of microclimate from the present authors' work relates to CO_2. In the rain forest canopy, CO_2 builds up to high concentration at nights when the external conditions are stably stratified (Fig. 17.3). This is the outcome of high rates of ecosystem respiration and the development of internal convection cells that can mix the ground level air with air in the mid-canopy. Lloyd et al. (1996) estimated that in the early morning, 6.00–9.00 a.m., a high proportion of the CO_2 molecules in the canopy are of respiratory origin (between 7 and 25%), much higher than occurs in a Siberian coniferous forest. Thus, in the early morning the leaves will experience high CO_2 and they re-fix a significant part of it.

This canopy microclimate is altered when the forest becomes fragmented, by logging or clearing for agriculture. We will return to this later.
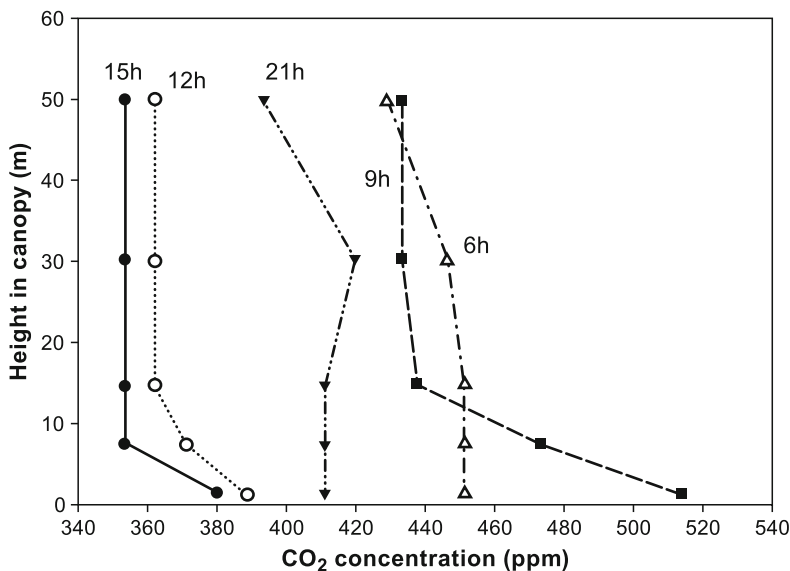
Fig. 17.3 Profiles of CO_2 in the canopy for a typical day/night at Reserva Jaru, Rôndonia, Brazil. Local time is shown on the labels e.g. 15h is 1500 hours. From Kruijt et al. (1996)

17.3 Physiological Attributes

The leaves of rain forest trees and seedlings have rates of photosynthesis that are similar to their counterparts in deciduous temperate forests, though possibly slightly lower on average (Chazdon and Field 1987; Riddoch et al. 1991; McWilliam et al. 1996; Carswell et al. 2000b; Domingues et al. 2005; Meir et al. 2007; cf. Sect. 4.5.2 in Chap. 4 by Kutsch et al., and Chap. 6 by Messier et al., this volume). Maximum photosynthetic rates of leaves are generally correlated to the foliar nitrogen content (Wong et al. 1979), and tropical rain forests are considered to be relatively well-supplied with nitrogen so therefore might be expected to have high rates of photosynthesis (Reich et al. 1994). However, photosynthetic rates in the rain forest, measured under natural light and at ambient CO_2 concentration, seldom exceed 12 μmol CO_2 m^{-2} s^{-1} (Reich et al. 1994; Carswell et al. 2000a; Dominguez et al. 2007). Exceptions may be the fast-growing pioneers like *Cecropia* (Bazzaz and Pickett 1980; Reich et al. 1995; Ellsworth and Reich 1996). Sometimes the broad-leaved species of temperate regions, when not stressed, have light-saturated rates exceeding 12 μmol CO_2 m^{-2} s^{-1} (Bassow and Bazzaz 1998; Kull and Niinemets 1998; Raftoyannis and Kalliope 2002). Attempts to compare world-wide photosynthetic rates suggested that leaves of tropical trees may have somewhat lower stomatal conductances than deciduous temperate trees, but the differences are not large (Schulze et al. 1994; Reich et al. 1999; Wright et al. 2004). The physiological characteristics of the leaves also show vertical profiles in the capacity to

photosynthesise, and some physiological differentiation into 'sun leaves' and 'shade leaves', much as reported in broadleaved trees from the temperate zone (Meir et al. 2002). When comparisons are made carefully, and at different heights in the canopy, it appears that maximum carboxylation rates from tropical rain forests are somewhat lower than for broadleaved temperate species (Fig. 17.4), despite the fact that these leaves may have relatively high nitrogen contents on an area or mass basis (Meir et al. 2007). These lower rates may be the result of adaptations for survival for longer periods: most leaves in the rain forest canopy are retained for 1–4 years instead of a few months (Reich et al. 2004), and to survive attack by biological agents especially insect herbivores they may require adaptations such as thick cuticles and high levels of plant secondary compounds (Coley and Kursar 1996), with corresponding reduced investment in photosynthetic machinery. In-
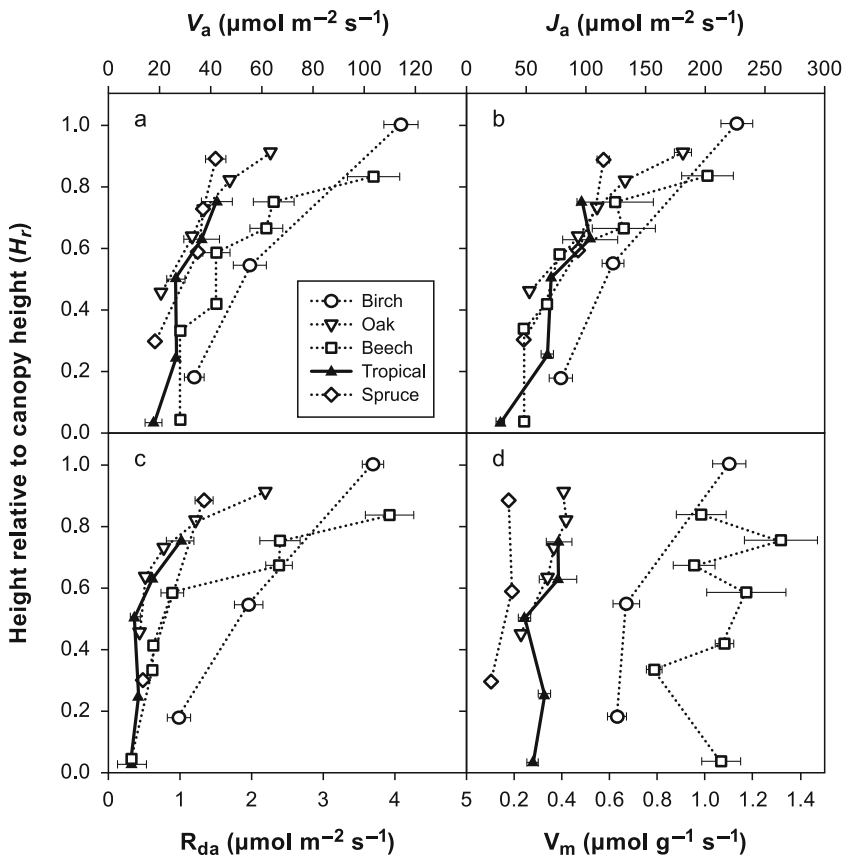
Fig. 17.4a–d Leaf-level gas exchange characteristics within forest canopies. Quantities are: **a** V_a maximum carboxylation rate on an area basis, **b** J_a maximum electron transport capacity on an area basis, **c** R_{da} leaf respiration on an area basis, **d** V_m maximum carboxylation rate on a leaf mass basis. From Meir et al. (2002)

deed, Reich et al. (1999) have shown a strong negative relationship between the longevity of leaves and their capacity to photosynthesise. On the other hand, the lower rates may be the result of a shortage of phosphorus: several studies now suggest that phosphorus rather than nitrogen limits the photosynthetic capacity of the leaves of rain forest species (Meir et al. 2007; Kattge et al. 2009), although the overall productivity may nevertheless be limited by the nitrogen supply in many cases (LeBauer and Treseder 2008).

At canopy level, the response of gas exchange, measured by the micrometeorological technique of eddy covariance, is quite similar to that found in deciduous temperate forests, with maximum rates of ecosystem gas exchange in rain forests of 15–25 µmol CO_2 m^{-2} s^{-1} (Grace et al. 1995; Malhi et al. 1998; Carswell et al. 2002; Saleska et al. 2003). The important difference is that the rain forest functions more or less continuously all year, whilst temperate deciduous forests shed their leaves in the winter, and boreal forests cease photosynthesis in the cold dark winters. Thus, when annual totals are compared, the rain forest has about twice the annual total of photosynthesis, a consequence of photosynthesising for 12 instead of about 6 months (Malhi et al. 1999; Luyssaert et al. 2007). This is not to say that rates are constant all year: they are likely to vary according to the length of the 'dry season' and are probably influenced greatly by variations in solar radiation and temperatures (Carswell et al. 2002; Saleska et al. 2003). When the estimated productivity of all rain forests are summed, it is thought that they contribute about one-third of all the terrestrial biological productivity of the world (Roy et al. 2001).

17.4 Are Rain Forests Carbon Sinks?

The net ecosystem exchange is the balance between the CO_2 entering the ecosystem by photosynthesis and the losses by autotrophic and heterotrophic respiration. A basic postulate, often heard, is that old-growth forests are carbon neutral, i.e. gains by photosynthesis are equal to losses by respiration. This view is perhaps forged in the ecological paradigm that assumes a process of ecological succession that leads to a 'climax forest' in equilibrium with a more-or-less constant climate. Nowadays we know that the climate fluctuates considerably and has always done so, and we also are more aware that forests are disturbed and most are in a stage of recovery from damage. The circumstances whereby an old-growth forest might be a sink would be in a trend of an increasingly favourable environment that stimulates photosynthesis more than respiration and consequently accumulates carbon, above- and/or belowground. Several authors suggest this can occur as a result of elevated CO_2 or N-deposition (Taylor and Lloyd 1992; Lloyd and Farquhar 1996). Taylor and Lloyd (1992) first devised a very simple theoretical model to show how this depends on the extent of the stimulation and the turnover rate of the carbon pools. Later, Lloyd and Farquhar (1996) made 'reasonable' assumptions and showed how rain forests might accumulate carbon at a rate of around 0.6 t C ha^{-1} year^{-1}.

In fact, rain forests in Amazonia have been shown by direct measurement to be acting as carbon sinks (Grace et al.1995; Malhi et al. 1998). These results were strongly challenged by Saleska et al. (2003), who reported a case where a rain forest was apparently a net source of carbon, using essentially the same measurement technique as the previous authors. However, the same forest moved towards a sink over a period of 4 years, and is now considered to have been recovering from disturbance (Hutyra et al. 2007). There are uncertainties in eddy covariance measurements, especially at night, and it is now clear that the technique has a tendency to under-record night respiration and thus to exaggerate the size of the sink. Moreover, because it is known that spatial variations in the carbon balance of rain forests are large, and in some areas the forest may still be recovering from disturbance, there is always a large sampling problem. Consequently, the issue of whether the Amazonian rain forest *as a whole* is a sink cannot be resolved by eddy covariance alone (Araújo et al. 2002; Kruijt et al. 2004; Rice et al. 2004; Miller et al. 2004; Ometto et al. 2005; Sierra et al. 2007). Rather, it is necessary to deploy other methods as well.

Another way to assess whether ecosystems are carbon sinks is by thorough repeated inventory, involving many sample plots, over a decadal time scale. By showing increases in above ground biomass of up to 0.5 t C ha^{-1} year^{-1}, analysis of large scale inventories of aboveground biomass have also suggested the rain forests are indeed a sink (Phillips et al. 1998, 2004; Baker et al. 2004). Of course, this approach neglects to study changes in the soil, which may be quite significant. A third way is by analysis of atmospheric CO_2 concentrations, and inferring what the land surface must have been exchanging with the atmosphere to give the observed concentrations. However, this approach also suffers from insufficient sampling densities; although the recent indications it provides suggest a carbon sink in the tropics (e.g. Rödenbeck et al. 2003; Stephens et al. 2007). Clearly, the four approaches – modelling, eddy covariance, forest inventory and atmospheric inversion – all have their own particular weaknesses and are subject to errors that sometimes compromise the estimate; nevertheless, they are completely independent techniques and they point to the same conclusion – that the tropical rain forest is a carbon sink. Is it possible that all these forests are sinks because they are responding to elevated CO_2? Although Clark et al. (2003) demonstrated a statistical correlation between tree growth at one site in Central America and atmospheric CO_2 concentrations as measured at Mauna Loa, it seems unlikely that rain forests are especially stimulated by elevated CO_2. In other nature forest ecosystems where it has been possible to carry out long term fumigation with twice-normal CO_2, the enhancement of growth has been hard to detect (Asshoff et al. 2006).

Moreover, Carswell et al. (2000a) showed seedlings of two rain forest species to be rather unresponsive to twice-normal CO_2, although a greater response was found for a (temperate) liana species by Granados and Körner (2002) and Zotz et al. (2006). There is a possibility that rain forests are responding to long-term trends in other factors. Malhi and Wright (2004) found that since 1970, the rainfall in the humid tropics as a whole has declined by 1%, the N-deposition has increased by 10% and the CO_2 concentration has increased by about 20%. The decline in rainfall

was probably associated with an increase in solar radiation, and that may have been beneficial.

Another way in which carbon fluxes might change is through shifts in species composition over periods of several decades ('long term'). Given that climate and CO_2 has changed over the last century or so, it is possible that changes in species composition will show up in data from permanent sample plots.

17.5 Are There Recent Changes in Species Composition?

The analysis of forest inventory data to test the hypothesis that species composition is changing is a long term project in several centres that is still in progress. There are strong indications of gradients, determined by moisture and nutrient availability, at a regional scale (ter Steege et al. 2006; Swaine and Grace 2007). One indication from the literature is that lianas are increasing in abundance (Phillips et al. 2002; Wright et al. 2004). It is difficult to generalise about the relevant features of lianas because they are taxonomically diverse. However, they have very deep roots and an efficient water transport system (Holbrook and Putz 1996; Restom and Nepstad 2004; Cai 2007; Swaine and Grace 2007). Those in the top of the canopy a have a lower stomatal conductance than trees, and a correspondingly higher $\delta^{13}C$ value (Domingues et al. 2007). Schnitzer (2005) examined floristic data from 69 tropical forests worldwide and found a negative correlation between mean annual precipitation and liana abundance. He found that lianas grew seven times faster than trees in the dry season, and twice as fast during the wet season, and attributed this to the tendency of lianas to produce deeper roots than trees. More recently, an examination of the floristics along a rainfall gradient in Ghana, showed that the abundance of liana species (as a proportion of the total species) increased linearly with dryness (Fig. 17.5, from Swaine and Grace 2007). According to Londre and Schnitzer (2006), lianas succeed in disturbed regimes and fragmented forests affected by fire. We may hypothesise that part of the response to a drying trend in the climate might be an increased contribution to the carbon balance by lianas. This hypothesis should now be tested in other regions of the tropics. The implications of a liana-enriched canopy are not clear, but there could be strong feedbacks for the light climate at the forest floor, the microclimate in general and the interaction with the climate system.

17.6 How Will Rain Forests Behave in a Hotter and Drier Climate?

There are rather few studies where it has been possible to measure the growth rates of rain forest trees by repeated annual measurements on the same individuals, and then relate the trends to climatological variables. Inevitably, these studies have a rather small sample size and need to be taken as 'indicative' at this stage. Clark
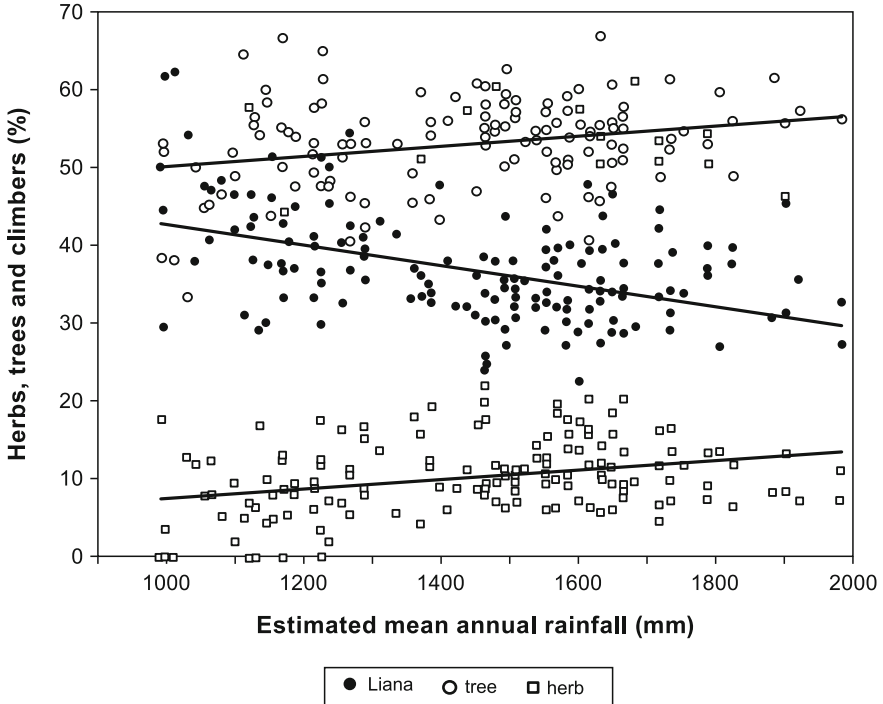
Fig. 17.5 Liana (●), tree (○) and herb (□) species as a percentage of all species in 154 sample plots on a rainfall gradient in Ghana (Swaine and Grace 2007)

et al. (2003) examined the diameter growth of six species in Costa Rica, and found evidence for a decline in growth rates associated with increasing night temperatures. More recently, the data of Feeley et al. (2007) from Panama and Malaysia show a negative correlation with minimum temperature, and a positive correlation with precipitation. It seems highly likely from these two examples that warming will reduce the growth rates.

Another line of evidence comes from eddy covariance. The technique enables an exploration of the short-term patterns of CO_2 flux into, and out of, whole ecosystems. Based on data from a forest in southwest Brazil, Grace et al. (1995) showed that the gas exchange of rain forest may be expected to depend critically on temperature and irradiance. The sensitivity to temperature results from the empirical observations of a very strong dependency of plant and soil respiration on temperature, and a non-saturating relationship between incoming solar radiation and canopy gas exchange. A small increase in temperature (1°C) in model simulations was enough to turn the carbon balance from a carbon sink to a source. Thus, one would expect that interannual variability would have a very large impact on carbon balance. Later authors came to a similar conclusion using more sophisticated models (Cramer et al. 2001; Tian et al. 1998; Cox et al. 2000). The model of Tian et al. (1998) additionally showed a high sensitivity to precipitation. The paper

by Cox et al. (2000) is especially interesting, as it is the first in which a simple carbon cycle model has been coupled to a global circulation model (HADCM3) – HADCM3 estimates the climate and ecosystem carbon fluxes of the next 100 years. Large scale climatic phenomena such as the El Niño-Southern Oscillation ('El Niño') are emergent properties and, in this model, the El Niño development is especially strong. The coupled model predicts that the warming of the Amazon will be so large as to trigger a replacement of rain forest by savanna (Cox et al. 2000). However, other models are less conclusive (Friedlingstein et al. 2006). Nevertheless, large El Niños, with an impact on the Amazon forest, may have happened several time since the Holocene. Meggers (1994) found evidence for such phenomena at 1,500, 1,000, 700 and 450 years before the present, and periods of rain forest extinction and re-emergence have been identified in the pollen record from lake sediments (Whitmore 1998; Mayle et al. 2007). The difficulties in modelling the process of rain forest decline relate to our uncertain knowledge of the controls of microbial respiration (Trumbore 2006; Davidson and Janssens 2006), phenology (Hutyra et al. 2007), and fire.

The fire effect is likely to be paramount, and is linked to disturbance and fragmentation. It is well known from field measurements that when rain forest is fragmented, the canopy microclimate is affected, and necromass becomes drier and thus more prone to burning (Kapos 1989). Laurance and Williamson (2001) presented a speculative hypothesis to draw together our knowledge of the interactions between people, fire, forests and climate (Fig. 17.6). Dense forests have a characteristic microclimate with high humidities and daytime temperatures that are lower than those at the top of the canopy. At forest edges the situation is different, with free horizontal ventilation and mixing of canopy air with air from outside.
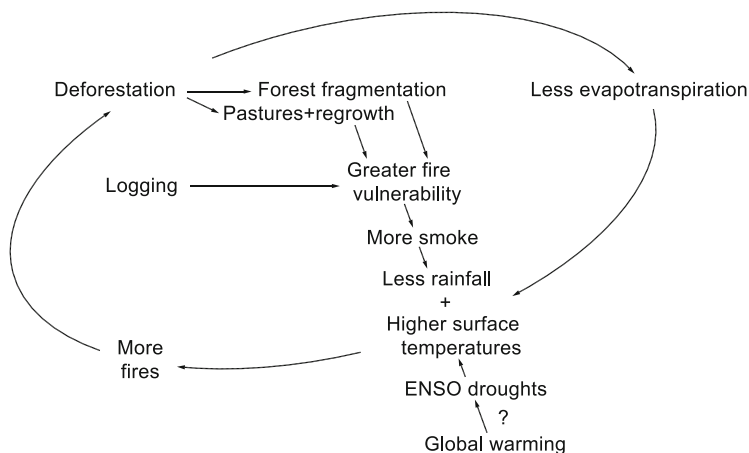
Fig. 17.6 Conceptual model of the positive feedbacks in the interactions between global warming, humans and deforestation. *ENSO* El Niño-southern oscillation. From Laurance and Williamson (2001)

When drought occurs, relatively dry air penetrates the canopy, and reductions in humidity and increases in plant mortality have been measured at up to 100 m from the canopy's edge (Benitez-Malvido and Martinez-Ramos 2003). Humans light fires, and these fires are likely to ignite more easily and spread more rapidly in the dry conditions of the forest edge. Hence, the forest is damaged and possibly destroyed at a faster rate than would occur in the absence of humans. Such processes have been implicated in the conversion of rain forest to Savanna at a large scale (Bowman 2000). The processes involved are quite complex and collectively amount to a strong positive feedback. In the Laurance–Williamson model, deforestation causes less evaporation, which in turn leads to less rainfall and hence droughts are exacerbated (Laurance and Williamson 2001). Logging can also be important as it thins the canopy and increases vulnerability to combustion.

17.7 The Future

17.7.1 A Pessimistic View of the Future

The dynamics of old-growth forest are likely to change as the environment changes. It is easy to see how it might happen: the duration of the dry season is likely to increase and impact negatively on biodiversity; occasional severe droughts will become more common and lead to extensive forest fires; the encroachment of people into the forest will lead to attrition exacerbated by the processes proposed by Laurance and Williamson (2001); the carbon cycle will be impacted and the tropical regions will rapidly become a source of carbon to the atmosphere. The effects of loss of forest area will alter the albedo and the water balance of whole regions and, through teleconnections, this will impact upon the climate in other parts of the world (Werth and Avissar 2002). So far, coupled climate and vegetation models are at a primitive stage of development and they provide insufficient insight into how soon the changes may occur. Truly useful areas of research are rather difficult to define, but it is clear that the general vegetation–atmosphere linkage is still poorly understood, and more work is needed in many areas before we can make good predictions.

17.7.2 An Optimistic View of the Future

On the other hand, if fossil fuel emissions are less extreme than suggested by predictions (IPCC 2007), and if the Cox et al. (2000) model-prediction turns out to be pessimistic because of the rather coarse assumptions made in that model about heterotrophic respiration, we may expect a different outcome. Rain forests would still be degraded to a large extent, but secondary rain forest has useful

characteristics (Brown and Lugo 1990). If the global CO_2 concentration could be held at 550 ppm and the temperature increase to 1°C, and if measures for forest protection at a global scale were stronger, we might preserve much of the rain forest and some of the environmental services it provides. Forest protection might be achieved by extending the terms of the Kyoto Protocol to include not just 'afforestation' but also 'avoided deforestation' (cf. Chap. 20 by Freibauer, this volume), especially if this is linked to the development of carbon-cycle surveillance techniques using advanced satellite remote sensing techniques, which are already developing fast (Xiao 2006; Grace et al. 2007; Chap. 18 by Achard et al., this volume). Essentially, this means that many poorer countries of the world would be paid for keeping the rain forest intact for the benefit of the Earth and humankind.

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Part V
Human Dimensions

Chapter 18
Detecting Intact Forests from Space: Hot Spots of Loss, Deforestation and the UNFCCC

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18.1   Introduction

Changes in forest cover have become recognised as an important global environmental issue. This chapter aims to synthesise what is known about areas and rates of forest-cover change in the tropics and boreal Eurasia from the 1990s onwards, based on data compiled from expert opinion and earth observation technology. Since the early 1990s, changes in forest area can be measured with confidence from space from the global to the regional scale (Mollicone et al. 2003).

Forest-cover change (including deforestation) at the regional scale is the process of land-cover change that is most frequently measured. During the 1990s, rates of forest-cover change were much higher in the tropics than in other parts of the world. In particular, the Amazon basin and Southeast Asia contain a concentration of deforestation hotspots, and more regional remote sensing studies cover the tropics than boreal zones. However, forest degradation in Eurasia, related mostly to unsustainable logging activities or increases in fire frequency, has been growing in recent years.

In addition to reviewing the results from Earth observation studies, this chapter presents a potential accounting mechanism in the context of the United Nations Framework Convention on Climate Change (UNFCCC) question of reducing emissions from deforestation in developing countries (UNFCCC 2006), which builds on recent scientific achievements related to the estimation of tropical deforestation rates from Earth observation technology.

18.2   Monitoring of Forest Areas from the Global to the Regional Scale using Satellite Imagery

Combined with ground measurements, remote sensing plays a key role in determining the loss of forest cover. Technical capabilities have advanced since the early 1990s and operational forest monitoring systems at the national level are now a

feasible goal for most developing countries (DeFries et al. 2006). Several appropriate methods are now available to analyse satellite data to measure changes in forest cover. These methods range from visual photo-interpretation to sophisticated digital analysis, and from wall-to-wall mapping to hot spot analysis and statistical sampling. Clearings for large-scale mechanised agriculture are detectable with medium resolution data (hundreds of metres spatial resolution), whereas small agricultural or settlement clearings of 0.5–1 ha require higher resolution data (tens of metres) to be detected accurately.

Analysis of remotely sensed satellite data is the only practical approach to measure changes in forest area at the regional to global scale. High resolution data, with almost complete global coverage, are available at low or no cost for the 1990s, early 2000s and around year 2005, in particular Landsat satellite data from NASA (https://zulu.ssc.nasa.gov/mrsid), the USGS (http://edc.usgs.gov/products/satellite/landsat_ortho.html) or from the University of Maryland's Global Land Cover Facility (http://glcfapp.umiacs.umd.edu/). It has been demonstrated that estimates of deforestation can be provided by using such data at the global or continental level (Achard et al. 2002; FAO 2001), or at national level for very large countries such as Brazil or India (INPE 2005; Forest Survey of India 2004). Deforestation, defined as the conversion of forest land to non-forest land, is most easily monitored. Estimating forest degradation resulting from practices such as unsustainable timber production, harvesting of wood for fuel, and fires clearing the edge of forest fragments is more technically challenging than measuring deforestation. Quantifying the accuracy of the result and ensuring that consistent methods are applied at different time intervals is critical. Accuracies of 80–95% are achievable for monitoring with high resolution imagery to discriminate between forest and non-forest (DeFries et al. 2006). Accuracies can be assessed through in-situ observations or analysis of very high resolution aircraft or satellite data.

18.3   Information on Global Forest Extent and Deforestation Rates

18.3.1   Distribution of Forest Areas at Global Scale

In the late 1990s, data from AVHRR (advanced very high resolution radiometer) sensors at 1.1 km resolution on board the United States National Oceanic and Atmospheric Administration's polar orbiting meteorological satellites were used to produce pan-tropical forest maps at around 1 km resolution (Fig. 18.1) with classification techniques adapted to the ecological conditions of these areas, e.g. low seasonality and nearly permanent cloud coverage (Achard et al. 2001). Recently, the VEGETATION sensor on board SPOT-4 and SPOT-5 satellites, and the MODIS sensor on board the Terra and Aqua satellites allowed for a spatial and thematic refinement of the previous global maps. In the framework of the Global Land-Cover 2000 project

(GLC-2000), teams of regional experts mapped each continent independently using VEGETATION data for the year 2000 at 0.01° geographic resolution, i.e. at around 1.1 km resolution at the equator (Bartalev et al. 2003; Eva et al. 2004; Latifovic et al. 2004; Mayaux et al. 2004; Stibig et al. 2003, 2004). To complement mapping data, a "vegetation continuous fields" algorithm has been developed using MODIS data to map the global percent tree cover at 500 m resolution (Hansen et al. 2003).

To produce estimates of the global extent of tropical forests, different approaches have been developed so far, based mainly on: (1) compilation of national inventories or maps; (2) statistical sampling with high spatial resolution satellite images; or (3) global coverage of forested areas by remote sensing data at medium to coarse resolution.

Each method suffers from its own limitations as detailed in Mayaux et al. (2005), and each assessment uses its own definition of 'forest', e.g. based on a different cover threshold or with some specific land-use characterisation. Therefore, forest area figures vary considerably among the assessments, as illustrated in Table 18.1.

18.3.2 Distribution of 'Intact Forests': from Boreal Eurasia to the Global Scale

There are many definitions of forest degradation relating to canopy cover, ecological function, carbon stocks, and other attributes of forests (Penman et al. 2003). Degradation defined by changes in canopy cover is most readily observable with remote sensing. The concept of 'intact forest landscapes' was first applied by the Global Forest Watch network over Russia (Yaroshenko et al. 2001; Aksenov et al. 2002). It was extrapolated across the world using a consistent set of criteria and high-resolution satellite imagery from throughout the year 2000 (Greenpeace 2006). This new map of the world's intact forests depicts the remaining large forest areas where it can be assumed that human influence is limited (Fig. 18.2).

Table 18.1 Tropical forest areas derived from the GLC 2000 map and from the FAO FRA exercise. *CS*: Country Survey (compilation of national statistics), *RSS*: Remote Sensing Survey

	GLC 2000[a]			FAO FRA 2000[b]		
	Humid tropics (10^6 ha)	Dry tropics (10^6 ha)	Flooded forests (10^6 ha)	CS		RSS
				Closed forests (10^6 ha)	Open forests (10^6 ha)	Forests (10^6 ha)
South America	630	147	25	858	69	780
Africa	233	415	13	353	289	518
Southeast Asia	231	145	13	416	58	272
Global	1,094	707	52	1,627	416	1,572

[a]Global Land-Cover 2000 project (Mayaux et al. 2005)
[b]FAO Forest Resources Assessment 2000 (FAO 2001)

This forest distinction between 'intact' and 'non-intact' is based on experience with satellite-based forest mapping and uses a 'negative approach'; disturbance such as the development of roads can be detected easily, whilst the absence of such visual evidence of disturbance can be taken as evidence that what is left is 'intact' (Yaroshenko et al. 2001). Intact forest areas were originally defined for the boreal ecosystems according to the following six criteria: situated within the forest zone; larger than 50,000 ha, and with a smallest width of 10 km; containing a contiguous mosaic of natural ecosystems; not fragmented by infrastructure; without signs of significant human transformation; and excluding burnt lands and young tree sites adjacent to infrastructure objects (with 1 km wide buffer zones). This definition has been applied to all forest ecosystems of the world (Greenpeace 2006) but could be easily adapted for other purposes (see Sect. 18.4). Disturbance is easier to identify unequivocally from satellite imagery than the forest ecosystem characteristics that would need to be determined if we followed the 'positive approach' i.e. identifying intact forest and then determining that the rest is non-intact. Following the negative approach, forest conversions between intact forests, non-intact forests and other land uses can be measured easily worldwide through Earth observation satellite imagery. In contrast, other definitions of forest status (e.g. pristine, virgin, primary/ secondary, etc.) are very difficult to quantify at large scale (Chap. 2 by Wirth et al., this volume).

18.3.3   Hot Spots of Forest Loss

For the humid tropics, areas of rapid deforestation were first identified through expert knowledge (Achard et al. 1998). This information was used to sample areas to be analysed with high resolution data (Achard et al. 2002). Experts with detailed knowledge at the country or regional level ensured that areas of major change were not overlooked. Databases such as transportation networks, population changes and locations of government resettlement programmes can also be used to help identify areas where the pressure to deforest is likely to be high and where a more detailed analysis is required. Globally, the main forest conversion process in the humid tropics is the transformation of closed, open or fragmented forests to agricultural land. The major forest changes are largely confined to a number of "hot spot" areas where forests are increasingly fragmented, heavily logged or burnt, and where rates of change are alarmingly high. In Latin America, the transformation from forest to agriculture by clear-cutting predominates. In addition, areas of mosaics or savannah woodlands have been transformed for agriculture.

A more recent study based on this 'hot spot' assessment in the tropics identified areas of recent and current rapid forest-cover change at a global level from expert knowledge, and characterised the main drivers of these changes (Lepers et al. 2005). It concluded that, at the end of the 1990s, Asia had the greatest concentration of areas of rapid land-cover changes, and that the Amazon basin remained a major

hotspot of tropical deforestation. These results were supported by a national Brazilian assessment through the PRODES monitoring system (INPE 2009), which identifies 'critical areas' based on the previous year's monitoring to prioritise analyses for the following year.

More recently still, the broad geographic patterns of rapid forest-cover change have been mapped for boreal Eurasia, with characterisation of their main causes from expert opinion and remote sensing data (Achard et al. 2006). Around 40 million ha of rapid change with clear-cutting activities and 70 million ha with increased fire frequency were depicted. Rapid land-cover change is not randomly or uniformly distributed but is clustered in some locations, e.g. high intensity logging takes place mostly in the European part of Russia (e.g. in the Karelian Isthmus) and along the southern border of the Taiga. Forest degradation in Siberia – related mostly to an increase in fire frequency and development of logging activities– is extending rapidly. Annual rates of forest-cover change in areas identified as 'rapid change areas' may range from 0.26% $year^{-1}$ for diffuse logging activities to around 0.65% $year^{-1}$ for areas affected by intense clear-cutting activities, up to 2.3% $year^{-1}$ for areas affected by fires or a combination of fire and logging (Achard et al. 2006). While such an approach does not lead directly to quantitative estimates of forest-cover changes, it highlights those areas where intensive monitoring would be required for an improved estimation of the changes at the continental scale (Potapov et al. 2008).

18.3.4 Estimates of Forest Conversion Rates in the Tropics

During the 1990s, rates of forest-cover changes were much higher in the tropics than in other parts of the world. To estimate deforestation over the whole tropical belt, three main methods have been tested. (1) Gathering information through reports, national statistics and independent expert opinions (FAO 2001). This approach is limited by the heterogeneity of the applied methods and forest definitions used. (2) Measuring change using fine resolution satellite imagery on a sampling basis (FAO 2001; Achard et al. 2002). This approach exploits the fine spatial resolution of satellite images but requires a well designed sampling strategy. (3) Measuring change using coarse resolution satellite imagery (DeFries et al. 2002; Hansen et al. 2005). This approach measures changes in "percent tree cover" but must be carefully calibrated with local studies.

The TREES (tropical ecosystem environment observations by satellites) project (Achard et al. 2002) estimated deforestation rates for four regions of the humid tropics: (1) Pan Amazon and Central America, (2) Brazil Amazonia and Guyana, (3) Africa and (4) Southeast Asia. The TREES forest definition corresponds closely with the FAO definition of 'closed broadleaved forest' (FAO 2001). The resulting estimates of global humid tropical forest area change for the period 1990–1997 showed a marked reduction of closed forest cover: the annual deforested area for the humid tropics is estimated at 5.8 ± 1.4 million ha with a further 2.3 ± 0.7 million ha of

forest where degradation can be visually inferred from satellite imagery. Large non-forest areas were also re-occupied by forests, mostly by young re-growth on abandoned land along with some forest plantations, both very different from natural forests in ecological, biophysical and economic terms, and therefore not appropriate compensation for the loss of mature forests. The three continents revealed considerable differences in percentage change rates. Forest degradation is most prominent in Southeast Asia, intermediate in Africa and lowest in Latin America but these estimates represent only the proportion of degradation identifiable using our methodology and do not include processes such as selective logging.

The comparison of annual deforestation rate estimates between the three remote sensing surveys, 'TREES', FAO Remote Sensing Survey (FAO 2001) and 'AVHRR' coarse resolution survey (DeFries et al. 2002) shows a similar result, i.e. 2.0 million ha year^{-1}, for Southeast Asia where the spatial extent covered by the three studies is the same (Table 18.2). Estimates for Latin America and Africa cannot be compared directly as the three surveys do not cover the same areas. To provide indicative estimates of conversion rates between intact forests, non-intact forests and non-forests during the time period from 1990 to 2005, we used FAO net change figures (FAO 2006). Intact and non-intact forest areas are taken as the FAO's primary and secondary forest areas, respectively. Gross deforestation is taken as changes from intact and non-intact forests to non-forests. The change rates from intact forests to non-intact forests are approximated by applying a ratio of 0.52 to the gross deforestation rates. This ratio of 0.52 is the 2002 ratio between the logging area rate (Asner et al. 2005) and the gross deforestation rate (INPE 2005) in Brazilian Amazonia. In FAO (2006) primary/secondary forest areas are not reported for a number of countries (e.g. Venezuela and India). Consequently, the global estimates correspond only to part of the tropical forest domain, namely to 1,303 million ha from a total of 1,810 million ha in 2005. For these 1,303 million ha of tropical forests, the loss of intact forests is estimated at 5.8 million ha per year (0.72% year^{-1}) between 1990 and 2005 (Table 18.3). This 5.8 million ha year^{-1} loss of intact forests is the sum of 2.8 million ha year^{-1} of changes from intact forests to non-forest areas and 2.9 million ha year^{-1} of changes from intact forests to non-intact forests (it should be noted that, for the same portion of tropical forests, a further 5 million ha year^{-1} of intact forests are estimated to be transformed into non-forest areas).

Table 18.2 Comparison of estimates of annual deforestation rates in the tropics in the 1990s

	All tropics (10^6 ha year^{-1})			Humid tropics (10^6 ha year^{-1})	
	AVHRR[a]	FAO CS	FAO RSS	TREES[b]	FAO CS
Tropical Asia	−2.0	−2.5	−2.0 ± 1.2	−2.0 ± 0.8	−2.5
Tropical Africa	−0.4	−5.2	−2.2 ± 0.8	−0.7 ± 0.3	−1.2
Tropical America	−3.2	−4.4	−4.1 ± 2.2	−2.2 ± 1.2	−2.7
Pan-tropics	−5.6	−12.0	−8.3 ± 2.6	−4.9 ± 1.3	−6.4

[a]Advanced very high resolution radiometer
[b]Tropical ecosystem environment observations by satellites (Achard et al. 2002)

Table 18.3 Estimates[a] of forest areas in 2005 and conversion rates between intact forests, non-intact forests and non-forests for the period 1990 to 2005. *CR* Conversion Rates

	Forest area in 2005 (10^6 ha)		Intact to non-intact	Intact to non-forest	Non-intact to non-forest
	Primary	Secondary	CR (%)	CR (%)	CR (%)
Congo	7,500	15,000	−0.04	−0.04	−0.10
Madagascar	10,300	2,200	−0.05	−0.05	−2.37
Nigeria	300	10,400	−5.79	−5.35	−3.62
Sudan	13,500	48,600	−0.43	−0.40	−1.00
Total Africa	37,100	193,300	−0.35	−0.21	−0.36
Indonesia	48,700	36,400	−1.35	−1.24	−3.45
Malaysia	3,800	15,500	0.00	0.00	−0.47
PNG	25,200	4,100	−0.52	−0.48	−0.31
Thailand	6,500	5,000	0.00	0.00	−2.55
SE Asia	62,900	104,800	−1.10	−1.13	−1.66
Costa Rica	200	2,200	−1.44	−1.33	−0.42
Central America	9,100	13,000	−0.42	−0.39	−2.50
Mexico	32,900	30,300	−0.48	−0.66	−0.29
Bolivia	29,400	29,400	−0.23	−0.22	−0.70
Brazil humid	300,600	40,800	−0.32	−0.31	−2.16
Brazil dry	115,300	15,600	−0.44	−0.43	−2.98
Colombia	53,100	7,300	−0.05	−0.05	−0.48
Peru	61,100	6,900	−0.10	−0.09	−0.98
Suriname	14,200	600	0.00	0.00	0.00
South America	597,300	129,200	−0.27	−0.27	−1.57
Total tropics[b]	764,500	474,800	−0.36	−0.36	−1.03

[a]These estimates are extrapolated from FAO net change figures (FAO 2006) and should be considered as indicative
[b]The global estimates correspond only to part of the tropical forest domain

18.3.5 Monitoring of Intact Forests in Northern European Russia

Approximately 289 million ha remain as intact forest landscapes in Russia, representing 26% of the total forest area. Eastern Siberia is the part of Russia that is least affected by human impact, with 39% of the forest zone still intact, followed by the Russian Far East (31% intact) and Western Siberia (25% intact). European Russia is the most affected region of Russia (9% intact) (Aksenov et al. 2002). Here we consider the original definition of 'intact forest landscape', which typically contains a 'natural mosaic of forest and non-forest ecosystems' (Yaroshenko et al. 2001).

The 'intact forest landscape' of Northern European Russia was monitored for the period 2000 to 2004. The area of intact forest landscapes decreased during this 4-year period by 277,000 ha, or 0.9% of the initial 'intact forest landscape' area. For some patches, a very high speed of area reduction (up to 7% of the area) was registered.

The decrease in intact forest landscape area occurred in two ways: through direct transformation and through fragmentation. The main causes of conversion are logging operations and, associated with them, the construction of transportation infrastructure. Most of the logging occurred in the southern and middle zones of the taiga, leading to a degradation of large intact forest areas in the southern and middle taiga of this region. The majority of logging is in the form of clear cuts with a size of up to 50 ha. Forest fires represent another threat. Most forest fires are connected with the oil extraction infrastructure in the north-eastern part of the region. While fragmentation of intact forest landscape patches by new disturbances and road construction represents 58% of the total decrease in intact forest landscape area, conversions to non-forest areas represent 27% (logging) and 14% (fires). The rate of intact forest loss remains low only in northern taiga regions, near the Ural Mountains, and in large patches of swamp areas in the southern part of the region.

18.3.6   Options for Future Monitoring

In the field of global forest and land-cover mapping, new emphasis is now given to the use of moderate resolution data from the MODIS sensors (250–500 m) on board
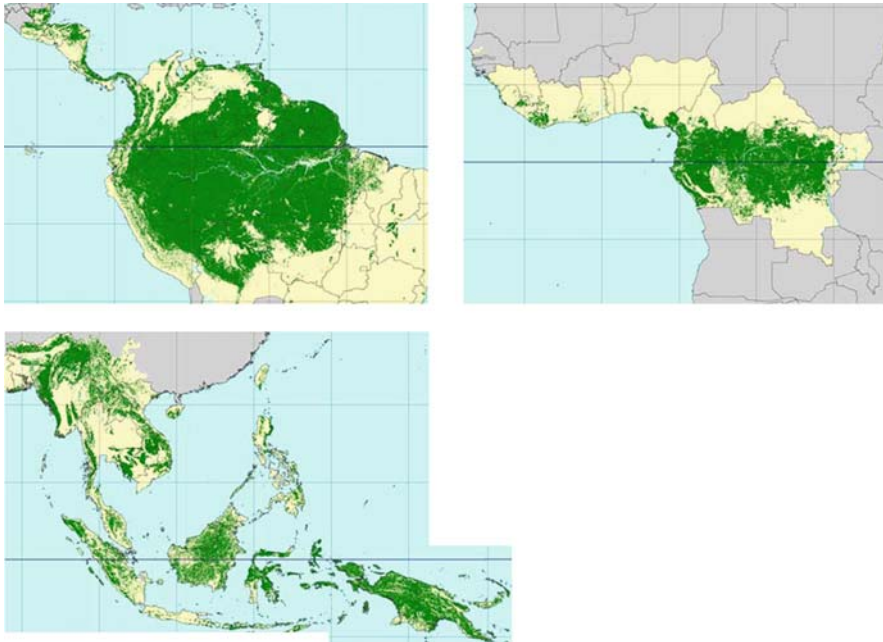
Fig. 18.1 Example of humid tropical forest biome as depicted from advanced very high resolution radiometer (AVHRR) sensors in the late 1990s

the Terra and Aqua platforms (Hansen et al. 2005; Morton et al. 2005), or from the MERIS sensor (300 m) on board the ENVISAT platform (Arino et al. 2007). While still maintaining a global or regional view of the Earth's surface, the improved spatial detail of such images allows the prospect of better addressing land-cover information needs not only at global and regional levels, but also at sub-regional and national levels. Indeed such data could establish the link between global and local observations.

For future operational assessments of forest cover change, the main lesson from previous exercises is to make use of approaches similar to TREES and FAO remote sensing surveys, with the following recommendations (Mayaux et al. 2005): (1) to integrate pre-existing knowledge on deforestation hot spots (to make the procedure more efficient); (2) to use a higher number of observations (to increase precision), and (3) to expand the assessment spatially (to consider global coverage) and temporally (back to the 1980s and after 2000 to improve understanding of deforestation trends).

Technological improvements and better access to remote sensing data make it possible to expand the scope of previous surveys. The FAO 2010 remote sensing survey will be extended to all countries (not just those in pan-tropical zone), and will be based on a much higher number (about 13,000) of smaller samples, covering 1% of total land area, sampled systematically. A 10 km × 10 km sample will be located at each intersection of the 1° lines of latitude and longitude that overlie land. This approach should deliver regionally accurate estimates of forest cover change.

18.3.7 Processes of Deforestation and Forest Degradation

More regional remote sensing studies have covered the tropics than the boreal zones. However, forest degradation in Eurasia, related mostly to unsustainable logging activities or increases in fire frequency, has been growing in recent years. The vast majority of rapid land-cover changes in the 1980s and 1990s are believed to have occurred in the tropics (Lepers et al. 2005). The factors that drive tropical deforestation are complex, including the construction of roads and other infrastructure, international economic demands, and national circumstances (Geist and Lambin 2002). This renders making projections of future deforestation trajectories a challenge.

Degradation results directly from human uses of forest as well as from the indirect results of human activity. Managed and unplanned selective logging leaves forest gaps. Woody removal for wood fuels, particularly charcoal, can result in degradation. Edges of forest fragments exposed through deforestation and logging leave the forest susceptible to degradation through understorey fires (Laurance and Luizao 2007). Some land-use practices in forests, such as managed logging and shifting cultivation, result in a shifting mosaic of cleared areas that may expand into previously intact forest areas. All of these degradation processes

Fig. 18.2 Intact forest landscapes for the year 2000 (Greenpeace 2006)

promote the loss of forest cover and can be the first step towards total forest loss through deforestation.

The main processes of rapid forest-cover changes in boreal Eurasia are logging (both through clear-cutting and high-intensity selective logging) and increases in fire frequency (Achard et al. 2006; Mollicone et al. 2006). Ancillary forest-cover change processes include forest conversion for urban areas or dam construction, forest re-growths and conversion of bogs. Except for forest re-growths on abandoned agricultural land in the southern Taiga, all other processes lead to a decrease in forest cover or to its degradation. Logging activities are driven by regular timber harvesting and irregular cutting for public revenue or individual profit in response to growing demands in national and international markets, particularly in China and Japan. Forest degradation in Siberia, related mostly to an increase in fire frequency (Achard et al. 2008) and development of logging activities, is extending rapidly.

18.4 Tropical Forest Monitoring in the Context of the UNFCCC

18.4.1 Tropical Deforestation and Carbon Emissions

The removal of forest cover through deforestation is the primary contributor to greenhouse gas emissions resulting from changes in forest areas. Forest degradation from high impact logging, shifting cultivation, wildfires, and forest fragmentation also contributes to greenhouse gas emissions. Deforestation and other land-cover changes typically release carbon from the terrestrial biosphere to the atmosphere as CO_2, while recovering vegetation in abandoned agricultural or logged land removes CO_2 from the atmosphere and sequesters it in vegetation biomass and soil carbon. Emissions from land-use and land-cover change are perhaps the most uncertain component of the global carbon cycle, with enormous implications for balancing the present-day carbon budget and predicting the future evolution of climate change.

A complete analysis of the carbon emissions from tropical deforestation involves the quantification of several key elements, including rates and dynamics of land-cover change, initial stocks of carbon in vegetation and soils, mode of clearing and fate of cleared carbon, response of soils following land-cover change, influence of historical land-cover legacies and, finally, the representation of processes in the models used to integrate all of these elements (Ramankutty et al. 2007).

Recently, several estimates of carbon emissions from land-cover change have emerged. Houghton (2003) compiled land-cover change information from various national inventory records and used them, within a carbon-cycle model, to estimate global carbon emissions of 2.2 Gt C year^{-1} in the 1990s (compared with 6.4 Gt C

year^{-1} from fossil-fuel emissions). Combining measurements of changes in forest area with estimates of changes in carbon stocks enables allows us to estimate emissions from deforestation over large regions. DeFries et al. (2002) and Achard et al. (2004) have used remotely sensed tropical deforestation data to estimate releases of 0.5–1.4 Gt C year^{-1} and 1.1 $\pm$ 0.3 Gt C year^{-1}, respectively, in the 1990s.

The average carbon emissions from land-cover change in the 1990s is of the same order of magnitude as the residual carbon sink of 1.9 Gt C year^{-1}, thereby highlighting the importance of accurately estimating land-use carbon emissions for balancing the global carbon budget.

18.4.2 Use of the Concept of 'Intact Forest' in a Potential Mechanism for Reducing Emissions from Deforestation in Developing Countries

Building on the recent scientific achievements related to the estimation of tropical deforestation rates and using the concept of 'intact' forest areas, a potential accounting mechanism has been elaborated in the context of the UNFCCC item of reducing emissions from deforestation and degradation (REDD) in developing countries (UNFCCC 2006).

18.4.2.1 UNFCCC Item REDD

International discussions initiated at the 11th UNFCCC Conference of Parties (COP-11) in December 2005 focussed on issues relating to reduce greenhouse gas emissions from deforestation in developing countries. No such policies are currently in place during the first commitment period of the Kyoto Protocol for countries without commitments, i.e. presently non-Annex I countries, which correspond mainly to developing countries (Schulze et al. 2003; see also Sect. 20.2.1 in Chap. 20 by Freibauer, this volume). The resulting COP-11 decision established a process for submitting recommendations on the implementation of policies to reduce greenhouse gas emissions from deforestation in developing countries and for examining related scientific, technical and methodological issues. Consequently a first ad-hoc workshop was organised in Rome in August 2006 (UNFCCC 2006). The discussion process continued at COP-13 in Bali in December 2007, where the relevant scientific, technical, and methodological issues were reported (see Sect. 20.2.1 in Chap. 20 by Freibauer, this volume). A new action plan was defined, which includes the consideration of "policy approaches and positive incentives on issues relating to reducing emissions from deforestation and forest degradation in developing countries; and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries" (UNFCCC 2008).

The implementation of policies to reduce emissions from deforestation depends on accurate and precise estimates of emissions averted at the national scale (Santilli et al. 2005). Several components must be estimated: (1) loss of forest cover at the national level; (2) initial carbon stocks for the base period and their change caused by deforestation and degradation, and (3) emissions averted from a defined "baseline" or base period.

The following definition of forest was adopted at the UNFCCC COP-6 for the implementation of article 3:

> "Forest is a minimum area of land of 0.05–1.0 hectares with tree crown cover (or equivalent stocking level) of more than 10–30% with trees with the potential to reach a minimum height of 2–5 meters at maturity in situ. A forest may consist either of closed forest formations where trees of various storeys, and undergrowth cover a high proportion of the ground or open forest" (UNFCCC 2001: Decision 11/CP.7 of the Marrakesh Accords).

COP-6 further noted that the parties recognise that there should be a certain flexibility in applying the values in order to reflect national circumstances. With the above-mentioned UNFCCC definition that forests must have a tree cover of more than 10%, substantial loss of tree cover can occur through degradation while maintaining the designation 'forest.' A location would not be considered non-forest until forest cover fell below the canopy threshold. In tropical forests the conversion to other land uses is often preceded by forest exploitation, with significant losses in carbon stocks (Asner et al. 2005). Moreover, forest degradation may enhance susceptibility to fire and may result in a substantial loss of belowground carbon in peat areas.

18.4.2.2 A Potential Mechanism for Reducing Emissions from Deforestation in Developing Countries

In order to address the forest degradation issue, we will first divide the forest land-use category into two sub-categories: (1) intact forests: fully-stocked (tree cover can be anything between 10% and 100% but must be undisturbed, e.g. there has been no timber extraction); (2) non-intact forests: not fully-stocked (tree cover must be higher than 10% to qualify as a forest under the existing UNFCCC rules, but in our definition this forest may have undergone some level of timber exploitation).

In the proposed mechanism, the degradation process is considered as a conversion between these two forest sub-categories: 'intact' and 'non-intact'. Making the distinction between intact and non-intact forest is important given the current limitation in knowledge on the spatial distribution of carbon stocks. In the future, this proxy parameter of carbon stocks ('intactness') could be substituted by accurate, spatially explicit estimates of carbon stocks when available. This distinction allows us to account for carbon losses from forest degradation, i.e. from the conversion of intact to non-intact forest, without introducing a forest degradation definition, which has not yet been achieved in the context of the IPCC. The definition of intact forests applied by Greenpeace at a global scale (Greenpeace 2006; see also Sect. 18.3.2) could be easily adapted for this purpose to tropical ecosystems, e.g. situated within the forest zone according to current UNFCCC

definition; larger than 1,000 ha and with a smallest width of 2 km; containing a contiguous mosaic of natural ecosystems; not fragmented by infrastructure; without signs of significant human transformation (minimum size of isolated deforested or degraded patches to be considered from satellite imagery: 5 ha); and excluding burnt lands and forest re-growths. This forest distinction between 'intact' and 'non-intact' could be applied worldwide.

The proposed system would use forest area conversion rates as input data. A solution to set baselines would be to use historical average figures during the time period from 1990 to 2005. The system introduces two different schemes to account for preserved carbon: one for countries with high forest conversion rates where the desired outcome would be a reduction in these rates, and another for countries with low rates. A 'global' baseline rate would be used to discriminate between these two country categories (high and low rates). Carbon stock estimates of forests undergoing defor-estation and the subsequent carbon dynamics are uncertain for many developing countries but default data and guidelines for carbon accounting already exist in the IPCC Good Practice Guidance Report (Penman et al. 2003).

For the hypothetical accounting period 2013–2017, and considering 72% of the total tropical forest domain for which data are available, the scenario of a 10% reduction of the high rates and of the preservation of low rates would result in reduced emissions of approximately 1.6 billion t CO_2 (Mollicone et al. 2007). The resulting benefits of this reduction would be shared between those high-rate countries that reduced deforestation, and low-rate countries that did not increase their deforestation over an agreed threshold.

18.5   Conclusions

During the 1990s, forest-cover changes were much more frequent in the tropics than in other parts of the world. In particular, the Amazon basin and Southeast Asia contain a concentration of deforestation hotspots. Forest degradation in Eurasia, related mostly to unsustainable logging activities or an increase in fire frequency, has been growing in recent years. While old-growth forests are difficult to identify from space, it is possible to detect intact forest areas with low human impact. Intact forest landscapes are becoming a rarity in many parts of the world, in particular in temperate and dry tropical zones. Remaining intact forests are generally broken into fragments, too small to sustain the full array of functions characteristic of a natural forest landscape (see also e.g. Sect. 16.3 in Chap. 16 by Armesto et al., and Sect. 17.6 in Chap. 17 by Grace and Meir, this volume).

Although rates of forest-cover changes are now better assessed, in particular over the tropics, where systematic analysis is carried out because of the interest in tropical deforestation, uncertainties still exist about rates of change in intact forest areas. Monitoring of forest cover should be made operational as a priority for this category of forests. Based on FAO estimates of change rates in 'primary forests', tropical intact forests are estimated to have been converted at a rate of 0.72% per

year between 1990 and 2005 (non-intact forests have been converted to non-forests at an annual rate of 1.04% per year). Without decisive action within the next few years, intact forest landscapes may disappear within entire ecological zones. Decisions about the conservation and use of the remaining intact forest landscapes must take into account a complex range of ecological, social, and economical roles, including the role of preserving existing carbon pools in mitigating global climate change. A potential mechanism presented in the context of the UNFCCC item REDD uses the concept of intact forests to account for degradation losses.

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Chapter 19
Impacts of Land Use on Habitat Functions of Old-Growth Forests and their Biodiversity

Dorothea Frank, Manfred Finckh, and Christian Wirth

19.1 Introduction

While this book has a clear focus on the biogeochemical function of old-growth forest, the pivotal role of old-growth forests in the conservation of biodiversity has been a recurring theme in several chapters [e.g. Chap. 15 (Schulze et al.); Sect. 16.3 in Chap. 16 by Armesto et al.; Sect. 17.1 in Chap. 17 by Grace and Meir; Sect. 13.5 in Chap. 13 by Bergeron et al.; and Sect. 20.3.2 in Chap. 20 by Freibauer, this volume]. It is because of their function of habitat provision that non-governmental organisations all over the world thrive to conserve old-growth forests[1]. This includes a plethora of activities ranging from raising public awareness of the threat to endangered species, to the promotion of environmental research and education, to concrete actions such land acquisition and anti-deforestation campaigns.

It is beyond the scope of this chapter to exhaustively review the science of species conservation in old-growth forests. Instead, we would like to provide a brief introduction to this fascinating subject by presenting examples that serve to illustrate the key habitat functions of old-growth forests in different biomes. In addition, we will discuss historic impacts and actual human threats to old-growth forests worldwide, and their respective consequences with regard to habitat function.

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[1] "WWF ["World Wide Fund For Nature"](http://www.panda.org/index.cfm); Greenpeace International (http://www.greenpeace.org/international/); Taiga Rescue Network (http://www.taigarescue.org/en//index.php; Finnish Nature League (http://www.luontoliitto.fi/metsa/forest/background/); Nature Conservancy (http://www.nature.org/); Friends of the Earth International (http://www.foei.org/); Ancient Forest International (http://www.ancientforests.org/); Ancient Forest Exploration and Research (http://www.ancientforest.org/afer.html); Primal Nature (http://www.primalnature.org); Australian Wilderness Society (http://www.wilderness.org.au/); etc.

19.2 Old-Growth Forests – Habitat Function

The internal environmental conditions of old-growth forests differ from those of earlier successional stages in two ways. On the one hand, the fine-scale heterogeneity of environmental conditions and structural elements tends to be higher in old-growth forests. On the other hand, the resulting mosaic of patches is stable over long time-scales. The habitat function of old-growth forests, and their propensity to host diverse animal and plant assemblies, is closely related to this special mix of spatial heterogeneity and temporal stability. The higher spatial variability and associated structural diversity is believed to provide a wider array of niches. The process that creates the spatial variability in old-growth forests is the mortality of single trees or groups of trees, often as a consequence of small-scale disturbances. In other words, the notion of habitat- and thus species-rich old-growth forest is fully compatible with the intermediate disturbance hypothesis of diversity (Connel 1978). In addition, temporal stability could promote speciation (Fjeldså and Lovett 1997) and thus the evolution of mutualistic interactions. On the flipside of this, specialised old-growth species are vulnerable to drastic regime-shifts and often disappear when stands are destroyed by disturbances or heavily altered by management.

It follows that plant and animal communities in old-growth forests are unique and often different from other types of forests, as the following examples show: winter bird populations in different forest types in west central Pennsylvania in the United States, showed significantly higher species richness and abundances in old-growth stands compared to other forest types (Haney 1994). Ernst et al. (2007) could show that amphibian communities of primary tropical forests were generally diverse and their composition unpredictable. In contrast, communities of logged or secondary forests were less diverse and more predictable due to strong environmental filters that reduced the number of species intolerant of strong fluctuations in microclimate. Similar results were found in a study on hawk moth assemblages in Southeast-Asia, with the relative frequency of subfamilies of *Sphingidae* changing significantly from primary to disturbed forests (Beck et al. 2006), and in species changes in Malayan arboreal ant communities due to anthropic forest degradation (Floren and Linsenmair 2005; Floren et al. 2001). These shifts in species composition indicate environmental constraints acting on the community.

If gradients of 'old-growthness' can induce changes in diversity and composition, we may also expect to see differences in individual performance. Lomolino and Perault (2007) analysed the body size of selected mice or shrew species in fragmented and extensive stands of old-growth temperate rainforests in the northwestern United States. Individuals from three species (*Peromyscus keeni*, *Sorex monticolus*, *Sorex trowbridgii*) were significantly smaller in small forest fragments than in more extensive stands of old-growth forest. The comparison between large old-growth stands and small fragments surrounded by monospecific plantations or early-successional stands points to the importance of stand extent for the fitness of individuals and populations. Woltmann (2002) analysed bird community responses to human disturbance in lowland Bolivia and found several species, e.g. the ringed

antpipit (*Corythopis torquata*) and the spot-backed antbird (*Hylophylax naevia*), that avoid exploited forests.

In the following sections we will discuss how different environmental characteristics of old-growth forests are related to their function as a habitat for flora and fauna.

19.2.1   Structure

The special structural features of old-growth forests (see Chap. 2 by Wirth et al., and Table 13.2 in Chap. 13 by Bergeron et al., this volume; Mosseler et al. 2003), such as multiple tree strata, uneven-aged or multi-aged structure, the presence of old individuals of late-successional species, canopy gaps and dead and dying trees in varying stages of decay (Mosseler et al. 2003), especially large-sized coarse woody detritus (Bobiec et al. 2005), provide niches and fulfil the structural and trophic habitat requirements of old-growth dependent wildlife. In this context, structure is a proxy for a complex mixture of nutritional and behavioural requirements.

Old-growth forests in humid climates normally host partly heterotrophic epiphyte communities, formed – depending on the geographical region – by fungi, bryophytes and lichens, ferns, *Orchidaceae, Bromeliaceae* and many other vascular plant taxa. As a general feature, epiphyte diversity and biomass increases with stand age. Lichen and bryophyte diversity depends on microsite heterogeneity, and bark roughness; stem structure and chemical surface properties become more diverse with tree diameter and age (Friedel et al. 2006; Belinchón et al. 2007). Vascular epiphytes generally depend on detritus accumulation on the trunk and branches, and on structural requisites such as broken branches and half fallen trees, which develop as stands age. The epiphyte communities themselves contribute to the structural diversity and provide habitat for a specialised fauna including arboricoulous amphibians, reptiles and mammals as well as stem-gleaning birds and a still insufficiently known number of invertebrates.

Many large woodpeckers occur only in late-successional or old-growth forests. Examples are the pileated woodpecker (*Dryocopus pileatus*) in North-American forests, the Magellanic woodpecker (*Campephilus magellanicus*) from temperate Patagonian *Nothofagus* forests, or the recently rediscovered ivory-billed woodpecker (*Campephilus principalis*) in the southeastern United States and Cuba (Hartwig et al 2004; Fitzpatrick et al. 2005; Hill et al. 2006; Vergara and Schlatter 2004). They serve as examples of animals that need large decaying and dead trees as feeding substrates and to carve out cavities for nesting. Thereby, they also act as keystone species as their abandoned large holes provide nesting, roosting, hiding and feeding sites for other birds, small mammals, reptiles, amphibians and invertebrates (Simberloff 1998; McClelland and McClelland 1999; Bonar 2000; Aubry and Raley 2002). The number and size of cavities is significantly related to tree diameter (Lindenmayer et al. 2000) and thus to tree age. Schlatter and Vergara (2005) observed higher abundances of three bird species around sap wells drilled by the Magellanic woodpecker. Other examples of old-growth-associated birds are

the seasonally frugivourous gray-cheeked thrush (*Hylocichla minima*) and the blackbacked woodpecker (*Picoides arcticus*), which feed on larvae and insects on dying conifers and occur predominantly in boreal old-growth forests (Thompson et al. 1999; Mosseler et al. 2003). The life-history requirements of the northern spotted owl (*Strix occidentalis caurina*), a federally listed "threatened" species in the Unites States, are associated with late-successional habitats, due to this species' preference for large caves (Hershey et al. 1998; Andrews et al. 2005; Forsman et al. 2005) and structural understorey requirements for foraging (North et al. 1999).

Two ground-gleaning tapaculo species of Southern American temperate rain-forests, the black-throated huet-huet (*Pteroptochos tarnii*) and the ochre-flanked tapaculo (*Eugralla paradoxa*), are regionally present only if some old-growth forest patches remain (see Sect. 16.3 and Table 16.1 in Chap. 16 by Armesto et al., this volume). Reid et al. (2004) explain this pattern with preferences for food resources and escape-cover.

19.2.2 Stand Microclimate

In all biomes, old-growth forests tend to have a structurally complex and dynamic vertical and horizontal light environment, with understorey light generally below 5% near the forest floor in closed forest and few microsites with high light levels (Chap. 6 by Messier et al., this volume). Although being variable at a micro-scale, relative microclimatic stability is a constant feature of old-growth habitats at the macro-scale. In other words, old-growth forests possess a high density and continuity of micro-sites that are buffered against variations in temperature, light and humidity.

Thus it is not surprising that a high number of stenoecous species evolved in old-growth forests. Many species closely bound to old-growth forests are poorly adapted to microclimatic changes (Laurance et al. 2006b). They lack resistance mechanisms against frost or desiccation, or depend on species that lack these properties, such as plethodontid salamanders (e.g. the North American genus *Aneides*; Spickler et al. 2006; Mahoney 2001), Chilean leptodactylid frogs (Correa et al. 2006) or desiccation-sensitive vascular plants (e.g. Chilean *Valdivia gayana*), *Hymenophyllaceae* (Dubuisson et al. 2003) and bryophytes (Friedel et al. 2006). These taxa typically depend on the usually moist and well-buffered microclimatic conditions typical of old-growth forests (Wilson 2003), and are often inserted in complex food webs or embedded in mutualistic interactions in terms of seed dispersal or pollination.

19.2.3 Spatiotemporal Stability

Until the beginning of the Neolithic period, old-growth forests prevailed in many parts of the humid ecosystems of the tropical, temperate and boreal zone (Asouti

and Hather 2001; Kalis et al. 2003; Marinova and Thiebault 2008). Extended forests in earlier successional stages predominated mainly in areas subject to intensive regimes of natural disturbances, such as wind, volcanic disturbances or natural fires.

Long-term spatiotemporal stability of forest ecosystems at meso- and macro-scale seems to be an important precondition for the occurrence of many obligate old-growth species. Hinojosa et al. (2006) analysed the relationships between early Miocene palaeofloras and the actual vegetation in the Chilean Coastal Cordillera in south-central Chile. They concluded that the notable evolutionary stability of many ancient lineages in the analysed vegetation in terms of morphological persistence and floristic similarity is due to the extremely conservative environment of the coastal forests. Smith-Ramirez (2004) describes the forests of the Chilean coastal range as a centre of endemism and explains this with pleistocenic forest continuity in coastal refugia and post-pleistocene stability of the respective forest ecosystems. Meijaard et al. (2008) found a positive correlation between phylogenetic age and susceptibility to timber harvest in Bornean mammals. Lineages that evolve in forest ecosystems that are stable on an evolutionary time scale apparently lack, in many cases, the plasticity to adapt to open conditions.

Complex functional plant–animal interactions have evolved in many ancient forest ecosystems. In tropical forests and to a lesser extent also in temperate and boreal forests, animals have crucial functions as pollinators (e.g. insects, birds, bats) and/or dispersal agents of plants (e.g. birds, mammals). They defend other species against herbivory or predation (e.g. ants) and they facilitate and accelerate nutrient recycling (e.g. termites, beetles). Fungi are key organisms for lignin decomposition and plant–fungi associations are mutualistic key strategies used to deal with nutrient poor sites (e.g. *Orchidaceae*) or with humid and cool environments (e.g. *Ericaceae*), to mention just a few selected groups of forest-relevant mutualisms.

Old-growth species often differ from early-successional species in their functional traits. Several studies (Hamann and Curio 1999; Kitamura et al. 2005; Tabarelli and Peres 2002) report higher percentages of zoochorous trees with larger fruits and specialised frugivore seed dispersers in old-growth compared to early-successional forests from central Philippines, north-eastern Thailand and south-east Brazil, respectively. Many large frugivore species are restricted to intact old-growth habitats, and early-successional stages or secondary forests do not fulfil their ecological requirements. To analyse old-growth specific habitat functions, species quality in terms of specific functional traits and ecological services matters.

The classical intermediate disturbance hypothesis predicts maximum species richness of ecosystems under intermediate disturbance intensity and is generally valid in forest ecosystems at the landscape level (e.g. Molino and Sabatier 2001). However, the increase in overall species richness under intermediate disturbance is the result of a gain in disturbance-adapted generalists and occurs at the expense of more specialised old-growth species intolerant of disturbances (Roxsburgh et al. 2004; Kondoh 2001).

19.3   Characteristic Human Impacts on Old-Growth Forests in Different Biomes and their Impact on Habitat Characteristics, Habitat Functions and Biodiversity

Neither the process nor the structural definitions of old-growth forest necessarily preclude human impact. However, the allowable degree of human impact is subject to debate. Armesto et al. (Chap. 16, Sect. 16.1) consider old-growth condition to have *"... a species composition that has not been significantly modified* (by recurrent human impact or other large disturbance at least during the past two centuries). Mosseler et al. 2003 require *"minimal evidence of human disturbance"* as an old-growth attribute. Many authors emphasise that anthropogenic disturbances of forests are common if not ubiquitous (Redford 1992; Chap. 17 by Grace and Meir, this volume).

Severe man-made disturbances in old-growth forests have persistent effects on species composition and are, in many cases, not completely reversible. This is especially true under ongoing human impacts[2]. Recolonisation of habitat is an extremely slow process for species that depend on stable environmental conditions, have limited (diaspore) mobility or are embedded in trophic or functional mutualisms.

Several authors describe the floristic legacy of ancient woodland fragments – i.e. woodland defined by the historic continuity of its forest cover – in temperate zones of Europe and the eastern United States, characterised by plant species that do not easily recolonise reestablished forests after agricultural land use (Bellemare et al. 2002; Hermy et al. 1999; Graae et al. 2004; Hérault and Honnay 2005). Traits correlated with historic continuity of forest fragments include, for example, barochory and myrmecochory, i.e. generally short-distance dispersal strategies and low diaspore production.

In most forest types, it takes several centuries of a low disturbance regime to develop old-growth conditions (see Sect. 2.4 in Chap. 2 by Wirth et al., this volume) and little is known about disturbance thresholds that impede or allow old-growth forests to develop. The spatial extent and the intensity of anthropogenic impacts on old-growth forests differ according to economic driving forces, and the type of impacts and factors. For example, impacts can be confined to property lines or natural boundaries, or can trespass in a diffuse manner into old-growth forests. The following section summarises typical human impacts on forest ecosystems within different biomes, and the consequences these human impacts have for the habitat function of old-growth forests. Table 19.1 shows the impacts caused by diverse socioeconomic driving forces on the habitat function of old-growth forests in different biomes.

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[2]Lawrence (2004) observed a reduction in tree species diversity in repeated cycles of shifting cultivation in west Kalimantan, partially due to long-distance dispersal limitations and changes in soil nutrients.

Table 19.1 Impacts of various anthropogenic drivers on the habitat function of old-growth (OG) forest ecosystems in different biomes. The grey scale indicates the importance of the impact (*dark grey* low, *mid-grey* medium, *light grey* high). The figures indicate specific types of impacts and processes on habitat functions

Driver	Spatial effect	Impact[a]		
Biome:	Confined/diffuse	Boreal	Temperate	Tropical
Governmental interior colonisation projects	Confined			1,2,3,4,5,6
Concession-based timber exploitation	Confined	1,2,3,4		1,2,3,4,5
Illegal logging	Diffuse	1,2,3		1,2,5
Industrial forestry (plantations)	Confined	1,3,4	1,3,4	1,3
Agro-industrial projects	Confined			1,3,4
Mining projects, hydropower and oil exploration	Confined	1,3,4		1,3,4
Anthropogenic fires	Diffuse	1,2,3		1,2,3,5
Smallholder slash and burn agriculture	Diffuse			1,2,3,4,5,6
Smallholder silvopastoral activities	Diffuse		6	2,3,4,6
Smallholder fuel wood extraction and/or charcoal production	Diffuse		3,6	2,3,4,5
Collection of fruits, ornamental and medical plants	Diffuse			3,4
Hunting	Diffuse	4	4	3,4
Poaching	Diffuse	4		4
Urbanisation	Confined		1,2,3,4,6	2,5,6
Fragmentation by roads and highways	Diffuse		1,2,3,4,5	1,5
Contamination and eutrophication	Diffuse	6	3,4,6	6
Global warming	Diffuse	3,5,6	3,5,6	3,5

[a] *1* Deforestation of native (OG-) forest; *2* reduction of forest cover; *3* shift in species composition, i.e. loss of specialised OG-species; *4* loss of dispersal agents, shifts in animal species composition and subsequent alteration of tree regeneration and vegetation; *5* increased vulnerability to disturbances with subsequent irreversible loss of forest integrity; *6* invasion by neophytes

19.3.1 Boreal Forests

The climatic and edaphic conditions of the boreal forest region had largely impeded agricultural land use until modern times. The local populations in Eurosiberian and North-American boreal forests have been predominantly hunters and/or transhumant reindeer nomads, with low population densities and thus little impact on forest cover (Wallenius et al. 2005). Thus, the boreal forests remained relatively intact until the beginning of industrialised forest exploitation; 300-year-old forests represent the natural state of *Picea*-dominated landscapes in north-eastern Fennoscandia and north-western Russia (Wallenius et al. 2005). Since human activities began in boreal areas, they have become the main agent of fire ignition (Wallenius et al.

2005; Mollicone et al. 2006), and fires have become more frequent (Mollicone et al. 2006). Illegal logging increases in boreal regions, particularly in the Russian Far East and the Baltic region (Taiga Rescue Network 2004).

Given that large stand-replacing fires are part of the natural dynamics of boreal forests (see Gromtsev 2002), the questions of how to evaluate the higher man-made fire frequency and whether clear-cut logging effectively mimics the effects of fires are pivotal for evaluating their impact on boreal old-growth forests.

Stand-replacing forest fires and clear-cut logging both eliminate canopy trees, but there are important differences, especially with respect to spatial patterns, temporal regularity and the amount of legacy deadwood: natural fires are always patchy, leaving parts of the landscape to escape fire for long periods (Chap. 13 by Bergeron et al., this volume; Gossow 1996), and opening the possibility of the development of old-growth islands or corridors. Large fires (2–20 × 10^3 ha) leave islands with a median size of about 10 ha (Eberhart and Woodard 1987) and thus fulfil the forest cover requirement for moose (Euler 1981, in Eberhart and Woodard 1987). In Eurasian boreal forests characterised by non-stand-replacing recurring surface fires (Wirth 2005), the effect of fire is to create a stable, fine-grained age-class mosaic with high structural β-diversity (Sannikov and Goldammer 1996). On the contrary, large-scale clear cuts (clear cuts up to more than 10,000 ha in size have been reported[4]) are very uniform and rarely exhibit remnant patches of the original vegetation. Remnant patches favour wildlife in several ways: first, they serve as stepping stones and seeds for recolonisation of the area; second, they create habitat 'edges' required by some species, and third, they function as refugia.

In contrast to the short and regular cycles of clear-cuts, the frequency of natural fires is highly irregular and unpredictable; they often spare wet microsites along river flood plains, swamps, lakes or river channels (Furayev 1996), and form irregular boundaries at the landscape-scale. Fire and timber harvest remove live wood but, although being highly variable, fire removes far less live wood than intensive timber harvest and, with the exception of extremely severe fires, it is unlikely that much of the large diameter live wood burns (Chap. 8 by Harmon, this volume).

In boreal forests, vascular plant diversity decreases from early-successional to late-successional forests, but cover and diversity of bryophytes increases in old-growth boreal forests (Sect. 6.4.2 in Chap. 6 by Messier, this volume; Hollingsworth et al. 2006). As dispersal distances for many bryophytes are less than 50 m, they need a local source of propagules and sufficient time to develop rich communities. These communities are thus threatened by large-scale clear-cuts and short rotations (Newmaster et al. 2003). Many cyanolichen taxa are associated with stands having sufficient 'old-growth characteristics' with regard to canopy micro-climate and throughflow, which cannot develop in even-aged hemlock stands with a

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[4]See Greenpeace Canada "Threats to the Boreal Forest" (http://www.greenpeace.org/canada/en/campaigns/boreal/threats-to-the-boreal-forest)

rotation of 120 years (Radies and Coxson 2004). Newmaster et al. (2003) reached similar conclusions for cedar-hemlock forests of British Columbia, where only old-growth forests provide a microclimate to form a rich community of rare dessication-sensitive liverworts.

A broad variety of forest-dwelling animals also depend on old-growth characteristics. The endangered woodland caribou (*Rangifer tarandus caribou*) is associated with late-successional or old-growth forests where arboreal hair lichens, their main winter food source, are abundant (Apps et al. 2001; Mosnier et al. 2003). Another of the many other examples is the endangered saproxylic beetle species *Pytho kolwensis*, which is restricted to virgin spruce-mire forests with a stand continuity of at least 170 years as it requires long-term continuous availability of suitable host trees (Siitonen and Saaristo 2000).

To summarise, the present industrialised exploitation of boreal forests, with its large-scale clear cuts often followed by monospecific reforestation[5] with a short and predictable rotation, does not mimic natural disturbance dynamics. It alters the boreal ecosystems substantially, and the proportion of old-growth boreal forests harbouring sensitive species decreases.

19.3.2 Temperate Forests

The land-use history of temperate forests differs greatly from that of the boreal regions. Since the beginning of the younger Neolithic, temperate forests have been cleared for agricultural land use or affected by fire wood and charcoal production and grazing (Asouti and Hather 2001; Kalis et al. 2003; Marinova and Thiebault 2008). Agrotechnical innovation led to human population increases and subsequent expansion of agricultural land. This gradual conversion of forests and the manifold small-scale exploitation of the remaining fragments produced diverse landscape patterns in the different temperate regions of the world, reflecting the socioeconomic conditions and the pace of the conversion processes.

In the following, we will discuss the driving forces of forest conversion, the resulting forest systems, and the consequences for old-growth biota, focussing on Europe and Chile as examples.

19.3.2.1 Europe

Almost no primary forests are left in Central Europe. Pollen records indicate that floristic changes had begun already in the middle Neolithic (Kalis et al. 2003). Forest degradation and clearing producing marked signals in pollen composition

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[5]Plantation forests often exclude pioneer shrubs, non-timber tree species and, especially, older age-classes are very scare or non-existent, thus food supply and cover availability for wildlife species are reduced (Gossow 1996)

started in the younger Neolithic period at about 6300 BP. Forest destruction started in regions with favourable soils and climate, and later extended into areas with minor productivity. Pollen composition further suggests a simultaneous increase of wood gathering, charcoal production and animal husbandry, causing large areas of secondary forests, dominated by early-successional tree species (Kalis et al. 2003).

With the population increase in the Middle Ages, extended old-growth forests remained only in the upper montane and subalpine belt and in royal hunting reserves. Most other forests, many of them used as commons, were heavily impacted by livestock husbandry, firewood and timber extraction, tannery (e.g. oak coppice) or charcoal production, and litter removal. Forest overexploitation and the removal of litter and topsoil caused soil degradation and the formation of extended heathlands on sandy soils. Mining regions and salterns in the Austrian alps had their own forest regulations and authorities to satisfy their specific demands for pine and spruce.

Systematic large-scale reforestation started early in the nineteenth century to fulfil the growing urban and industrial demand for timber. Species composition and structure of planted forests was different from natural forests, due to coeval stands, short rotation periods without large old trees and extensive utilisation of Norway spruce and scots pine outside their natural habitat. The latest important process that has impacted the Central European forests is the atmospheric nitrogen deposition that grew dramatically throughout the twentieth century, and reached a peak in the 1980s[6].

Currently, about 30% of central Europe is covered by forest (Güthler 2003), but unmanaged old-growth forests exist on less than 0.2% of the area, mostly in the mountains. Thus, there is little possibility to deduce the general features of primary old-growth forests in lowland areas from analyses of these fragments.

Nonetheless, we find a high diversity of management schemes, due partly to the historic legacy of a fine-textured land tenureship. The historic diversity of private and public stakeholders, each with their own interests in terms of productivity, investment return and weighting of contrasting environmental versus economic factors, generated a multitude of forest types[7]. Although this created forest landscapes characterised by a high γ (inter-stand) diversity, the mean size of the forest parcels is small. This combination has important consequences for biota requiring old-growth habitats. Due to the lack of extensive forest, the fauna of large woodland

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[6]Actually, air-borne nitrogen deposits in German forests fluctuate from 20 to 40 kg ha^{-1} a^{-1}, with important regional differences (Güthler et al. 2005). Wright et al. 2001 report a trend of slightly reduced atmospheric nitrogen deposition in Central Europe compared to the peak in the 1980s.

[7]Management schemes range from traditional concepts such as "coppice" for energy demand or "coppice with standards" for energy and construction over "shelterwood cutting" ("Schirmschlag", "Femelschlag") to "selection forestry" ("Plenterwald") for high quality timber. Management philosophies are quite diverse, from clear cut or age class forestry with low β diversity to "permanent forest" ("Dauerwald") concepts, and from plantation forestry with alien species to "close to nature" silviculture with site-adapted native species.

mammals is extremely impoverished. The largest herbivores, such as the Auerox and the Tarpan, have been extinguished; European bison or moose and top predators such as the brown bear and wolf have been mostly driven back to less populated areas in Northern and Eastern Europe.

Where we find remnants of ancient woodland, they still differ from post-agricultural secondary forests in terms of their floristic composition. Hermy et al. (1999) listed 132 plant species of deciduous forests of Central Europe significantly related with historic woodlands, and found long persistence of these plants even within very small forest fragments. Especially taxa with long-lived individuals, poor seed dispersers (gravity or ant dispersal) and short-statured geophytes are restricted to ancient woodlands (Graae et al. 2004; Hermy et al 1999; Herault and Honnay 2005). These findings are not restricted to the temperate forests of Europe, *". . . herbaceous understorey communities in the mixed-mesophyteic forests of the Appalachians appear unlikely to recover within the present planned logging cycles of 40–150 years, suggesting continuing loss of diversity of understorey herbaceous plants."* (Meier et al. 1996).

If we compare mature managed forests with natural old-growth in Germany, managed forests are dominated by few tree species with economic importance (*Pinus silvestris*, *Picea abies*, *Fagus sylvatica*, *Quercus robur* and *Quercus petraea*). Senescent and damaged trees are rare and typical old-growth features such as detritus, caves, snags and logs are largely missing. This structural depletion has a heavy impact on parts of the forest biota: 25% of dead-wood dependent macro-fungi in Bavaria are classified as threatened; of the ∼1,200 wood-dependent (xylobiont) coleopterae in Germany, about 50% are classified as endangered (Güthler 2005). Many insects depend on very specific structural requisites, in terms of dead wood diameter, dead wood insolation, and tree species, that are rarely realised in managed forests (Bobiec 2005; Ranius et al. 2005; Buse et al. 2008; Güthler 2005).

19.3.2.2 Chile

The region where temperate forest ecosystems occur in southern Chile has been populated by humans since at least 12,000 BP (Heusser et al. 1996). In the sixteenth century, the Spanish conquistadores reported a patchy mosaic of fields and clearances in a matrix of extended closed forests south of the Rio Bío-Bío (approx. 37°30′S) (Berninger 1929). By the mid-nineteenth century, in the course of the so called "pacification" and organised agricultural colonisation of South Central Chile, the indigenous population was settled in "reductions", and the majority of the land was given to European and Chilean settlers investors. Since then, the previously continuous temperate forest ecosystems of southern-central Chile have suffered substitution and fragmentation by extensive burning and logging for agricultural and forest land-uses (Berninger 1929; Lauer 1961).

Native forest fragments remained embedded in the subsistence agriculture system of indigenous Mapuche communities as well as in the more intensive land-use system

of the large wheat and cattle farms. These fragments, consisting mostly of secondary forests with different degrees of alteration and small old-growth remnants, were traditionally used as coppice woods for firewood and charcoal production.

Economic development in the 1970s and 1980s led to a dramatic expansion of fast-growing *Pinus radiata* and *Eucalyptus* monocultures, with profound changes in the landholders' structure[8]. In fewer than three decades, large timber companies established plantation forestry as a new co-dominant land-use system. These land-use changes have had a strong impact on biological diversity and the dynamics and functional aspects of the remaining forest ecosystems (Willson et al. 1995).

The primary forests of the lowlands and the Coastal Cordillera were species-rich temperate rainforests dominated by evergreen laurophyllous trees, such as *Aextoxicon punctatum,* with a high degree of endemism and complex biotic interactions[9] (see also Chap. 16 by Armesto et al., this volume). Chilean temperate old-growth forests are diverse in tree and liana species, as well as in epiphytes depending on detritus accumulation in the canopy layer, and provide habitat for disturbance-sensitive species such as the *Hymenophyllaceae*, which require high and constant air humidity[10]. Neophytes are completely lacking in undisturbed primary forests. In contrast to lower and mid elevations, mountains above 1,000–1,200 m are dominated by *Nothofagus* forests (*Nothofagus alpina, Nothofagus antarctica, Nothofagus dombeyi, Nothofagus pumilio)* and conifers.

Temperate old-growth forests have almost completely vanished outside protected areas. Lowland forests are especially endangered, as the national park system comprises principally mountain ecosystems above 1,000 m (Finckh 1996; Smith-Ramirez 2004). Extended forests still exist to some degree in the Coastal Cordillera (Smith-Ramirez 2004) and in the Andes.

Secondary forests show marked differences in structure and species composition compared to the remaining old-growth forests. Secondary forests are dominated by the deciduous *Nothofagus obliqua*, which indicates disturbances up to several centuries ago (Frank and Finckh 1998). Evergreen and laurophyllous species regenerate in their understorey, but old-growth specialists are scarce. Neophytic weeds comprise 5–20% of the species spectrum; they generally indicate the level of disturbance caused by cattle. The vegetation of pine plantations is constituted mostly of neophytes and native generalists adapted to edge conditions. Depending on previous land-use, the understorey vegetation of pine plantations shows a convergent development from different starting points. Pine plantations established on former pastures or fields are dominated by neophytic weeds (e.g. *Dactylis glomerata, Arrhenaterum elatior*). Native bird-dispersed plant species such as

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[8]The indigenous land-use systems remained quasi-unaltered, due to a protective legislation that strictly regulates the market for indigenous lands.

[9]For an detailed description of the present state of knowledge regarding plant–animal interactions and habitat functions of old-growth forests of temperate Chile, see Chap. 16 by Armesto et al., this volume.

[10]The fronds of most *Hymenophyllaceae* have a thickness of one (or a few) cells without stomata (Marticorena and Rodriguez 1995) making them very susceptible to desiccation.

Aristotelia chilensis or *Cissus striata*, and edge species (*Muehlenbeckia hastulata, Maytenus boaria*) invade gradually, together with neophytes such as *Rubus constrictus*. If native forests or shrub communities have been replaced directly by pine plantations, native species, especially resprouting woody plants and pioneers, dominate the understorey vegetation during the first rotation. Their number decreases over time in the plantations, a process that continues during the following rotation. Already within the second rotation of *Pinus* or *Eucalyptus* plantations, the differences between deforested and reforested lands have vanished and a small species group of generalists and relatively shade-tolerant neophytes dominates such plantations (Süsser 1997; Frank 1998).

Those plantations offer habitat neither for the highly diverse native arboreal flora, nor for the epiphytes, drought-sensitive herbaceous species, or native animal species depending on one of the aforementioned plant groups. Little is known about the role of landscape matrices for habitat functions. Native forest corridors are of high importance for endemic understorey birds like *Scelorchilus rubecula* and *Eugralla paradoxa* (Sieving et al. 2000; Willson et al. 1995), as those birds do not cross larger patches of open space and thus cannot move between forest fragments in open landscapes. Forest plantations may enhance the connectivity between fragmented old-growth patches, as the above-mentioned bird species move through *Pinus* plantations towards embedded fragments of native forest (Estades and Temple 1999). This is in agreement with Braunisch (1997), who found a significantly higher diversity of forest birds in forest fragments embedded in a plantation matrix compared to fragments within an agricultural landscape. For other taxa with minor mobility, exotic plantations might act as 'hard' barriers between habitat islands.

Diversity and abundances of the entomofauna of old-growth forests, secondary forests and pine plantations are markedly different (Pauchard 1998), but comparative studies on the invertebrates of old-growth forests versus secondary forests and pine plantations are scarce.

The destruction of small native forest patches and the spatial segregation of formerly overlapping land uses, together with the alignment of formerly fuzzy native forest edges is a current process of landscape dynamics (Frank 1998). Supra-national markets for agricultural and forestry products push the conversion of finely textured traditional land-use systems and native forests into coarsely textured agro-industrial landscapes. This coincides with landscape dynamics observed in other parts of the world, e.g. the famous 'arc of destruction' in the Brazilian Matto Grosso with its soy boom.

19.3.3 Tropical Forests

Tropical rainforests have been inhabited and used by humans for millennia. In colonial times, tropical rainforests started to be of interest for European economies, as exotic timber and spices were important merchandise. With the industrial

revolution, secondary products of tropical forests such as caoutchouc (natural rubber) and resin gained in importance, but during the second half of the twentieth century timber finally formed the main tropical forest merchandise (Whitmore 1993).

Nevertheless, large parts of the humid tropical lowland forest ecosystems remained relatively intact until the twentieth century, while other regions, mostly tropical highlands with fertile, often volcanic soils, were already densely populated during earlier civilisations. To some degree, these historical patterns are still visible in the contemporary landscape.

Forest destruction in tropical lowlands is often initiated and driven by government settlement and infrastructure projects (e.g. Brazil), by industrial logging concessions (e.g. West Africa, South-east Asia), or by export-oriented conversion of forests to cash-crop plantations such as oil palm (Sandker et al. 2007), bananas (Simon and Garagorry 2005), soy bean (Malhi et al. 2008; Fearnside 2001), or the expansion of cattle production, e.g. in Brazil (Malhi et al. 2008), whereas deforestation associated with the expansion of traditional smallholder agriculture appears to be a phenomenon mainly of upland zones (Geist and Lambin 2001). Periods of regeneration between agricultural uses of shifting cultivation have decreased (FAO 1996).

Human impacts such as (large-scale) clear-cutting, timber extraction, the conversion to agricultural land, commercial and subsistence hunting[11], result in the loss of forest cover, fragmentation of the forest matrix, and/or changes in the structures, process chains and species composition in remaining forest fragments.

Already in 1990, Brown and Lugo stated that secondary forests, having simpler structures in comparison to mature forests and being composed usually of generalist species, are increasingly abundant in the tropics (40% of the total forest area) with a rate of formation of about 9 million ha year^{-1}. This rate corresponds mostly to the destruction of old-growth forests and is probably still a conservative guess. Fragmented forests are greatly altered by 'cryptic' surface processes that are hard to detect by remote sensing (Peres et al. 2006). Along their edges, tropical forests become significantly drier and warmer, and fires enter more easily from the edge (Cochrane and Laurance 2002), as well as humans with their activities such as selective small-scale logging or understorey thinning. These effects cause elevated tree mortality of canopy trees (Ferreira and Laurance 1997; Laurance et al. 1998). Large trees (>60 cm diameter) die almost three times faster within 100 m of edges than in forest interiors (Laurance et al. 2006b). Forest fragments undergo drastic changes in their species composition, with a strong increase in disturbance-adapted non-biotically dispersed pioneer species and a significant decline of large-seeded, slow-growing and shade-demanding late-successional species (Laurance et al. 2006b).

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[11]Indications of the threatening amounts of animals taken by (subsistence) hunters are given e.g. in Redford 1992; Redford and Robinson 1987.

In tropical old-growth forests, animals have crucial functions as pollinators and/or dispersal agents. At least 50%, often 75% to over 90%, of the tree species produce fleshy fruits adapted to bird or mammal consumption (Howe and Small-wood 1982; Hamann and Curio 1999). Many of the largest tropical forest animals are frugivores that play an important role within the ecosystem for seed dispersal and/or pollination, and, at the same time, the largest species in the ecosystem are almost always the ones most commonly hunted (Redford 1992; Chapman and Chapman 1995; Peres and Palacios 2007). Regardless of the effects of body size, Peres and Palacios (2007) found more marked declines for frugivourous species in heavily hunted areas of Amazonian forests compared to seed predators and browsers. Similar observations exist worldwide for old-growth forests in other tropical areas: Most vertebrates of the Brazilian Atlantic forest threatened by local extinction within forest fragments are large-bodied or relatively specialised frugivores like primates or toucans, which often disperse medium- to large-seeded plant species occurring primarily in old-growth forests (Tabarelli and Peres 2002).

In large areas of neotropical forests, even though the forest still appears intact, many populations of large animals are already so diminished due to subsistence and commercial hunting that they can be considered as functionally or ecologically extinct. It must be taken into account that the number of animals subject to subsistence hunting is very high (see Redford 1992; Redford and Robinson 1987). Even without extensive habitat loss or fragmentation, spider monkeys and other ateline primates, being pivotal dispersers for many plant species in the Neotropics, are among the first animals to become locally extinct following human penetration into pristine forest areas (Link and DiFiore 2006). Also in Africa, primates rely on fruiting trees as important food resources, and play an important role as seed dispersers, pollinators and in plant dynamics (Chapman and Onderdonk 1998; Chapman et al. 2006), and both African tropical forests and their primates are seriously threatened (Cowlishaw 1999).

In a second line of attack, a decline in forest macrofauna is also caused by human activities not aimed directly at animals, especially habitat destruction by logging, burning, clearcutting etc., but also massive commercial fruit- and nut-collection (Redford 1992), or the destruction of key sites (spatial bottlenecks in the life history traits of a species), such as nesting or rest places of migratory birds or bats.

These worldwide tendencies are particularly alarming because narrow mutualistic interdependencies seem to be a pronounced feature in tropical old-growth forests. The disruption of those mutualisms due to the diminution and extinction of animal populations might have strong effects on whole-forest ecosystem processes. Large-seeded frugivorous plants – many of them late-successional tree species – may be especially vulnerable to the loss of specialised seed dispersal services under increasing hunting pressure or due to fragmentation (Chapman and Onderdonk 1998; Hamann and Curio 1999; Kitamura et al. 2005; Peres and Palacios 2007). Forest fragments in the Kibale National Park, Uganda, with dramatically reduced primate seed dispersers, had lower overall seedling density and fewer species of seedlings compared to areas with an intact frugivore community (Chapman and Onderdonk 1998). Losses of key pollinators and seed dispersers

could also affect tree communities in a surprisingly rapid dynamic. In less than two decades of a fragmentation experiment in Central Amazonia, Laurance et al. (2006a) found that typical old-growth tree genera, many of them requiring obligate outbreeding and animal seed-dispersers (Laurance 2005), declined significantly. The composition of the seed disperser fauna is probably one of the key factors for seedling recruitment in successional forest landscapes (Tabarelli and Peres 2002).

From a long-term perspective, conservation of tropical forest vegetation will not be possible without the associated forest fauna. Sustainable management of forest fauna is not just a popular flagship species theme for international conservancy trusts like the IUCN, CI or WWF, but remains a key issue for long-term conservation of the remaining old-growth forests in the humid tropics and beyond.

19.4 Conclusions

Structure and species-richness of old-growth habitats differ according to forest biomes. Nevertheless, many of the habitat functions are common to almost all old-growth forest ecosystems:

- Old-growth forests tend to have structurally complex and dynamic vertical and horizontal microclimatic environments. At the same time, old-growth habitats are to some extent resilient against variations in temperature, light and humidity at the meso- and macro-scale. Both are reasons for the high diversity of lichens and bryophytes in all old-growth forest ecosystems, and the high number of stenoecous old-growth species, such as amphibians, beetles, and ferns, and many other taxonomic groups.
- The amount and structural diversity of dead wood in terms of diameter classes, species composition and climatic conditions nourishes numerous saprophytic organisms (such as fungi, xylobiont beetles and termites), many of which are therefore strictly bound to old-growth forests. These saprophytic organisms in turn support a great number of species higher up in the food chain.
- Tall late-successional tree species create complex, vertically structured environments, characterised by highly diverse arrangements of foliage, branches, stems, logs and snags. Many endangered vertebrates depend on these spatial structures.
- Functional mutualistic plant–animal interactions like dispersal and pollination play an important role in old-growth forests. Their complexity increases from boreal to tropical forests and with ecosystem-stability over evolutionary time-scales. Fragmented populations of old-growth biota can have a very long persistence, thus slow genetic erosion leading towards extinction is hard to detect. Functional mutualisms are susceptible to human disturbances, and broken mutualistic process chains might cause irreversible long-term changes in forest ecosystem processes.

- The natural course of succession and the regeneration of true old-growth forests are often impeded by dispersal limitation of late-successional species. Since intact forest landscapes are becoming rare in many parts of the world, and complete biotic assemblages can recover only from remaining intact fragments, the spatial array and permeability of the non-forest matrix become important in fragmented, intensively used landscapes.
- Impacts on old-growth forests differ according to key factors; economic driving forces largely determine land-use systems. There is no scientific consent about a minimum threshold for acceptable anthropogenic disturbances in old-growth forests. The future will show to what degree old-growth biota will be able to cope with global and local change processes.

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Chapter 20
Old-Growth Forests in the Context of International Environmental Agreements

Annette Freibauer

20.1   Introduction

Forests are included in several political negotiations and legal documents under the United Nations (UN). This chapter focusses on the three most relevant and dynamic UN political processes in the context of old-growth forests: The UN Framework Convention on Climate Change (UNFCCC), the Convention on Biological Diversity (CBD), and the UN Forum on Forests (UNFF). Forests are also addressed by the UN Convention on Combating Desertification and the Ramsar Convention on wetlands.

Old-growth forests are defined by biological and ecological criteria, which differ from the criteria and categories applied in international environmental agreements. The absence of human impact is no clear criterion for old-growth forests. Old-growth forests can be managed or unmanaged, and can be primary or secondary forests (see Chap. 2, by Wirth et al., this volume).

Following the definitions in Chap. 2 of this book, old-growth forests are characterised by

1)   a relatively old age (existence of large old late-successional tree species with ages close to their life expectancy; mean age half the lifespan of the dominating trees),
2)   structural and compositional features witnessing self-replacement through gap-phase dynamics (uneven-aged, regeneration of shade-tolerant species, presence of canopy gaps, large snags and logs in varying stages of decay).

The question arises whether it matters in the context of international environmental agreements if forests are in their late stages of succession. This chapter summarises the present status of old-growth forests in global environmental agreements and discusses promising options to include old-growth forests in future phases of these agreements.

The following sections (1) give an introduction to the UNFCCC, CBD and UNFF and show the role of forests in these UN political processes; (2) highlight characteristics of old-growth forests relevant for the UNFCCC, CBD and UNFF,

and analyse how they are reflected in the context of the agreements; and (3) assess how and to what extent old-growth forests could be considered in future stages of these international environmental agreements.

20.2   Forests in UN Processes

20.2.1   UN Framework Convention on Climate Change

The ultimate objective of the UNFCCC (Article 2) is the "stabilisation of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system. Such a level should be achieved within a time-frame sufficient to allow ecosystems to adapt naturally to climate change , to ensure that food production is not threatened and to enable economic development to proceed in a sustainable manner" (UNFCCC 1992, 1997, 2002).

According to this objective, the UNFCCC addresses only anthropogenic greenhouse gas emissions and abatement of adverse consequences of their emission. This objective was interpreted by policy makers, and in the IPCC Good Practice Guidance (IPCC 2004), as a restriction to managed forests. Unmanaged forests hosting the great majority of old-growth forests are not considered in the current activities under the UNFCCC and the Kyoto Protocol. As of October 2007, 191 countries, with some exceptions, e.g. Iraq and Somalia, have ratified the UNFCCC. Almost the entire global forest area (99.8%) is located in signatory states of the UNFCCC.

However, it is left to the individual signatory states to define what constitutes "managed forests" (Höhne et al. 2007). Depending on the choice of definition of "managed forest", the UNFCCC addresses as much as 92% of global forests if all types of uses are included, but down to 34% of global forests if only the production function is included (see Table 20.1). The 24% of global forests that are used for protection, conservation or social services (see Table 20.1) are likely to bear a significant share of old-growth forests. These forest uses, however, can be missed by a narrow definition of "managed forest" restricted to timber production.

The member countries of the UNFCCC need to submit national inventory reports including the carbon stock changes in forests. Five ecosystem carbon pools have to be considered unless it can be proven that a pool is not a carbon source: Aboveground biomass, belowground biomass, deadwood litter and soil. In practice, most of the reports concentrate on biomass. This is also true for the country reports for the FAO Forest Resource Assessment (FAO 2005; Marklund and Schoene 2006). Changes in non-biomass carbon pools – particularly relevant for old-growth forests [cf. Chaps. 5 (Wirth and Lichstein), 6 (Harmon), and 11 (Gleixner et al.), this volume for dynamics of dead wood and soil carbon, respectively] – are associated with large uncertainties or are currently ignored by more than half of the reporting countries to the FAO (Fig. 20.1).

Table 20.1 Forest area and its primary use in 2005 (FAO 2005)

Region	Total forest area (1,000 ha)	Production (%)	Protection (%)	Conservation (%)	Social services (%)	Multiple purpose (%)	None or unknown (%)
Eastern and Southern Africa	226,534	19.4	2.8	9.5	n.s.	39.0	29.1
Northern Africa	131,048	35.2	10.0	10.4	n.s.	16.8	27.7
Western and Central Africa	277,829	44.6	1.9	35.0	0.3	8.1	10.1
South and South-east Asia	283,127	42.4	20.9	20.2	0.1	13.3	3.2
Western and Central Asia	43,588	22.2	30.0	6.4	2.1	39.3	n.s.
Europe	1,001,394	73.1	9.1	3.8	2.3	10.7	1.0
Caribbean	5,974	28.1	37.0	20.2	0.1	1.4	13.3
Central America	22,411	14.8	4.8	37.8	0.2	34.6	7.8
North America	677,464	6.0	0.1	11.8	0.0	78.9	3.3
Oceania	206,254	11.0	0.2	14.4	n.s.	63.5	10.8
South America	831,540	11.6	11.3	14.4	13.7	34.6	14.5
World	3,952,025	34.1	9.3	11.2	3.7	33.8	7.8
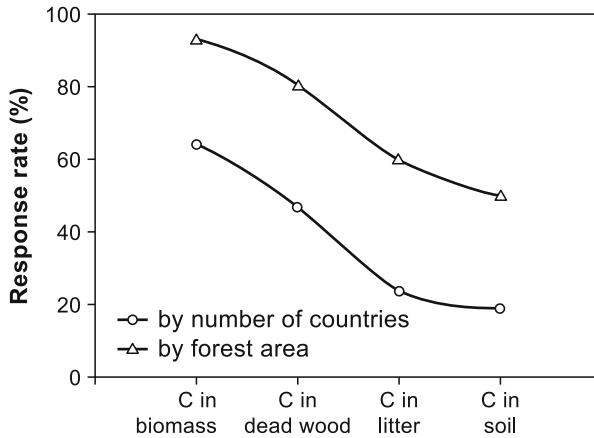
Fig. 20.1 Response rate (in %) for carbon reporting by countries to the Food and Agriculture Organization Forest Resources Assessment (FAO FRA) 2005 (FAO 2005). Adapted from Marklund and Schoene (2006)

Article 4(d) of the UNFCCC commits countries to "promote sustainable management, and promote and cooperate in the conservation and enhancement, as appropriate, of sinks and reservoirs of all greenhouse gases" (UNFCCC 1997). The Marrakech Accords set principles for the first commitment period under the Kyoto Protocol (2008–2012), e.g. "that the implementation of land use, land-use change and forestry activities contributes to the conservation of biodiversity and sustainable use of natural resources" (UNFCCC 1997).

However, these principles are not legally binding. The term "sustainable use of natural resources" is not defined.

The Kyoto Protocol (UNFCCC 1997) sets mandatory emission limitation targets for industrial countries. The Kyoto Protocol has been ratified by 84 states, among which are the European Union (EU) and its Member States, Russia, Japan, Canada, and Australia, but not the United States. The Kyoto Protocol originally aimed at reducing emissions from fossil fuel use, but also includes some land use options (Höhne et al. 2007). Carbon stock changes created by afforestation, reforestation and deforestation (Article 3.3) are accounted on a mandatory basis even though several countries opted to report other categories of land management, such as forest management (Article 3.4). Twenty signatory countries, including the Russian Federation, Japan and many EU member states, but not Canada, have decided to account for forest management. These countries host 25% of the global forest area; 72% of these forests are used primarily for production, 13% for multiple purposes, 9% for protection, 4% for conservation, and 2% for social services (FAO 2005). It can be expected that most, if not all of the forest area in these countries will be included in the national accounting under the Kyoto Protocol.

20.2.2 Convention on Biological Diversity

The objectives of the Convention on Biological Diversity CBD (Article 1) are "...
the conservation of biological diversity, the sustainable use of its components and
the fair and equitable sharing of the benefits arising out of the utilisation of genetic
resources..." (CBD 1992). Among other means, the objectives shall be achieved
via national strategies, plans and programmes for the conservation and sustainable
use of biological diversity (Article 6), and in situ conservation, e.g. by national
systems of protected areas (Article 8).

The 2010 Biodiversity Target with various Focal Areas, Goals and Targets was
decided together with indicators of success. As of April 2009, the CBD has 9
member countries, excluding e.g. Brunei Darussalam, Iraq, Somalia and the United
States. Ninety-two percent of the global forest area is located in member countries
of the CBD.

The CBD addresses all managed and unmanaged forests and urges its parties to
apply the principles of the ecosystem approach. Forest ecosystems receive special
attention under the CBD via the working programmes on forest biodiversity and on
protected areas. Forest protected areas do not exclude commercial use.

Even more than the UNFCCC, the implementation of the CBD relies on the
intentions of individual signatory states to act because the CBD has no international
compliance regime. In Europe, cooperation among countries for forest biodiversity
is fostered by the Ministerial Conference on the Protection of Forests in Europe
(MCPFE) as well as by the Pan-European Biological and Landscape Diversity
Strategy (PEBLDS).

The synthesis of progress reported in the third national reports to the CBD
shows that among all ecosystem types, forests have received the greatest attention
(CBD-WGRI 2007b). The thematic programme of work on forest biodiversity has
been implemented with high priority by almost 70% of the reporting countries,
sometimes even with quantitative national targets for total forest area, the increases
in forest area, and protected areas coverage (CBD-WGRI 2007b, 2007a). Forest
biodiversity targets have been integrated into forestry and development plans.
Measures for forest protection, rehabilitation, restoration, conservation of
threatened species, taxonomic research and activities, sustainable forest manage-
ment and reforestation, and improving the knowledge basis have been introduced
by 94% of the reporting countries. Many countries have established protected forest
area networks (CBD-WGRI 2007a). However, it has to be noted that the reports on
which the synthesis was based are voluntary and reports are not reviewed. There are
no criteria to substantiate, quantify or compare progress among countries, thus,
despite the large number actions described, the high amount of attention paid to
forest ecosystems does not necessarily equate to significant progress in the protec-
tion of forests.

20.2.3   *UN Forum on Forests (UNFF)*

The UNFF is a forum towards an international agreement on forests "to promote the management, conservation and sustainable development of all types of forests and strengthen long-term political commitment to this end" (IFF 2000).

The 1992 Rio summit failed to agree on an international forest convention. Since then, 25 years of negotiations at three successive UN fora have failed, by April 2009, to set up any legally binding international agreement. Between 1995 and 1997, proposals for action to support the management, conservation and sustainable development of forests were developed by the Intergovernmental Panel on Forests (IPF) under the UN Commission on Sustainable Development (CSD). The recommendations of the IPF were further negotiated between 1997 and 2000 under the Intergovernmental Forum on Forests (IFF). In February 2000, the IFF issued its final report, which included a recommendation for an international arrangement on forests. As a consequence, the United Nations Economic and Social Council (ECOSOC) adopted a resolution outlining an international arrangement on forests and establishing the UNFF as a subsidiary body of ECOSOC. Since 2000, international negotiations have continued under UNFF.

In 2006, UNFF agreed on "shared global objectives on forests" (UNFF 2006):

1) Reverse the loss of forest cover worldwide through sustainable forest management (SFM) including protection, restoration, afforestation and reforestation, and increase efforts to prevent forest degradation;
2) Enhance forest-based economic, social and environmental benefits, including by improving the livelihoods of forest-dependent people;
3) Increase significantly the area of protected forests and other sustainably managed forests, and increase the proportion of forest products derived from sustainably managed forests; and
4) Reverse the decline in official development assistance for sustainable forest management and mobilise significantly increased new and additional financial resources from all sources for the implementation of SFM.

A non-legally binding instrument on all types of forests was adopted under UNFFF on 28 April 2007. The purpose of this instrument is (UNFF 2007):

a) to strengthen political commitment and action at all levels to implement effectively sustainable management of all types of forests and to achieve the shared global objectives on forests;
b) to enhance the contribution of forests to the achievement of the internationally agreed development goals, in particular with respect to poverty eradication and environmental sustainability;
c) to provide a framework for national action and international cooperation.

The instrument is voluntary and non-legally binding[1]. Each state is responsible for the sustainable management of its forests and for the enforcement of is forest-related laws, so that the instrument remains without international control.

International negotiations about forests proved a lot more difficult than those about climate change, biodiversity or desertification. Major resistance has emerged from fears of losing some of the national control over forests and forest products and of national sovereign rights to exploit forest resources. The definition of sustainable forest management was also controversial. In conclusion, UNFF has not achieved any mandatory international obligations nor international control of unsustainable forest use.

20.3   Consideration of Old-Growth Forests in UN Processes

20.3.1   Old-Growth Forests and the UN Framework Convention on Climate Change

Old-growth forests are usually characterised by high carbon stock densities [t C ha^{-1}] in all carbon pools considered under the UNFCCC (cf. Chaps. 5 (Wirth and Lichstein), 6 (Harmon), and 11 (Gleixner et al.), this volume, for dynamics of dead wood and soil carbon, respectively). However, due to the sensitivity of the carbon pools in biomass, dead wood and litter, large and fast carbon losses can be triggered by disturbance.

Existing carbon stocks are not a criterion under the UNFCCC and the Kyoto Protocol, which consider only carbon stock changes. But high carbon stock densities are relevant in the context of potential emissions by disturbance, e.g. by degradation and deforestation.

Old-growth forests are treated by the UNFCCC as all other forests. In cases where old-growth forests fall under the category "managed", their carbon stock changes are reported under the UNFCCC. The industrial signatory states of the Kyoto Protocol need to account for CO_2 emissions from the deforestation of forests, including old-growth forests (Article 3.3), and if they have elected to adopt Article 3.4 (Forest Management) they need to account for disturbance and degradation occurring in their forests, including old-growth forests. But if old-growth forests are considered "unmanaged" they are excluded from the UNFCCC and the Kyoto Protocol, because for unmanaged forests it is assumed that carbon stocks do not change by direct human action. This assumption is based on the paradigm that, as succession proceeds, ecosystem carbon stocks finally reach an equilibrium where gains and losses of carbon are balanced (Odum 1969).

Negotiations about an international climate change agreement for the period after 2012 are in progress. Although the scope and rules for the future are yet

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[1]Details of the negotiations and the final text of the non-legally binding instrument can be found at http://www.iisd.ca/vol13/enb13162e.html.

unclear, it can be anticipated that forests will be more comprehensively included. A new mechanism is being developed for incentives to reduce emissions from deforestation and degradation (REDD) in developing nations. This is especially important since most developing countries are in the tropics, where the fraction of old-growth forest within the primary forest landscape is particularly high compared with other biomes (see Fig. 2.7 in Chap. 2 by Wirth et al., this volume). Old-growth forests in developing nations endangered by deforestation or degradation could be conserved under REDD mechanisms.

20.3.2   Old-Growth Forests and the Convention on Biological Diversity

The high structural and species richness, the existence of large old trees, and the significant amounts of standing and lying dead wood in old-growth forests create habitats of high value for the conservation of biodiversity [see e.g. Chaps. 13 (Bergeron and Harper), 15 (Schulze et al.), 16 (Armesto et al.), and 19 (Frank et al.), this volume]. Old-growth forests should therefore be, and have already partly been, priority areas for CBD targets such as protected areas, conservation of threatened species, and management guidelines ("ecosystem approach"). Old-growth forests are specifically addressed by some countries. For example, Estonia's Nature Conservation Development Plan includes the target to maintain at least one-third of all forests more than 100 years old (CBD-WGRI 2007b). Methods for mapping old-growth forests based on forest inventories or remote sensing have been devised for many regions [see Chaps. 2 (Wirth et al.) and 18 (Achard et al.), this volume].

Old-growth forests are not an official forest category under the CBD. Nevertheless, of all the existing international environmental agreements, the CBD is best suited to promote the conservation of old-growth forests because it specifically addresses forests rich in biodiversity. However, unlike the compliance regime under the UNFCCC, there is no enforcement of national commitments, e.g. to achieve the 2010 Biodiversity Target.

20.3.3   Old-Growth Forests and the UN Forest Focus

The UNFF would ideally provide an integrative platform on which the various specific features of old-growth forests for carbon, biodiversity, ecosystem functions and sustainable management could be balanced. However, as mentioned above, the UNFF process has so far failed to achieve an international agreement on its implementation, and still has the weakest legal structure of all UN processes relevant for old-growth forests.

20.4 Potential Role of Old-Growth Forests in Future International Environmental Agreements

The high amount and long residence time of carbon stored in old-growth forests is not valued in climate policy (WBGU 1998; Schulze et al. 2002). However, Article 4.1(d) of the UNFCCC (see above) includes the conservation of carbon in ecosystem pools. In contrast, the link between the mitigation of climate change and the conservation of biodiversity remains vague and non-binding. No priority or specific rule for old-growth forests can be derived from the mandate or commitments under the UNFCCC. Therefore, expectations for direct support for the conservation of old-growth forests by future activities under the UNFCCC need to remain realistic. The target entity of the UNFCCC will likely remain the change in carbon stocks in forests at the national level, rather than any management or conservation targets for a specific forest type.

Nevertheless, global negotiations on the REDD mechanism could give value to and allow a certain protection for forests in developing countries, where large areas of old-growth forests exist. The REDD mechanism will likely be implemented by a national approach (Mollicone et al. 2007) so that countries receive incentives to reduce carbon losses from their forests. The conservation of old-growth forests endangered by forest degradation and deforestation may be one of several promising approaches within broader national policies for sustainable resource management and good governance. Such favourable national conditions go beyond the scope of individual international agreements and can therefore not be directly enforced at the international level. However, old-growth forests need long-term strategies for their conservation. Sustained incentives will be critical, but it is as yet unclear how this will work under the REDD mechanism (Mollicone et al. 2007). Such incentives need to be financial and institutional and need to be associated with international progress control, ideally with sanctions for non-commitment.

In parallel, a future climate change agreement under the UNFCCC may also be broadened towards a comprehensive inclusion of all forests. For equity reasons, if developing countries take a national approach under a future climate change agreement, the industrial countries, to which the REDD mechanism does not apply, need to follow with similar efforts to protect their forest carbon stocks. In addition, although deforestation in industrial countries is currently small, forest degradation through illegal or unsustainable logging and increased forest fires are not confined to developing countries (Mollicone et al. 2007).

Old-growth forests, which are "managed" in the broad sense, are subject to the UNFCCC and CBD. The streamlining of activities between the various conventions remains a major challenge. Whilst the UNFCCC will address the national total forest carbon stock, most of the potential synergies with the CBD will arise from activities at a national to local level. A network of forest protected areas such as proposed under the CBD could form part of a wider (voluntary) national portfolio of forest policies under the UNFCCC. Old-growth forests declared as unmanaged, however, remain under the domain only of the CBD. The ongoing efforts to

establish a global network of forest protected areas under the CBD (Schmitt et al. 2007) can support old-growth forests but will also continue to rely on voluntary national commitments for the foreseeable future.

The common denominator of the UNFCCC and CBD are the efforts towards sustainable forest management via the CBD mandate, the UNFCCC principles, the principles of the Marrakech Accords and the REDD "degradation" mechanism.

At the project level, a common evaluation standard for climate change and biodiversity projects should be developed that takes into account the specific type of activity, e.g. land-use change, avoided deforestation, and the protection of carbon stocks, among which old-growth forests could be included (De Vrede et al. 2005). A system of multiple scores for various international environmental agreements would allow investors to choose the level of environmental integrity they wish to achieve in their projects (De Vrede et al. 2005).

20.5   Conclusions

None of the UN processes was specifically targeted at old-growth forests. The successional stage of a forest is not a criterion used to distinguish forest ecosystems in national or international legal documents. Instead, forests are holistically addressed or distinguished by the degree of human impact or indicators related to the environmental goals to be achieved. Old-growth forests could emerge as a prime area of synergy between the UNFCCC and CBD as a cross-cutting issue.

The failure of the UNFF to move to action can be seen as a warning about the difficulty of establishing a legally binding international instrument exclusively for forests with their multiple local, national and international interest groups. Using existing and emerging mechanisms under existing international environmental agreements for the protection of old-growth forests may turn out to be the most effective strategy for the near future. However, existing agreements should not be overburdened with details that would make their implementation and control difficult and expensive.

International environmental agreements can only set a broad legal framework of goals, principles and commitments for the conservation of old-growth forests and may offer support by international funding. Old-growth forests will profit only when these agreements are implemented by the individual countries through national and local action. Designing, implementing and maintaining adequate incentive schemes for the conservation of old-growth forests remains a critical challenge, which cannot be solved solely at the international level.

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**Part VI
Synthesis**

Chapter 21
Old-Growth Forests: Function, Fate and Value – a Synthesis

Christian Wirth

21.1 Challenges in Functional Old-Growth Forest Research

The total number of scientific articles on old-growth forests has increased drastically over the last 10 years (Chap. 2 by Wirth et al.), and yet papers on old-growth forests make up only about 1% of all forest- or forestry-related articles listed in the Web of Science. The availability of process information – as reviewed in this book – decreases exponentially with stand age irrespective of the ecosystem function considered (Fig. 21.1). One likely reason for the scarcity of information on old-growth forests is their seemingly low economic relevance and consequently limited research funding. Another possible reason is the scarcity of old-growth forests themselves in the countries where most scientific research is carried out. Surely, this may be compensated for by the fact that rarity tends to spark interest. Like anyone else, ecologists are fascinated by tall, majestic forests. This is clearly reflected by the dominance of old-growth studies carried out in the famous temperate rainforests of the western United States. However, the same features that make old-growth forests attractive (tall trees, complex structure, organismic diversity, remoteness) pose tremendous challenges to ecosystem research. Old trees are usually tall, and access to the canopy requires expensive infrastructure such as canopy cranes or towers, not to mention the difficulties involved in studying root systems. Old-growth forests are highly heterogeneous, in both the vertical and horizontal dimensions. Spatial heterogeneity in soil conditions is caused by tree falls (Chap. 10 by Bauhus). Thus, soil sampling aimed at a reliable estimate of element stocks and fluxes requires a large number of spatial replicates (Chap. 11 by Gleixner et al.). To complicate matters further, mere soil sampling is not sufficient to quantify ecosystem processes such as mineralisation or heterotrophic respiration, because decomposition also takes place in aboveground compartments such as snags, dead branches, rotting heartwood in live trees and detritus produced by epiphytes (Zabel and Morrell 1992). Epiphytes are difficult to reach, but may contribute significantly to net primary production (Clark et al. 2001). Micrometeorological investigations of water, energy and CO_2 exchange using the eddy covariance method require homogenous vegetation surfaces on level terrain, but
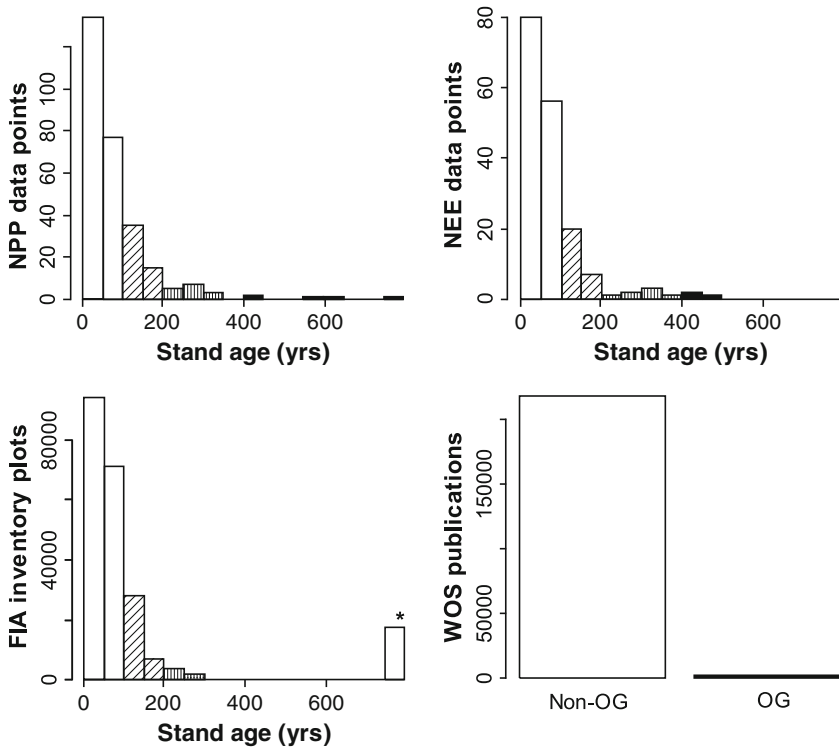
Fig. 21.1 Frequency of information on net primary productivity (NPP; *top left panel*) and net ecosystem exchange (NEE; *top right panel*) based on the datasets used in Kutsch et al. (Chap. 4) and Knohl et al. (Chap. 7), respectively, according to stand age. The *left lower panel* shows the age distribution of inventory plots in the United States forest inventory assessment, and the *right lower panel* the number of publications indexed in Web of Science referring to either 'forest' or 'forestry' (*left bar*) or one of the terms defined by Wirth et al. (Chap. 2) related to old-growth forests (*right bar*). The different shadings of the bars (except in the *lower right panel*) indicate, from left to right, the developmental stages: pioneer, transition, early old-growth and late old-growth; *stand age not known

old-growth forests often exhibit structurally irregular canopies and occur often on complex sloped terrain unsuitable for agriculture or forestry operation (Chap. 7 by Knohl et al.).

According to the classical view, tree species composition and process rates tend to stabilise with age as forest stands approach the climax state (Clements 1936; Odum 1969), i.e. younger stands are expected to change faster and are more different from each other than old stands. Under this scenario, the sampling effort should concentrate on young stands and the data scarcity in old stands would be of little concern. However, temporal and between-stand variability may indeed be substantial in old-growth forests. At annual time-scales, old-growth stands may switch from carbon sinks to sources in response to inter-annual climate variability (Chap. 7 by Knohl et al.). At longer time scales, successional species turnover and

the legacy of synchronised mortality influence the net exchange of carbon over many centuries. The model analysis and the chronosequence data presented in Chap. 5 suggest that it may take 400 years or more before ecosystem carbon stocks eventually equilibrate, if they ever do so. In contrast to Clements' view, the longer the time-scale over which a forest ecosystem develops, the higher the likelihood that it is affected by stochastic perturbations. This is likely to induce a divergence of successional pathways and associated trajectories of matter pools with stand age (Chapin III et al. 2004). In fact, variability may increase with stand age as the biomass chronosequences for *Pseutotsuga menziesii* and *Tsuga heterophylla* illustrate (see Fig. 5.8 in Chap. 5 by Wirth and Lichstein). Under this scenario, sampling effort should increase with successional age, which is in stark contrast with the actual situation. Finally, the above-mentioned sequences illustrate another severe problem in old-growth forest research. The quantification of successional time since stand initiation becomes extremely difficult after the even-aged founder cohort has completely turned over. This is why, in many studies, e.g. Janisch and Harmon (2002), old-growth stands are assigned an arbitrary high age. Alternatively, the age is given as a range (e.g. 200–500 years), a minimum value (>200 years) or a category ('old-growth').

Despite data limitations and the many difficulties in carrying out research in old-growth forests, the reviews and novel analyses presented in this book shed new light on how old-growth forests function differently from younger and managed forests.

21.2 Functional Consequences of Old-Growth Forest Structure: the Spatial View

The structure of old-growth forest is special. This is reflected by the fact that existing definitions of 'old-growth forest' are based largely on structural criteria (Chap. 2 by Wirth et al.). Although there might be pronounced differences in forest structure between biomes – some of which are reviewed in this book – old-growth forests across the world share a number of common structural features: Old-growth forest canopies are usually tall. Single tree death and subsequent gap phase dynamics create a higher spatial heterogeneity in the horizontal and vertical dimension as compared to managed or younger stands. This aboveground heterogeneity is partly reflected in the forest floor and soil properties. This poses the question of whether, and how, greater stature and spatial heterogeneity translate into differences in functioning.

21.2.1 Tall Stature

Tall forests occupy a greater ecosystem volume in which to accumulate carbon. This is why canopy height is a good predictor of biomass carbon stocks (Chap. 5 by Wirth and Lichstein). On the other hand, tree growth usually follows a sigmoidal function,

implying reduced growth rates in tall trees and, by the same token, lower biomass increment in tall forests. The most prominent (but still controversial) explanation for size-related growth reduction is provided by the hydraulic limitation hypothesis: as trees grow taller, increasing gravitational potential and path length lead to decreased leaf water potential (Chap. 4 by Kutsch et al.). To prevent leaf water potential from dropping below the wilting point, stomatal conductance is reduced, and thereby also photosynthesis and growth. I will summarise the extensive debate on age- or size-related productivity decline in Sect. 21.3. At this point, it is important to note that tall stature – as a structural feature – may induce reduced growth rates.

Another aspect of forest stature is that tall forests enclose a large volume of air between the soil surface and the canopy. This favours the development of internal convection cells that transport ground-level air, which is enriched in CO_2 from soil respiration, into the canopy where it can be re-fixed and increase growth rates if trees are carbon-limited (see Chap. 17 by Grace and Meir). Without this convection, respiratory CO_2 might be lost with lateral air flow. The belowground analogue of tall stature is a deep rooting depth. In addition to their anchoring function, deep roots provide access to ground water. During summer, when the top soil has dried out, old-growth forests may therefore maintain a higher stomatal conductance and photosynthesis than shallow-rooted young forests (Chap. 7, Knohl et al.). Deep roots thus help overcome the hydraulic limitation of photosynthesis in tall trees by increasing the water supply. In addition, deep roots act as channels for hydraulic lift of ground water (Caldwell et al. 1998). This passive redistribution provides surplus water to the ground vegetation and thus contributes to the maintenance of under-storey productivity under dry conditions (Dawson 1993).

21.2.2   The Imprint of Aboveground Structural Complexity

It may appear that canopy gaps in old-growth forests reduce the overall light use of the vegetation, thereby lowering gross primary productivity (GPP). However, the average light availability at the forest floor does not seem to differ between old-growth and secondary growth forests (Chap. 6 by Messier et al.), suggesting that light is not 'wasted' in old-growth forests, but simply harvested across a wider height gradient: gaps quickly fill from below with understorey herbs and tree regeneration, or are filled laterally by the expanding crowns of surrounding trees. This represents a form of resilience of GPP against canopy mortality and gap formation. This is supported by Knohl et al. (Chap. 7), who compared an old-growth multi-layered beech stand with an otherwise similar mono-layered managed stand and detected no differences in GPP. Given the above evidence, it is not surprising that the mean light experienced by the understorey vegetation in old-growth forests is low in temperate and tropical forests (Table 6.1 in Chap. 6 by Messier et al.). Under these conditions, the above-mentioned 'gap filling' is enhanced by the presence of sapling banks formed by trees with a high degree of shade-tolerance (Table 6.2 in Chap. 6 by Messier et al.;

Chap. 17 by Grace and Meir, see also Sect. 21.3.4). The resilience of GPP thus also hinges on diversity of plant function.

Another line of argument suggests that GPP should be even higher in old-growth forests (Chap. 7 by Knohl et al.): old-growth canopies possess a 'rough' topography and exhibit a high contact surface with the atmosphere (up to 12 times higher than the ground surface). Radiation therefore penetrates deeper into the canopy and is trapped more efficiently because radiation back-scattered from lower layers is less likely to escape the canopy (Weiss et al. 2000). A lower surface reflectance (which implies higher radiation absorption) over old-growth forests has indeed been verified by remote-sensing (Ogunjemiyo et al. 2005). To maintain non-lethal leaf temperatures in the face of higher net radiation, energy is dissipated by elevating the leaf transpiration rate. This requires a higher stomatal conductance, and thus indirectly induces an increase in GPP. This link between canopy surface roughness and higher transpiration rates represents yet another process that partly offsets a size-related hydraulic limitation of photosynthesis in tall trees (Chap. 4 by Kutsch et al.).

21.2.3   The Imprint of Belowground Structural Complexity

Single tree mortality may create not only canopy gaps but also root gaps. If so, this could lead to a leakier system with less efficient uptake of water and nutrients in old-growth forests with frequent gaps. Unfortunately, literature on this topic is scarce and results are far from conclusive (Chap. 10 by Bauhus). On the one hand, there is some evidence that belowground gaps are less abrupt and close faster than canopy gaps, mostly because the root systems of adjacent trees overlap more than their crowns. In fact, tree mortality does not seem to punch a hole in the root layer, but merely reduces fine-root biomass by about 20–40%. On the other hand, high nutrient losses via leaching have been reported even under small gaps (Chap. 10 by Bauhus), and a reduction in stand basal area of only about 10% can increase the water yield of a forest catchment (Chap. 7 by Knohl et al.). This paradox (little structural change, but large increases in 'leakiness') may be explained by the fact that, although the uptake capacity is barely affected, the supply of both leachates and water is strongly increased as a consequence of higher mineralisation rates (warmer, wetter soil) and reduced interception losses and transpiration. In any case, this leakiness calls into question the uptake efficiency of mycorrhizal networks. Such leakiness is likely reversed as the gap is re-colonised by herbs, shrubs and tree regeneration, but whether fine-root density is higher in such vegetated patches than in the surrounding matrix of old trees is unclear, as age-trends of fine-root density are idiosyncratic.

The mere existence of large trees induces a patchiness in the forest floor structure. Trees grow on top of their own woody litter (i.e. the heartwood) in order to lift their leaves above those of their competitors. This growth strategy concentrates organic matter into a comparatively small volume (i.e. the stem), in which it may be locked up for many centuries. After tree death and subsequent tree

fall, the carbon and nutrients contained in the stem are deposited in an area that is significantly smaller than the area from which these elements were initially gathered. For example, a deciduous broad-leaved tree with a breast-height diameter of 80 cm occupies a horizontal growing space of about 130 m^2, while the projection area of its downed stem is only about 17 m^2, i.e. 7.5 times smaller. This 'concentration effect' increases linearly with tree diameter and is thus most pronounced in old-growth forests and in young forests that are rich in legacy deadwood after stand-replacing disturbances. A special situation arises when trees are uprooted following a windstorm (Chap. 10 by Bauhus). Root plates are tipped up and, with progressive decay, the elevated stem bases and any attached roots and soil sink down to form mounds, whereas the exposed mineral soil remains as pits. This process disrupts any continuous layering of the soil and accumulates carbon and nutrients in mounds. Up to 33% of the forest floor might by covered by pits and mounds. The question arises whether and how this heterogeneity affects the net ecosystem balances of carbon and nutrients. Given the same total amount of organic material, does a forest floor with a patchy distribution lose more or less carbon and nutrients per unit area than one with homogeneous layering? The chapters in this volume do not directly answer this question, but they do allow us to formulate hypotheses: (1) the high concentration of easily degradable carbohydrates in and under woody detritus may help to overcome an energy-limitation of decomposition, thereby inducing a 'priming' effect (Chap. 12 by Reichstein et al.). This effect will be most pronounced around coarse roots in deeper soil layers where energy-limitation is most severe. As a result, the heterotrophic loss per unit organic matter would be higher in patches with high loads of carbon, which would translate into higher losses in ecosystems with a clumped distribution of fresh organic matter (mounds, logs). (2) We further hypothesise important interactions with site conditions. Snags, logs and mounds represent elevated structures that tend to be drier than the surrounding forest floor (Chap. 10 by Bauhus). For a patchy distribution in a dry climate, this could mean that a large amount of organic matter is locked up in places too dry for microbial activity. In a wet climate the opposite is true: elevated microsites might be the only places providing the oxic conditions required for decomposition (Chaps. 8 by Harmon, and 11 by Gleixner et al.).

21.2.4 Habitat Structure

Of all functions, the provision of habitat for plants and animals is the most obvious and by far the best studied in old-growth forests. There is a massive literature on this subject: out of 1,347 original papers in the Web of Science referring to 'old-growth' 1,125 (or 83.5%) were published in the fields of either conservation biology or general ecology (Chap. 2 by Wirth et al.). The chapters by Frank et al. (Chap. 19) and Armesto et al. (Chap. 16) suggest that the complex horizontal and vertical structure created by gap phase dynamics provides a diverse array of habitat structures, and thus probably allows more and different species to dwell in old-growth forests.

More specifically, because of the high spatial variability of light and temperature, the fine scale of these patterns ensures that moist microhabitats with a low temperature amplitude are never far apart from each other. This allows typical old-growth species with low desiccation tolerance and limited dispersal distances, such as lichens, mosses, snails or newts, to form viable populations. Large old trees create structures that cannot be provided by smaller trees, such as a fissured bark, cavities, small canopy ponds, and branches strong enough to carry high loads of epiphytes. The development of epiphyte communities further diversifies the habitat, as does the activity of woodpeckers and other habitat-structuring organisms. As reviewed by Bauhus (Chap. 10), the process of tree fall itself forms special microsites for plant growth and tree regeneration. Uprooting exposes mineral soil and creates a seedbed for those species that cannot germinate in organic substrates. Microsites on elevated root plates have higher light availability and allow shade-intolerant plant species to establish. The impenetrable tangle of branches where the crown hits the forest floor is usually avoided by ungulate herbivores and thus provides safe sites for tree regeneration. The dead trees themselves add significantly to the mosaic of habitat. Snags and logs support a great variety of specialised organisms that depend on decaying wood as food sources, hideouts and hunting territories, and nesting or rooting substrates (Chap. 8 by Harmon).

21.3   Old-Growth Forests in the Context of Succession: the Temporal View

Old-growth forests are the result – but not the end result – of primary or secondary succession. Succession is a process that unfolds over time, and the underlying temporal view recognises that old-growth forests have a history. Their structure and function is a transient manifestation of various processes that operate on different time-scales but are nevertheless interdependent. For example, the decay of legacy woody detritus after disturbance is completed within several decades (Chap. 8 by Harmon), successional tree species replacement may take centuries (Chap. 5 by Wirth et al.), and the development of phosphorous limitation may require millennia (Chap. 9 by Wardle et al.). The rate of change is highest initially, with later transformations being more subtle. Nevertheless – as will be argued below – the time since stand initiation matters at any successional stage, including old-growth. This dynamic view of old-growth contradicts the equilibrium view, according to which forests reach a self-perpetuating condition without long-term memory. While the equilibrium view is most likely incorrect for any old-growth forest, this view is certainly incorrect for most forests labelled 'old-growth' in existing studies. These have a mean age of only 300 years (Chap. 2 by Wirth et al.) and are thus strongly influenced by the legacy of earlier developmental stages (Chaps. 5 by Wirth and Lichstein, and 6 by Harmon). The notion that old-growth forest functioning can be understood only in the context of successional history is common to the sections that follow.

C. Wirth

21.3.1 Long-Term Trends in Tree and Stand Productivity

The debate about the so-called 'age-related decline' in forest net primary productivity (NPP) had its peak in the 1990s and was spearheaded by ecophysiologists. Discussions about age-trends of stand biomass (B) were lead by forest ecologists and started much earlier. Although these discussion have been largely separate in the literature, simple differential equation models from classical ecosystem theory show that productivity and biomass dynamics are tightly linked (Olson 1963; Odum 1969; Shugart 1984). For example:

$$\frac{dB}{dt} = NPP - \mu B \;\rightarrow\; B(t) = \frac{NPP}{\mu}(1 - \exp^{-\mu t}) \qquad\qquad 21.1$$

where t denotes time, and NPP and μ (the loss rate per unit biomass) are assumed constant. The equation on the right illustrates that, under the assumption of constant productivity and loss rate, biomass equilibrates at NPP/μ. Should either of the two terms change over time after equilibrium has been reached, as would be the case in 'age-related decline' for NPP, this would cause biomass to change over time as well. In short, given a constant loss rate, an 'age-related decline' in productivity would induce a biomass decline.

According to Binkley et al. (2002), age-related NPP declines are one of the most universal patterns in the growth of forests. Do such declines actually exist outside plantations, and, if so, do they have anything at all to do with age? Growth rates of individual trees usually decline after some peak, but it may take a long time before this peak is reached. There are numerous examples of tree-ring sequences that show constant or even increasing ring widths over many centuries, indicating increasing volume growth rates with age (Chaps. 3 by Schweingruber and Wirth, and 15 by Schulze et al.). Moreover, old trees remain responsive to sudden improvements in growing conditions (e.g. Fig. 7.1 in Chap. 7 by Knohl et al.; Wirth et al. 2002; Mund et al. 2002). Schulze et al. (Chap. 15) presented an example of an unmanaged old-growth forest where almost all individual large trees grew at high rates, and the stand accumulated carbon in the above-ground biomass at the exceptional rate of 232 g C m^{-2} year^{-1}. However, we also know that trees do not grow forever. Hypotheses on the age and size constraints on tree productivity are discussed by Kutsch et al. (Chap. 4). The original hypothesis, which stated that an increasing respiratory burden suppresses the growth rate of large trees, was not supported by experimental data. From the early 1990s on, the hydraulic limitation hypothesis became popular. According to this hypothesis, stomata close because hydraulic conductivity decreases with tree height (not age!). Since then, two lines of argument have challenged the hydraulic limitation hypothesis (Chap. 4 by Kutsch et al.), namely: (1) that trees can adjust their hydraulic architecture and fine-root biomass to compensate for size-related reductions in hydraulic conductivity, and (2) that reduction in growth in old trees might not be driven by supply (i.e. by changes in

carbon assimilation rates) but by demand (i.e. the ability to create carbon sinks through growth).

To what extent these individual-scale responses translate into a stand-level decline in NPP is still subject to debate. The 13 chronosequences presented in the seminal review by Ryan et al. (1997) clearly exhibited an age-related decline at the stand-level, but these even-aged, mostly managed coniferous monocultures are by no means representative of the world's forests. The reviews and new data presented in this book indicate that age-related decline in the productivity of natural stands is not as 'universal' as previously thought. At the time-scale of years to centuries (much shorter than the time-scale of ecosystem retrogression; see Chap. 9 by Wardle), we identified several processes that work against an age-related decline in NPP. These include a stand age-related increase in rooting depth exploring new belowground resources (Chaps. 4 by Kutsch et al., and 7 by Knohl et al.); increased canopy roughness in old forests, leading to more efficient light use and higher rates of transpiration and photosynthesis (Chap. 7 by Knohl et al.); and succession from light-demanding to shade-tolerant species, resulting in increased leaf area index and a change in leaf traits suggesting high net carbon gain per unit leaf investment (Chap. 4 by Kutsch et al.). Finally, if an age-related decline in productivity were such a universal feature, then, according to the equation above, biomass declines should also be common. However, various chapters conclude that late-successional biomass declines are the exception rather than the rule [Chaps. 5 (Wirth and Lichstein), 14 (Lichstein et al.) and 15 (Schulz et al.) – see also below].

The data presented in this book also suggest that physiological processes related to either size or age are probably less important than structural changes. The reanalysis of the Luyssaert dataset (Chap. 4 by Kutsch et al.) revealed only a subtle negative stand age-effect on NPP in coniferous forests and none in deciduous forests. Instead, leaf area index was an important predictor of both aboveground- and total-NPP. This suggests that structural changes reducing leaf display, such as gap formation, lateral crown abrasion or increased leaf clumping in bigger crowns, are more likely candidates for driving age-related decline in NPP (if it occurs). Schulze et al. (Chap. 15) apply the self-thinning rule to identify a minimum stand density below which the productivity cannot be maintained. They argue that productivity and biomass might decline with stand age only because large trees are more susceptible to disturbances than small ones. The above conclusions are in line with more recent assessments by Smith and Long (2001) and Binkley et al. (2002), who interpret a successional decline in productivity as an emergent stand-level property. Taken together, the established term 'age-related decline' is misleading. There are changes in productivity with succession (not necessarily with tree or stand age), some of them with a negative sign. The possible causes of these productivity declines include age- or size-related limitations of tree physiology, changes in canopy structure, trait-shifts due to species turnover, and interactions between succession and site development. The relative importance of factors that increase or decrease productivity as succession proceeds is likely to vary between biomes and forest types.

21.3.2   Are Old-Growth Forests Carbon Neutral?

This question can generally be approached from two directions (Chap. 12 by Reichstein et al.). One can monitor carbon stocks over time in different ecosystem compartments and infer the net ecosystem carbon balance (NECB) (Chapin et al. 2006); or one can directly measure the net exchange fluxes, the integral of which should, in principle, be equal to the net stock changes if temporal and spatial scales are similar (Baldocchi 2003). The first, 'bottom-up', approach is generally based on repeated inventories or chronosequences of biomass, woody detritus and soil carbon, while the second, 'top-down', approach uses the micro-meteorological eddy-covariance technique. Aggregated estimates from these two approaches for different developmental stages are presented in Fig. 21.2. It should be noted that the analyses presented in this book differ from an earlier review by Pregitzer and Euskirchen (2004), who considered dynamics only up to a stand age of 200 years for most pools and fluxes. Their study thus does not allow inferences on processes during the old-growth stage.

Knohl et al. (Chap. 7) and Luyssaert et al. (2008) reviewed the evidence for boreal and temperate forests from 'top-down' eddy covariance studies, and concluded that most old-growth forests (eight out of nine stands older than 200 years) remain carbon sinks. Not only the sign but also the magnitude was surprising (a mean of 130 ± 42 and 257 ± 246 g C m^{-2} year^{-1} for boreal and temperate forests, respectively), suggesting that these stands were far from carbon equilibrium. For mature humid tropical forests, only seven eddy covariance sites (with unknown ages) are available (Luyssaert et al. 2007). Considering upland sites only (six of the seven), the mean net C exchange was 231 ± 249 g C m^{-2} year^{-1}. This suggests that tropical and temperate old-growth forests function similarly as carbon sinks (see also Chap. 17 by Grace and Meir).

Several chapters in this volume also present bottom-up estimates for carbon stock changes in biomass, woody detritus, and soil. These numbers represent component fluxes of the net ecosystem carbon balance. Several lines of evidence

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Fig. 21.2a,b Synthesis of carbon flux estimates based on different approaches presented in the book. **a** Inventory- and model-based estimates: *AGB chrono*, *CWD chrono*, and *SOC chrono* represent changes in carbon stocks in the aboveground biomass, the woody detritus, and soil, respectively, and were calculated from the chronosequence studies presented in Wirth and Lichstein (Chap. 5) and Gleixner et al. (Chap. 11). *AGB FIA* mean estimates of change in aboveground biomass based on the Forest Inventory Assessment of the United States (Lichstein et al. Chap. 14); *AGB model* and *CWD model* estimates from the trait-based carbon succession model in Wirth and Lichstein (Chap. 5); *asterisks* sum of the stock changes in the biomass (mean of chronosequence and FIA estimates), woody detritus, and soil. Two different sums are shown, one excluding the high repeated sampling estimates (*large filled asterisks*) and one including them (*small open asterisks*), in which case the median of the chronosequence and repeated sampling estimates was used. No distinction is made between biomes, but there is a clear dominance of data from the temperate and boreal zone. **b** Comparison of inventory based (bottom-up) estimates of the net ecosystem carbon exchange (*asterisk*) and the estimates from eddy covariance studies in different biomes (Knohl et al. Chap. 7)

Carbon flux (g C m^{-2} yr^{-1})

Pioneer (0–100 yrs) | Transition (101–200 yrs) | Early OG (201–400 yrs) | Late OG (> 400 yrs)

a

b
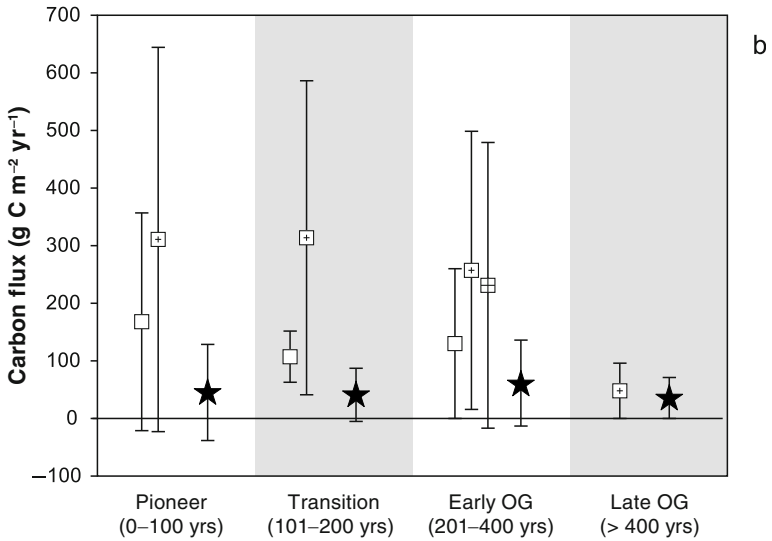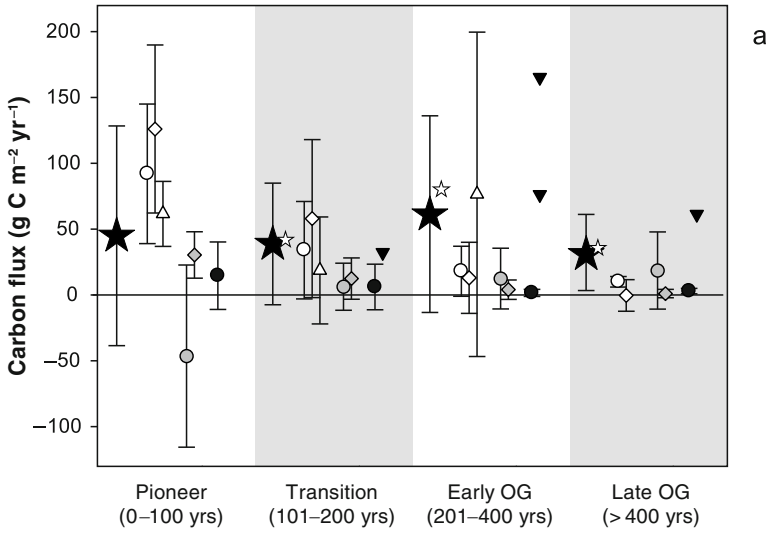
★ ☆ Σ Inventory-based
◇ AGB chronosequence
○ AGB model
△ AGB FIA
◒ CWD chronosequence
◇ CWD model
● SOC chronosequence
▼ SOC resampling

□ Eddy (boreal)
⊞ Eddy (temperate)
⊞ Eddy (tropical)

emanating from an analysis of forest inventories (Chap. 14 by Lichstein et al.), a literature evaluation (Chap. 15 by Schulze et al.), a review of long-term forest chronosequences and a model-data integration based on plant traits and succession descriptions (Chap. 5 by Wirth and Lichstein) suggest that late-successional biomass declines are the exception rather than the rule. The significance of this finding for the ecological theory of secondary forest succession is discussed in Chaps. 5 (Wirth and Lichstein) and 14 (Lichstein et al.). Figure 21.2 shows the mean rates of biomass carbon change [as estimated in Chaps. 5 (Wirth and Lichstein), 14 (Lichstein et al.) and 15 (Schulz et al.)] during progressive stages of succession. Forests in the early old-growth stage (201–400 years) accumulate aboveground biomass carbon at mean rates of between 10 and 30 g C m^{-2} year^{-1} (Fig. 21.2). The four chronosequences containing stands older than 400 years suggest a continued (albeit low) accumulation of about 10 g C m^{-2} year^{-1}.

The temporal course of woody detritus (standing and downed) stocks during secondary succession typically shows a 'reverse-J' or 'U'-shape resulting from an initial decay of legacy woody detritus and the build-up of *de-novo* woody detritus as the stand reaches the old-growth stage (Chap. 8 by Harmon). The long-term (>200 years) woody detritus chronosequences presented in Wirth and Lichstein (Chap. 5) reveal a high variability of stock changes of *de-novo* woody detritus that can be explained partly by climate and the peculiarities of species-specific decay rates. Along the four stages, the mean rates of woody detritus stock-change increased from –46 ± 69 ($n = 14$; pioneer), to 6 ± 18 ($n = 17$; transition), to 12 ± 24 ($n = 14$; early old-growth), to 18 ± 29 g C m^{-2} year^{-1} ($n = 4$; late old-growth) (Fig. 21.2). The chronosequence data show that, during the early old-growth stage, the accumulation rate of woody detritus was slightly lower than the biomass accumulation rate (12 vs 18 g C m^{-2} year^{-1}, respectively), while this trend reverses in the late old-growth phase (18 vs 10 g C m^{-2} year^{-1}). These data indicate that rates of woody detritus and biomass accumulation are of similar magnitude in old-growth forests, and that the relative contribution of woody detritus increases with forest age.

Soil pools are less well defined than biomass and woody detritus pools because of varying depth and definition of horizons. Gleixner et al. (Chap. 11) presented different estimates of changes in soil organic carbon stocks. This included estimates from chronosequences containing stands older than 150 years but also from repeated inventories and carbon balance approaches. Averaging across biomes and different methods, the chronosequence-based accumulation rates during the old-growth phases were in the order of a few grams (1.5 ± 2.7 and 2.8 ± 2.1 g C m^{-2} year^{-1} in the early and late old-growth phases, respectively). In stark contrast, the three old-growth studies using repeated sampling report rates that are higher by a factor of 50, namely, 61, 76, and 165 g C m^{-2} year^{-1} (cf. Table 11.4 in Chap. 11 by Gleixner et al. – see discussion below).

If we add the component fluxes of carbon accumulation in biomass, woody detritus, and soil for each stage (Fig. 21.2, asterisks), we find that our bottom-up estimates of NECB remain remarkably constant over succession. Old-growth forests appear to have the same sink strength as early-successional stands: roughly 40 ± 58 g C m^{-2} year^{-1}. This is true regardless of whether we include the high soil

carbon sequestration rates obtained by repeated sampling (Fig. 21.2, small aster-isks) or exclude them (large asterisks). The higher biomass accumulation rates during the first 100 years are compensated by the decomposition of legacy dead-wood. During the two old-growth stages, a continued accumulation of biomass and an increasing accumulation rate of *de-novo* woody detritus maintain a net carbon sink. The top-down eddy covariance estimates show a similar age pattern of sustained sink activity but at far higher levels (Fig. 21.2b).

What is the nature of this discrepancy? The eddy covariance method is known to overestimate carbon fluxes as it misses lateral advection of carbon dioxide under non-turbulent conditions (Chap. 17 by Grace and Meir). However, the bias intro-duced by this tends to be lower than 30%, and therefore explains only part of the discrepancy (Chap. 7 by Knohl et al.). On the other hand, our bottom-up estimate ignores some pools. We did not include the accumulation of carbon in coarse roots, and, for the most part, soil carbon estimates did not include the forest floor organic layer or deep soil horizons (see below). The chronosequence approach is also blind to the continuous export of dissolved organic carbon in groundwater. There is also a more generic difference: the eddy covariance method quantifies instantaneous fluxes and thus – unlike chronosequence approach – captures high-frequency temporal variability. For example, forest ecosystems that are influenced by recur-ring disturbances (fire, herbivory) are in a permanent state of recovery. Such ecosystems follow a steeper carbon trajectory than suggested by chronosequence fits, which cut through the characteristic saw-tooth pattern of carbon stock changes created by repeated carbon losses and subsequent recovery of pools (Wirth et al. 2002). And, finally, most stands might be forced onto a transient steeper trajectory because of ubiquitous carbon dioxide and nitrogen fertilisation via the atmosphere (Schimel 1995; Mund et al.2002; Vetter et al. 2005). This is difficult to detect using the chronosequence approach since carbon stocks that are compared along the time axis are the result of century-long ecosystem history, most of which was unaffected by contemporary atmospheric changes. The inability of chronosequences to capture transient dynamics might also partly explain the discrepancies in soil carbon storage between the low chronosequence estimates, and the high rates suggested by repeated soil sampling. Irrespective of the nature and extent of the discrepancy, both estimates independently suggest that old-growth forest maintain their capacity to sequester carbon, i.e. they are not carbon neutral. The various bottom-up methods suggest that the continued carbon sink is almost equally distributed between the biomass and the woody detritus. The actual and potential contribution of the soil pool is still unclear (cf. second paragraph in Sect. 21.5.2).

21.3.3   Nutrient Dynamics

Secondary forest succession starts with an exceptionally high availability of nutri-ents (Peet 1992). This is because stand-destroying disturbances result in a large input of necromass to the forest floor that is then rapidly mineralised. In the case of

fire, organic matter is combusted, which further speeds up mineralisation (Neary et al. 1999). Immediately following the disturbance, the amount of live biomass available to reabsorb the nutrients is small, so there will be a short-lived, but high, net loss of nutrients from the system (Bormann and Likens 1979). Next follows a phase where uptake by the recovering biomass exceeds the losses, and nutrient cycles are extremely tight. As the forest approaches the old-growth phase, large individual trees die and losses through decomposition again increase until uptake and losses roughly balance. This classical model of Vitousek and Reiners (1975) predicts that old-growth forests are less efficient in nutrient retention than the preceding stage, which implies that nutrient availability for the remaining trees not subject to further mortality increases. A contrasting scenario is presented by Wardle (Chap. 9), according to which the rates of mineralisation monotonically decline as succession progresses. The processes involved are immobilisation of nutrients in trees and understorey vegetation, a decline in litter quality (cf. Chap. 11 by Gleixner et al.), and a reduction in the activity of soil biota, which jointly lead to additional immobilisation of nutrients in the forest floor. The latter scenario was presented as an alternative mechanism inducing a successional decline in net primary production (Gower et al. 1996). In this context, it is relevant to note that the growth-stimulating hormone cytokinin is produced mainly by the fine-roots and its level depends on the nitrogen availability sensed by these roots (Lambers et al. 1998). Via this signalling, a low availability of nitrogen can partly explain a progressive sink-limitation of growth in old trees.

There is empirical support for both scenarios. Increased 'leakiness' according to the first scenario was found in watershed studies (Vitousek 1977; Bormann and Likens 1979) and is further supported by the observation of nutrient losses even under small root gaps (Chap. 10 by Bauhus – see also Sect. 21.2.3 above). However, recent studies in unpolluted temperate rainforests of South America suggest that old-growth forests do not 'leak' inorganic forms of nitrogen (Chap. 16 by Armesto et al.). Instead, they lose substantial amounts of dissolved organic nitrogen. Whether the trees in old-growth forests can make use of this organic nitrogen in the soil solution either by direct uptake or uptake via mycorrhiza is not clear. It appears that the second scenario (progressive decline in availability) is more commonly realised in boreal forest or on less fertile sites, as exemplified by the island study of Wardle and colleagues (Chap. 9) and the compensatory increase in fine-root biomass with age in coniferous forests (Chap. 10 by Bauhus).

During our symposium, Peter and Mona Høgberg formulated an interesting alternative hypothesis explaining progressive nitrogen limitation in boreal forests, and presented supporting data. They argued that dominant late-successional plants (conifers and ericoid shrubs) actively drive the system to nitrogen limitation 'using' ectomycorrhizal fungi as agents. The plants invest large amounts of their photosynthate in their symbionts, which hence play a particularly important role as nitrogen sinks among the soil biota. Contrary to the conventional assumption, a large share of the nitrogen taken up by these fungi may be locked up in cell wall components of their extensively growing mycelial networks, rather than being passed on to the host plants. This mechanism, and the dominant role played by these fungi, leads to a

condition where those plants that depend on arbuscular mycorrhiza fungi and high nitrogen supply face severe difficulties in becoming established and prospering.

The dynamics discussed so far unfold over the course of several decades to a few centuries and are thus relevant for the time-window most often considered in this book. A longer-term perspective is provided by Wardle (Chap. 9). As forest ecosystems age on the order of thousands of years without major disturbance, phosphorous availability may become the major factor limiting growth and biomass. Unlike carbon and nitrogen, phosphorous cannot be biologically fixed. Losses from the system via leaching or runoff cannot be replenished internally, and external input via dust deposition and sea spray is usually very small. In addition, phosphorus becomes increasingly physically occluded or bound in relatively recalcitrant organic compounds. The consequences, as evidenced by six long-term chronosequences, are increases in plant nitrogen-to-phosphorus ratios, a reduction in total biomass and canopy height, and decline in tree diversity. Belowground changes involve declines in microbial biomass and soil fauna activity and, consequently, lower decomposition rates. Collectively, the six chronosequences show that there is no such thing as a steady-state climax old-growth forest from the long-term perspective.

21.3.4   Consequences of Successional Species Change

Although old-growth forests may by extremely diverse, they do not contain a random sample of tree species. A strong biotic filter selects species that are able to cope with the specific conditions prevailing during the later stages of forest succession. Several chapters in this book compare old-growth tree species with those of earlier successional stages, e.g. with respect to leaf physiology [Chaps. 4 (Kutsch et al.), 6 (Messier et al.) and 17 (Grace and Meir)], nutrient acquisition (Chap. 9 by Wardle) and life history traits [Chaps. 5 (Wirth and Lichstein) and 6 (Messier et al.)]. Typical old-growth species have to be able to germinate in the shade. Their seeds must be large enough to supply enough resources so that the primary roots can penetrate a thick organic layer. Once established, they need to endure long periods of light starvation before a gap opens above them. They do so by maximising light capture, decreasing maintenance and construction costs, avoiding self-shading and efficiently exploiting sun flecks. During this time, they barely grow and stay small. This is a disadvantage in itself, because only by growing can trees escape shading by understorey herbs, browsing, trampling, surface fires, flooding and bending under high snow load. To withstand damage, trees must allocate carbon to chemical defence, structure, and storage. Once a gap opens, they need to mount a rapid growth response. Thus, they must be highly plastic, as fast growth requires completely different attributes than those required for survival in the shade. Once in the canopy, the formerly shaded tree will be fully illuminated. That this may exceed the plasticity limits for some old-growth species was illustrated by a case study for European Beech, which essentially uses the outer shell of leaves as a sunscreen (Chap. 4 by Kutsch et al.). The 'understorey legacy'

might also be reflected by our finding that sun-leaves of old-growth species tended to have higher specific leaf area, lower photosynthetic capacity, and lower dark respiration rates than pioneer species – all typical features of plants in the shade (Chap. 4 by Kutsch et al.).

But how is all this related to old-growth forest functioning? Because of their inherent shade-tolerance, old-growth trees are able to sustain a shade crown and thus can form a dense canopy (Horn 1974; Pacala et al. 1996), allowing them to harvest light more efficiently and profit more from diffuse radiation than typical pioneer species (Chap. 7 by Knohl et al.). Their offspring are able to cope with the low light underneath them and hence can develop a sapling bank ready to fill canopy gaps with new leaf area from below. This ensures an efficient light harvest and prevents a decline in GPP even in the face of gap formation.

There are many successions where the typical old-growth trees grow taller and are longer-lived than their early-successional predecessors and thus can accumulate higher carbon stocks (Chap. 5 by Wirth and Lichstein). Pioneer species, due to their superior colonising ability and/or high-light growth rate, often dominate early in succession, delaying the growth of old-growth species and thus carbon accumulation (Kinzig and Pacala 2001). However, there are also cases where competitive old-growth species are smaller (Chap. 14 by Lichstein et al.) or turn over faster than their predecessors (Schulze et al. 2005). These examples provide support for the 'shifting traits hypothesis' of biomass dynamics developed in Wirth and Lichstein (Chap. 5). The traits reviewed in this book differ more between conifers and broad-leaved trees (hardwoods) than between successional guilds within these groups. A compositional change between conifers and hardwoods therefore has the strongest effect on ecosystem functions. Modelling studies [Chaps. 5 (Wirth and Lichstein) and 8 (Harmon)] and the data presented in Lichstein et al. (Chap. 14) showed that carbon trajectories in both the biomass and woody detritus increase if succession changes from hardwoods to conifers and decreases vice versa. This effect was predicted in Chap. 5 to be most pronounced during the early old-growth phase, which covers stand ages between 201 and 400 years, i.e. the range that applies to most studied old-growth forests. Other processes likely to be affected by a change from deciduous to coniferous cover are stand transpiration and water yield (catchment studies in Chap. 7 by Knohl et al.), litter decomposition (Chap. 9 by Wardle), and NPP (Chap. 4 by Kutsch et al.).

21.3.5 Shapes of Responses

The dominant shapes of stand age-related responses of various ecosystem processes are summarised qualitatively in Fig. 21.3. Response shapes of carbon stocks differ according to compartment. A non-saturating increase with stand age was found to be the dominant shape for the biomass [Chaps. 5 (Wirth and Lichstein), 14 (Lichstein et al.) and 15 (Schulz et al.)] while woody detritus mostly follow a U- or inverse J-shaped trend [Chaps. 5 (Wirth and Lichstein), and 8 (Harmon)]. Soil

Group	Process	1	2	3	4	5	6	7
Diversity	Habitat provision	■ (large)				■ (medium)		
Diversity	Soil heterogeneity					■ (medium)		
Diversity	Tree species diversity	■ (medium)	■ (medium)	■ (large)	■ (small)			
Diversity	Structural diversity	■ (large)				■ (small)		
Resist.	Susceptibility to wind	■ (large)						
Resist.	Resilience to drought	■ (medium)	■ (medium)					
Resource acquisition	Water yield						■ (medium)	■ (medium)
Resource acquisition	Litter quality							■ (large)
Resource acquisition	N to P ratio	■ (large)						
Resource acquisition	Nutrient retention			■ (large)				
Resource acquisition	Light interception	■ (medium)	■ (medium)		■ (medium)			
Fluxes	NECB (Δ Carbon)				■ (large)		■ (small)	
Fluxes	NEE (Eddy covariance)			■ (small)	■ (large)			
Fluxes	NPP		■ (medium)	■ (medium)				
Fluxes	GPP		■ (large)					
Stocks	Soil carbon	■ (medium)	■ (medium)		■ (medium)			
Stocks	Woody detritus	■ (small)	■ (medium)	■ (small)		■ (large)	■ (medium)	
Stocks	Biomass	■ (large)	■ (medium)	■ (small)				

Shape of response / Stand age

Fig. 21.3 Qualitative assignment of age-related response shapes to various ecosystem processes. Ecosystem processes are grouped according to carbon stocks, carbon fluxes, resource acquisition, as well as indicators related to resilience and diversity. *Filled rectangles* Relative frequency of response shapes (*large* dominant, *medium* often, *small* sometimes). The individual response shapes are (from *left* to *right*): non-saturating increase with age; rise to upper asymptote; hump-shaped function, mid-successional peak; no change with stand age; U-shaped function, mid-successional trough; inverse J-shaped decline to lower asymptote; almost linear decline

carbon stocks stay constant or increase continuously with stand age, but hardly ever decrease (Chap. 11 by Gleixner et al.). Carbon fluxes tend to saturate (GPP; Chap. 7 by Knohl et al.), peak or saturate (NPP; Chap. 4 by Kutsch et al.), or stay more or less constant at positive values (NEE: Chap. 7 by Knohl et al.; NECB this chapter). The near constancy of the fluxes related to the overall carbon balance indicates that assimilatory and respiratory fluxes tend to compensate each other but, interestingly, not to the extent that the overall balance would approach zero. The temporal trend in resource acquisition efficiency was highly dependent on the resource. While light interception tends to increase either continuously or rises to a maximum (Chap. 7 by Knohl et al.), nutrient retention is low immediately after disturbance, reaches a mid-successional peak, but then declines again. The latter is reflected over the long-term by a decline in litter quality and an increase in the N:P ratio (Chap. 9 by Wardle et al.). Catchment water yield, which is inversely related to water acquisition (Chap. 7 by Knohl et al.), declines with stand age indicating higher transpiration rates. While resilience to drought increases with age, reflecting an increase in rooting depth (Chap. 7 by Knohl et al.), susceptibility to size-selective disturbances such as wind-throw increases too (Chap. 15 by Schulze et al.). Indicators related to diversity or spatial complexity generally increased with stand age, mostly because of small-scale disturbances and gap-phase dynamics.

21.4   The Fate of Old-Growth Forests Worldwide

21.4.1   Current Status of Old-Growth Forests

Evaluating the current status of old-growth forests is in fact very difficult because old-growth forest *per se* is rarely inventoried. Instead, inventories typically target primary forest[1] or a satellite-derived proxy of it termed 'intact forest'[2] (Chap. 18 by Achard et al.). The only statements we can make are (1) that old-growth forest is unlikely to exist outside primary forests, and (2) that the fraction of old-growth forest inside the primary forests – at least according to its successional definition – depends on the interaction between the longevity of pioneer species and the natural stand-replacing disturbance regime (Chap. 2 by Wirth et al.). Using a simple model, we estimated that the fractional cover of the old-growth stage in primary forests under natural disturbance regimes is about 20% in temperate or boreal coniferous

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[1]According to the FAO, forest of native species, where there are no clearly visible indications of human activities and ecological processes are not significantly disturbed. The definition includes forests of any age and developmental status.

[2]Intact forest areas were originally defined for boreal ecosystems according to the following six criteria (Chap. 18 by Achard et al.): situated within the forest zone; larger than 50,000 ha and with a smallest width of 10 km; containing a contiguous mosaic of natural ecosystems; not fragmented by infrastructure; without signs of significant human transformation; and excluding burnt lands and young tree sites adjacent to infrastructure objects (with 1 km wide buffer zones).

forest, about 60% in temperate deciduous forests, and exceeds 90% in tropical forests (Chap. 2 by Wirth et al.). Using a similar method, Bergeron and Harper (Chap. 13) estimate that 24% of the Canadian boreal forest would be older than 200 years under a historical fire regime. We conclude that old-growth forests have been a common, if not dominant, feature of natural forest landscapes. How does this compare with the current situation on our planet?

According to one bottom-up estimate, the fraction of primary forest in the eastern United States, a region primarily covered by deciduous forest, is about 0.5%, and the fraction of old-growth forests – which is only a subset of the primary forest – accordingly less (Davis 1996). Compared to the estimated 60% old-growth forest cover under a natural disturbance regime (see above), the estimate of something less than 0.5% under the actual disturbance regime illustrates how massive the destruction of old-growth forest has been in this region. In Central Europe, where forests have been cleared for agriculture since the late Neolithic, old-growth forests are almost non-existent outside nature reserves [Chaps. 15 (Schulze et al.) and 19 (Frank et al.)]. Forest scientists working in Europe know that old-growth research sites need to be handpicked. Only in South America can we find temperate forest regions where the fraction of primary forest is still as high as 32% (Chap. 16 by Armesto et al.). One of the biggest threats for the remaining parcels of old-growth forest in Europe, and to some extent in the Unites States, is artificially dense populations of ungulate herbivores such as roe deer or white-tailed deer (Chap. 15 by Schulze et al.). These essentially impede natural regeneration and thus prevent the future development of height-structured stands.

In boreal forests, historic land-use pressure has always been lower than in the temperate zone, mostly for climatic reasons (Chap. 19 by Frank et al.). In Russia, the amount of intact forest increases with increasing adversity for crop production along a continentality gradient from about 9% in European Russia to 39% in Eastern Siberia (Chap. 18 by Achard et al.). The maximum regional rate of deforestation in boreal Eurasia was 0.2% per year in Northern European Russia, with many other regions of Russia exhibiting lower rates. Currently, diffuse, unregulated logging, industrial forest exploitation, and man-made fires (and a combination of all three factors) have made the boreal forest another hot spot for the loss of primary forest.

Of all forest biomes, tropical forests are currently undergoing the fastest transition (Chap. 18 by Achard et al.). Remote sensing revealed that, during the 1990s, the global tropical forest has lost 0.52% per year of its intact area – half of it to non-forest area (deforestation) and the other half to non-intact forest (fragmentation). Another 0.20% per year were visibly affected by humans (degradation) but still qualify as intact. In absolute numbers, these transformations amount to 8.2 million ha – an area of the size of Austria every year. On top of this, 5 million ha year^{-1} of non-intact forest was deforested during the 1990s. Loss and degradation of intact forest were both highest in southeast Asia (0.91% and 0.42%, respectively), followed by Africa (0.43% and 0.21%) and Latin America (0.38% and 0.13%). As in the boreal forest, the agents of destruction were a mix of diffuse logging, industrial forestry, and fire. Moreover, even in areas where the forest structure remains intact, hunting and poaching of large frugivorous animals may lead to the local extinction of those

tree species that depend on these animals as dispersal agents. About 70% of all tropical tree species would be affected (Fenner 2000).

21.4.2 *Politics and the Future of Old-Growth Forests*

Old-growth forests provide important services to human society, many of which are discussed in this book. Destroying old-growth may initially serve individual groups or societies, but it will eventually have a negative impact on humanity as a whole. The two services provided by old-growth forests that we probably depend on most, now and for future generations, are (1) their capacity to host biodiversity, e.g. as a resource for medical and biotechnological research and tourism; and (2) their function as a stable carbon reservoir that plays a key role in regulating CO_2, the most important greenhouse gas (Körner 2003). The importance of these two services is reflected in the existence of two conventions of the United Nations (UN), the Convention on Biological Diversity (CBD) and the UN Framework Convention on Climate Change (UNFCCC), but only the former explicitly recognises the pivotal role of old-growth forests therein (Chap. 20 by Freibauer). The Kyoto Protocol of the UNFCCC refers only to managed forests, and it is left to the individual member state to define what 'managed' means. In simple terms, only if hunting or berry picking were considered management would some of the old-growth forest be included by the Kyoto Protocol's accounting schemes (Articles 3.3 and 3.4, cf. Chap. 20 by Freibauer).

This focus on managed forests goes back to Odum's (1969) ecosystem theory, according to which old-growth forests are supposed to be carbon neutral. This implies that humans cannot use old-growth forests to sequester carbon, which in turn implies that there is no reason for carbon accounting schemes to consider old-growth. This logic has far-reaching consequences. Irrespective of whether Odum was right or wrong (he probably was wrong – see Sect. 21.3.2 above), our book has shown that old-growth forests generally lock up more carbon than any other forest stage or alternative ecosystem. Thus, converting old-growth forest will inevitably induce emission of greenhouse gases to the atmosphere. If old-growth forests were included under 'managed' forests, these emissions would need to be reported – an unattractive prospect for those countries whose economies depend on the exploitation of primary forests of which old-growth forests are an important component.

The loopholes and perverse incentives created under the current Kyoto Protocol (Schulze et al. 2002) have initiated the development of a new mechanism: REDD (reducing emissions from deforestation and degradation in developing countries), with the goal of providing a more 'holistic' carbon accounting and, especially, to reward the protection of primary forests. Achard et al. (Chap. 18) outline a possible implementation that includes the following components: (1) the quantification of transitions between well-defined land-cover classes (such as intact and non-intact forests) that can be easily detected from space; (2) the local estimation of carbon stocks in each land-cover class, which is needed to quantify regional carbon stock

changes following class transitions; and (3) the quantification of emissions for the baseline period between 1990 and 2005 in order to reward countries that reduce their emissions relative to this period. Freibauer (Chap. 20) emphasises the strong synergies of the REDD mechanism with the CBD and is moderately optimistic that future negotiations will lead to the inclusion of incentives to protect old-growth forests. However, international treaties cannot enforce concrete conservation projects at the local scale. Countries have to develop their own conservation strategies, and this requires an open process of discussion between stakeholders, government, local authorities, and scientists. A successful example – the establishment of the Cape Horn Biosphere Reserve – is presented in Armesto et al. (Chap. 16).

21.5   Research Needs

Because of the many challenges involved in carrying out ecosystem research in old-growth forests, our understanding of the functioning of these systems is still limited. In the following, I identify key areas for future research:

21.5.1   Methods

- *Detection* Old-growth forests are disappearing at a fast pace and there is an urgent need to quantify how much is still left. Modern remote-sensing techniques based on optical sensors have been devised to differentiate between intact and non-intact forest, but the detection of 'old-growth' forest per se within the matrix of intact forest is still in its infancy. These techniques need to be complemented with new methods based on radar and LIDAR remote sensing in order to confidently identify old-growth forest from space.
- *Age Determination* Estimating the age since stand initiation in old-growth forests is a difficult task (Chap. 2 by Wirth et al.), and many chronosequence studies assign arbitrary high ages to old-growth forests or simply refer to them as a separate category. However, without a proper age determination of old-growth forest, the age-related shape of functional responses during the old-growth stage cannot be characterised. Clearly, more effort is needed, employing a wider array of methods such ^{14}C-dating of charcoal layers, historical reconstructions, age-determination of witness trees, etc.
- *Chronosequences* The chronosequence approach is a valuable tool with which to understand the age dynamics of structure, fluxes, and matter pools. However, only very few forest chronosequences consider all (or even the majority of) ecosystem pools (biomass, woody detritus, forest floor, soil), and hardly any study both biomass and nutrient pools. Surprisingly, there are currently fewer comprehensive chronosequences than eddy covariance sites, although the latter are expensive and difficult to maintain. The ideal situation, namely eddy covariance

towers, repeated inventories and a complete carbon inventory in stands forming a chronosequence has so far not been realised. Harmon (Chap. 8) makes a number of suggestions on how to improve chronosequences studies, with an emphasis on deadwood dynamics.

- *Repeated Soil Sampling* Currently, only four studies have followed soil carbon stock changes over time using repeated sampling schemes. There is an urgent need for more such studies in a larger variety of forest ecosystems. This method has great advantages over chronosequence studies: by appropriate stratification, it allows identification of the location of carbon storage or loss both vertically across the soil profile and horizontally between different microsites such as gaps and non-gap areas.

- *National Inventories* Many countries carry out regular inventories that – at least in some countries – also contain information on woody detritus stocks and understorey vegetation. This source of information is still underexplored and may provide a more spatially representative picture of old-growth occurrence, structure, and functioning.

- *Molecular Studies* An important topic not sufficiently reviewed in this book is the pivotal role played by microbial communities and other soil biota in matter cycling, organic matter stabilisation, and redistribution of resources in old-growth forests. This topic certainly needs more attention. Understanding the role of microbial communities in old-growth forest functioning will require the application of modern molecular methods that are able to identify organisms and determine their quantity and activity status. Suitable methods include phospholipid fatty acid (PFLA) profiling (Vestal and White 1989), genetic fingerprinting (Renker et al. 2003), proteomics (Schulze et al. 2005), and screening with metagenomic libraries (Daniel 2005). The latter technique is certainly the most powerful tool, but the development of libraries needs to be tailored to the study system and is extremely laborious.

- *Canopy Access* Cranes and other means of accessing the canopy have proven to be particularly important, not only to study the biota in tree crowns but also to carry out micrometeorological, biometric, and ecophysiological measurements in trees and epiphytes. More such facilities are needed in a wider range of forest types and biomes.

21.5.2   Knowledge Gaps

- What are the functional consequences of the 'matter concentration effect' in and under large woody detritus? Does it have the potential to induce a priming effect, thus speeding up decomposition? Are woody detritus logs hotspots of nutrient leaching, or can mycorrhizal networks effectively redistribute and homogenise the resources?

- Our knowledge of the mechanisms of soil carbon stabilisation and accumulation is still very limited. If soil carbon stabilisation hinges on the availability of binding sites on mineral surfaces, the sequestration capacity of soils is intrinsically limited and will decline with progressive weathering. If it depends on the formation of recalcitrant compounds, there is no theoretical limit, and old-growth forest could accumulate carbon as long as they persist. Furthermore, the origin of the 'recalcitrant' material is not known. It may be indecomposable residuals from incoming litter (classical view), newly formed material derived from microbial cell walls (cf. Chap. 11 by Gleixner et al.), or non-recalcitrant material transferred to deeper soil layers with low densities of decomposers. Reichstein et al. (Chap. 12) make suggestions for future experiments with the potential to differentiate between these mechanisms.
- After decades of dedicated research, we still do not know why growth rates of individual trees eventually decline. Is it because of hydraulic limitation of photosynthesis (size-related), a genetic program (age-related), or progressive nutrient limitation inducing a plant-internal sink limitation of growth (ecosystem-related)?
- Under which conditions do we expect a successional decline in NPP in natural forest ecosystems? If there is a decline, is it because of declining growth rates (see previous question), changes in canopy structure related to population turnover and tree stature, or depletion of soil nutrients (i.e. ecosystem retrogression)?
- The temporal changes reviewed in this book (biomass, productivity, woody detritus, soil carbon, nutrient ratios etc.) exhibit high between-site variability in magnitude and direction. Rather than searching for 'universal patterns,' we need to embrace the diversity of phenomena and work towards a theoretical framework that allows the contribution of different processes (population and community dynamics, biogeochemical feedbacks, above-/belowground linkages) to vary with site conditions, external forcing, disturbance regimes, and the composition and diversity of the regional species pool.
- Are old-growth forests leakier for water and dissolved compounds than earlier successional stages? What is the fraction of gaps below which the efficiency of nutrient retention declines? We still know very little about the extent, duration, and ecosystem effects of root gaps. Are root gaps just coarse root gaps, while the fine-root carpet and the mycorrhizal network remain more or less intact? If so, why does root gap formation increase leakiness? Which elements and compounds are lost and which are retained? Are the pronounced differences in the composition of leachates between southern and northern hemisphere old-growth forests (Chap. 16 by Armesto et al.) an idiosyncratic feature of the two regions or driven purely by differences in nitrogen deposition?

- We know a lot about how the occurrence of animal communities and endangered species relate to the specific habitat features of old-growth forest, but we need to know more about how these animal communities – by virtue of their diversity and/or identity – feed back to the functioning of the system.
- How much carbon is stored in old-growth forests and how much of it is lost if old-growth forest are degraded or converted to alternate land uses? Putting numbers to the various old-growth forest across the world is crucial for the application of the REDD mechanism aimed at rewarding avoided deforestation (Chap. 18 by Achard et al.).
- Even if we manage to set aside large parcels of old-growth forest, how responsive will they be to continuous external forcings such as global warming, changes in precipitation regimes, CO_2 and nitrogen fertilisation, and invasive species? Does their higher organismic, structural, and ontogenetic diversity increase their resilience, or does their complex canopy structure, and thus higher contact surface with the atmosphere, induce a stronger coupling with external forcings?
- Can we use old-growth forests sustainably? What is the threshold for acceptable disturbance and management impacts below which the essential features of old-growth forest functioning are maintained? Along the same lines, what are the population densities of ungulate herbivores that allow quasi-natural stand dynamics?
- To what extent can the findings in this book be transferred to old-growth forests in more arid systems, such as Miombo and Mediterranean forests?

21.6   Overall summary

The contributions in this book have explored many (but certainly not all) aspects of old-growth forest functioning. Our main findings can be summarised as follows:

- *Structural Complexity* We identified several processes that are influenced by the characteristic structural features of old-growth forests (e.g. tall stature and high horizontal and vertical heterogeneity). Old-growth forest structure is likely to enhance radiation inter-ception, resilience of productivity to drought stress (Chap. 7 by Knohl et al.), leakiness for nutrients (Chap. 10 by Bauhus), the local concentration of nutrients (this chapter), and the provision of habitat for plants and animals (Chap. 19 by Frank et al.).
- *Carbon Cycle* Up to an age of 600 years, old-growth forests remain carbon sinks and exhibit the same carbon sink strength as younger developmental stages. The size of the estimated sink varies between 40 and 300 g C m^{-2} $year^{-1}$, with the eddy-flux method yielding higher estimates than ground-based inventories.

Because the estimates are all positive, old-growth forests do not appear to be carbon neutral (cf. Odum 1969). The carbon sink is controlled mainly by the dynamics of biomass and woody detritus pools [Chaps. 5 (Wirth and Lichstein), 8 (Harmon), 14 (Lichstein et al.)]. Estimates of the carbon accumulation rate in mineral soil differ. Chronosequence studies suggest low rates ($\sim$1–5 g C m^{-2} year^{-1}), whereas repeated sampling studies yield far higher rates ($\sim$60 g C m^{-2} year^{-1}). Deep soil layers have been largely ignored but may play a crucial role in carbon sequestration (Chap. 11 by Gleixner et al.). Recent advances in theory suggest that forest soil carbon does not necessarily equilibrate (as previously thought) and may accumulate carbon indefinitely, but decisive data differentiating between the proposed alternative mechanisms are currently not available (Chap. 12 by Reichstein et al.).

- *Productivity* A successional decline in NPP is not a 'universal feature' of natural forests, and we identified several processes that work against successional decline. Changes in stand-level productivity are more closely related to changes in canopy structure than to age per se [Chap. 4 (Kutsch et al.) and 15 (Schulze et al.)].

- *The Imprint of Succession* Old-growth forests harbour a specific set of tree species (Chap. 6 by Messier et al.) and it often takes a long time to establish typical old-growth communities. In most old-growth forests studied to date, this process is not yet complete, and functions such as nutrient cycling, productivity, biomass and woody detritus accumulation are still influenced by changes in species composition and associated changes in functional tree traits [Chaps. 4 (Kutsch et al.), 5 (Wirth and Lichstein) and 9 (Wardle)].

- *Retrogression* There is evidence from all major biomes that forests undergo ecosystem retrogression over timescales of millennia. This is caused by a progressive loss and immobilisation of phosphorous and other nutrients that cannot be fixed biologically. The consequences are a reduction in total biomass and canopy height and a decline in tree diversity (Chap. 9 by Wardle).

- *Extent* Old-growth forests characterised by gap phase dynamics have been a common feature in natural forest landscapes comprising between 20 and 90% of the forest cover (Chap. 2 by Wirth et al.). This is in stark contrast with their current extent in the temperate region, which is below 0.5%. Current rates of old-growth forest destruction are alarmingly high in the tropics and also in some boreal regions.

- *Outreach* Ecological theory, namely the assertion of equilibrium behaviour and carbon neutrality in old-growth forests (Odum 1969), had a profound influence on the formulation of the Kyoto-Protocol, with negative consequences for old-growth forest protection (Chap. 20 by Freibauer). However unfortunate this is, it proves that political decisions are influenced by scientific ideas. It is one of the aims of this book to provide a refined and more comprehensive picture of the functioning of old-growth forests that shall serve as an additional basis for future political decisions.

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Abbreviations and Glossary[a]

AGB	Aboveground live tree biomass including stem, branch, foliage and fruit biomass
A_{max}	Photosynthetic capacity at light saturation level
AVHRR	Advanced very high resolution radiometer; space-borne sensor installed on the National Oceanic and Atmospheric Administration (NOAA) family of polar orbiting platforms
C/N	Carbon to nitrogen ratio
CBD	Convention on Biological Diversity; an international treaty adopted in Rio de Janeiro in June 1992 with the goals of conserving biological diversity and promoting its sustainable use
COP	Conference of Parties of the United Nation Framework Convention on Climate Change
CWD	Coarse woody detritus; dead trees left standing or fallen bigger than a certain diameter threshold in the order of 3–7 cm
dbh	Tree diameter at breast height (1.3 m)
ENVISAT	Environmental Satellite; an earth-observing satellite built by the European Space Agency
EU-15	Number of member countries in the European Union prior to the accession of ten candidate countries on 1 May 2004
FAO	Food and Agriculture Organisation of the United Nations
FAO FRA	FAO Global Forest Resources Assessment published in 2000
FCPF	Forest Carbon Partnership Facility; a facility of the World Bank that assists developing countries in their efforts to reduce emissions from deforestation and land degradation (REDD)
FIA	Forest Inventory and Analysis program run by the USDA Forest Service of the United States
FWD	Fine woody detritus; dead woody material smaller than a certain diameter threshold in the order of 3–7 cm
GHG	Greenhouse gas
GLC-2000	Global Land-Cover 2000 project coordinated by the Joint Research Center in Ispra with the goal of providing a harmonised land cover database over the whole globe for the year 2000

[a]Excluding symbols that were exclusively used in mathematical equations

GPP   Gross primary productivity, i.e. net photosynthesis at the ecosystem scale
g_s Stomatal conductance for water and CO_2
HLH   Hydraulic limitation hypothesis, according to which tree productivity is limited by a reduced stomatal conductivity as trees grow taller and path resistance and the gravitational potential increase
H_{max} Maximum tree height under normal conditions (as opposed to extreme height, i.e. the tallest tree ever measured)
ICBM   Introductory carbon balance model
IFL   Intact forest landscape; a territory within the forest zone that contains forest and non-forest ecosystems minimally disturbed by human economic activity, with an area of at least 500 km^2 and with a minimal width (diameter of the inscribed circle) of 10 km
IPCC   Intergovernmental Panel on Climate Change; a scientific body set up by the World Meteorological Organisation (WMO) and by the United Nations Environment Programme (UNEP) with the goal of providing decision-makers and others interested in climate change with an objective source of information about climate change
J_a Maximum electron transport capacity of photosynthesis expressed on a leaf area basis
k   Decomposition rate-constant (k)
K_L Whole tree hydraulic conductance to water flow through the xylem vessels
LAI   Leaf area index; ratio of total upper leaf surface of vegetation divided by the surface area of the land on which the vegetation grows
LMA   Leaf mass per unit leaf area
LMR   Leaf mass ratio: leaf biomass per total tree biomass
MCPFE   Ministerial Conference on the Protection of Forests in Europe
MODIS   Moderate resolution imaging spectroradiometer; an instrument aboard the Terra and Aqua satellites viewing the entire Earth's surface every 1–2 days, acquiring data in 36 spectral bands
NBP   Net biome productivity; gross primary productivity (net ecosystem photosynthesis) minus respiratory losses (heterotrophic and autotrophic) and carbon losses bypassing respiration (fire, harvest, DOC export)
NECB   Net ecosystem carbon balance; temporal derivative of all ecosystem carbon stocks; conceptually identical to NBP
NEE   Net ecosystem exchange between the land and the atmosphere as quantified by eddy covariance methodology
NEP   Net ecosystem production; gross primary productivity (net ecosystem photosynthesis) minus autotrophic and heterotrophic respiration
NGO   Non-governmental organisation

NPP	Net primary production; gross primary productivity (net ecosystem photosynthesis) minus autotrophic respiration; equivalent to plant biomass increment plus detritus production (litterfall, root turnover, whole-plant mortality)
PEBLDS	Pan-European Biological and Landscape Diversity Strategy; an initiative endorsed by the 3rd Ministerial Conference in 1995 with the goal of halting the degradation of biological and landscape diversity
PPFD	Photosynthetic photon flux density; measure of the availability of light at wavelengths relevant for photosynthesis
Q_{10}	Temperature coefficient; a measure of the rate of change of a biological or chemical system as a consequence of increasing the temperature by $10°C$
R_d	Dark respiration (i.e. excluding photorespiration)
REDD	Mechanism for positive incentives to reduce emissions from deforestation and degradation in developing nations
RGR	Relative growth rates, i.e. change in biomass during time interval $t + \Delta t$ divided by biomass at time t
SLA	Specific leaf area; leaf area per unit leaf mass
SRL	Specific root length, i.e. root length divided by root mass
TNC	Total non-structural carbohydrates; this involves storage carbohydrates such as starch but also low molecular metabolites such as e.g. saccharose and glucose
UNFCCC	United Nations Framework Convention on Climate Change; international treaty with the goal of reducing global warming and coping with whatever temperature increases are inevitable; this treaty has so far been ratified by 192 countries
UNFF	UN Forest Focus; an international policy forum to promote management, conservation and sustainable use of all types of forests
VAZ	Xanthophyll (violaxanthin + antheraxanthin + zeaxanthin, henceforth "VAZ"); accessory pigments (carotenoids) involved in the xanthophyll cycle that operates to protect photosystems from photoinhibition (non-photochemical quenching)
WWF	World Wide Fund For Nature
Ψleaf	Leaf water potential; the potential energy of water relative to pure water in reference conditions; this quantifies the tendency of water to move from one area to another due to various forces such as osmosis, gravity, pressure gradients or matrix effects such as surface tension
Ψsoil	Soil water potential; explanation see Ψleaf

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