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

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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

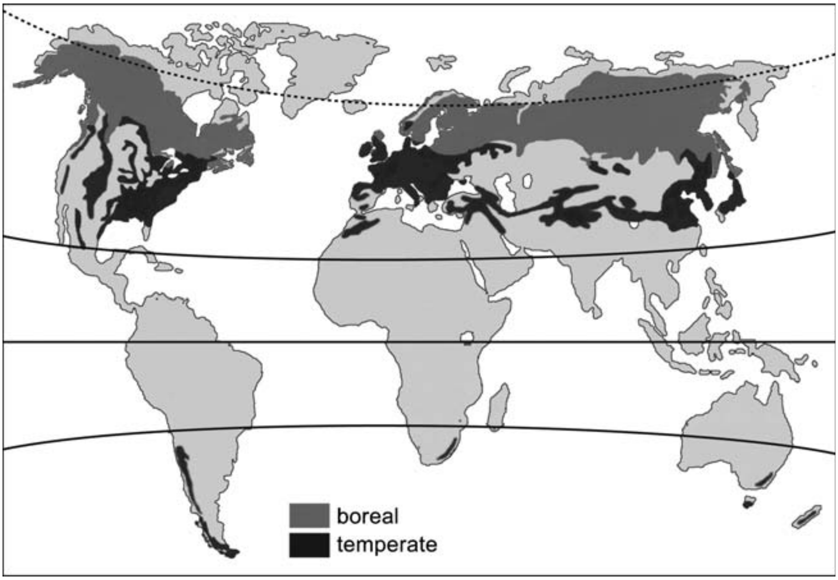

Fig. 15.1 Global distribution of temperate and boreal forests (after Sitte et al. 2005)

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

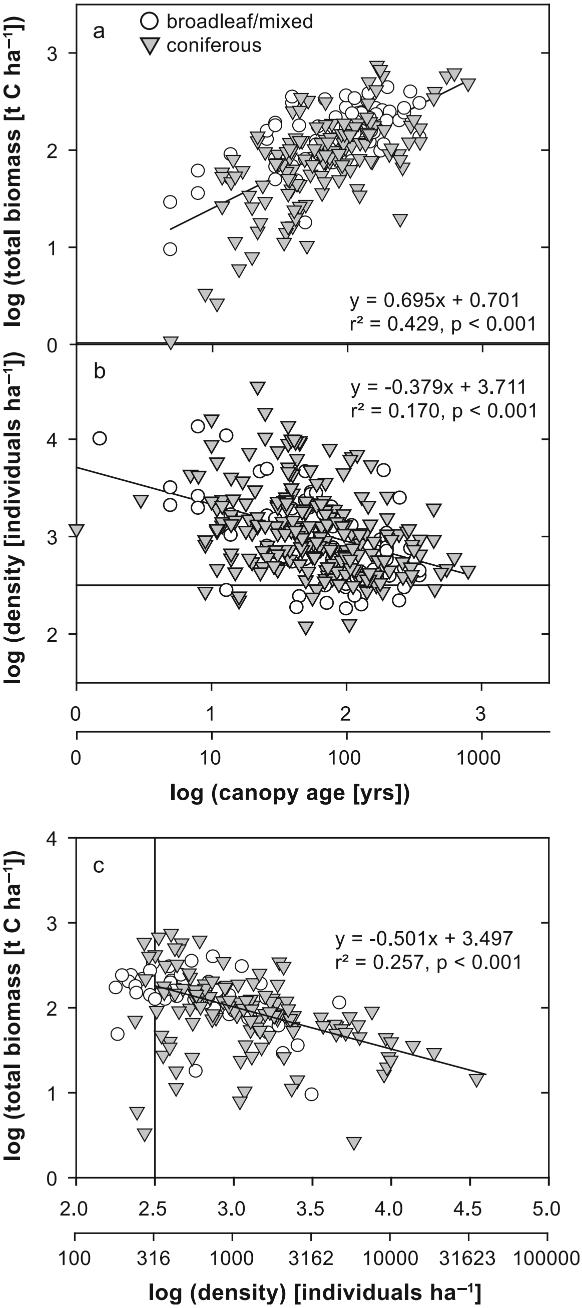

Fig. 15.2 **a** Total biomass accumulation and **b** stand density in temperate and boreal forests as related to the age of the emergent trees of the main canopy. The data show that low stand density is not restricted to old-growth forests, but can be found in all age classes. The *horizontal line* in **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

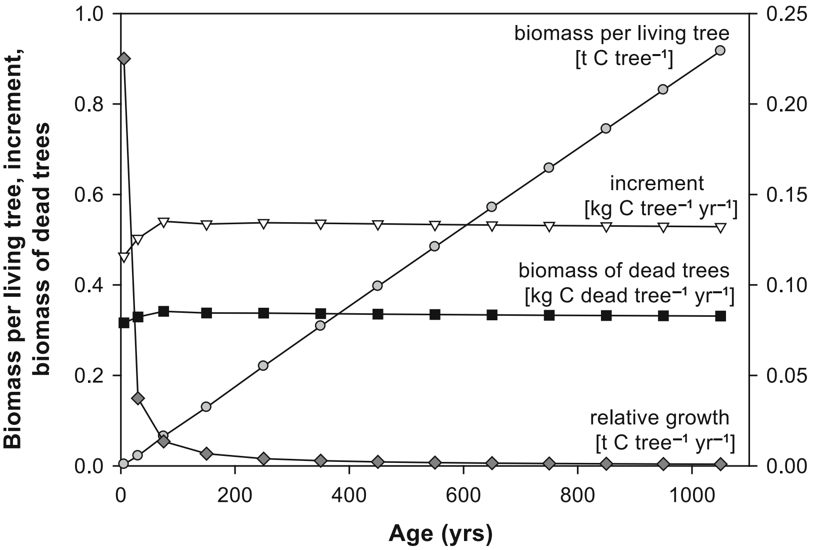

Fig. 15.3 Tree biomass and growth, tree mortality, and relative growth rates as related to stand age. The curves were calculated from the biomass and density relations shown in Fig. 15.2

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 respirationR_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

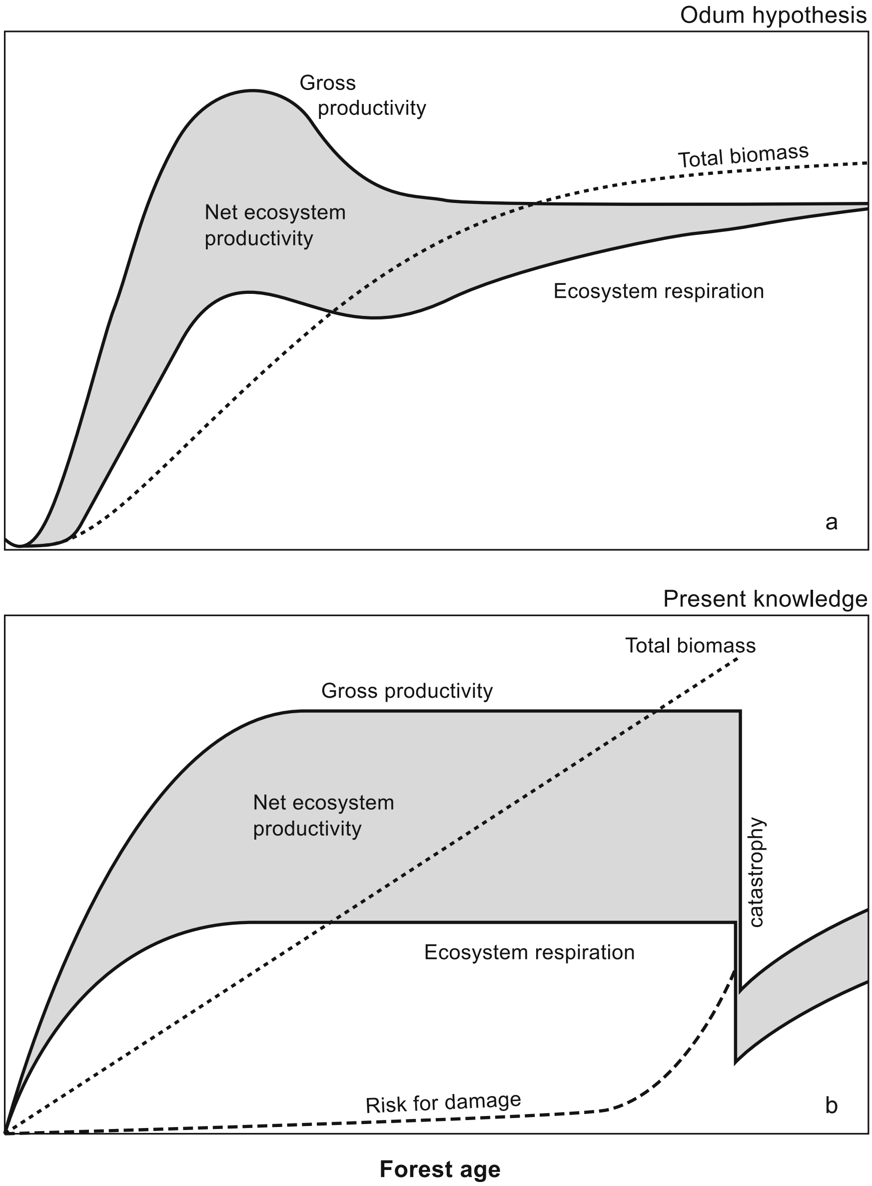

Fig. 15.4 **a** Schematic presentation of gross primary productivity, ecosystem respiration, net primary productivity and stand biomass as a function of forest age according to Kira and Shidei (1967) and Odum (1969, redrawn from Carey et al. 2001). **b** Proposed age dependency of gross primary production, 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

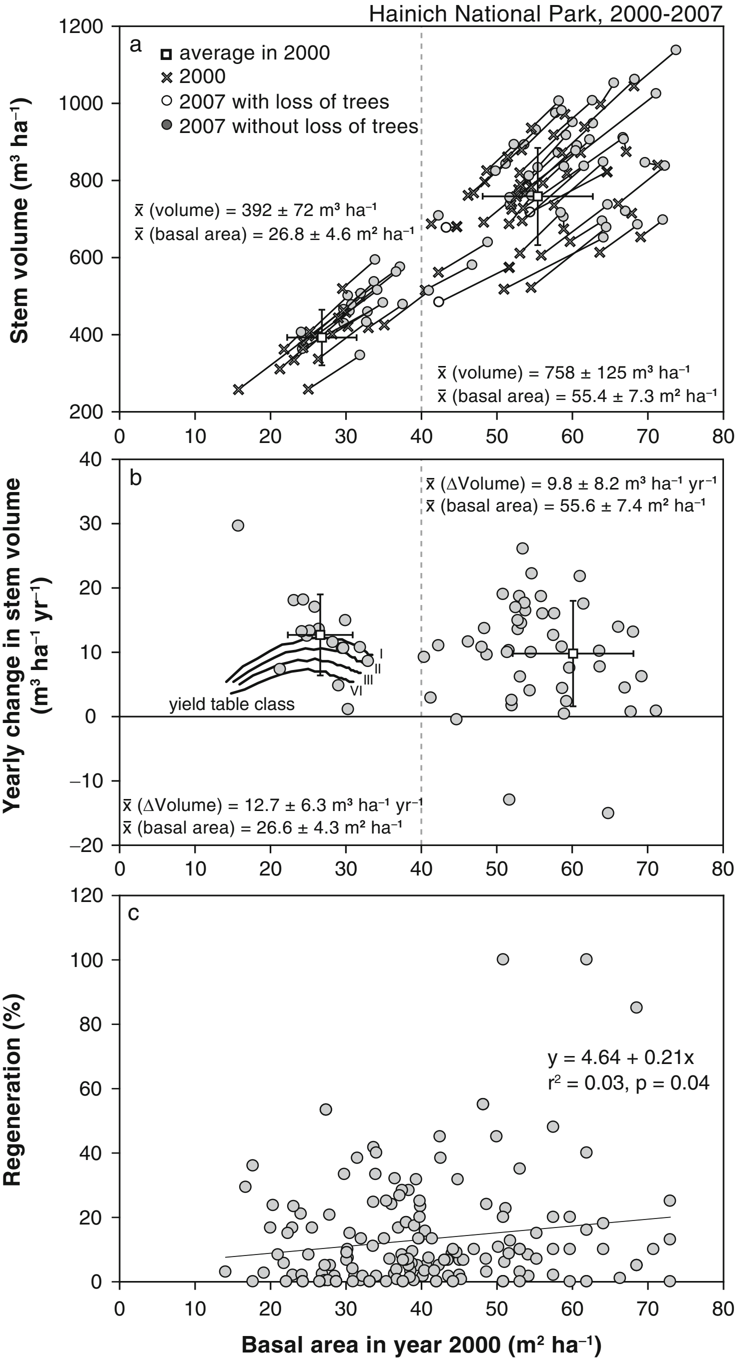

Fig. 15.5 **a** Stem volume as related to basal area on several plots of a repeated inventory of the Hainich National Park, Germany. The inventories were made in the years 2000 and 2007. **b** Annual change in stem volume between 2000 and 2007 as related to basal area in 2000. Negative

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 $9.3 \pm 0.6\ \mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{year}^{-1}$.

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)

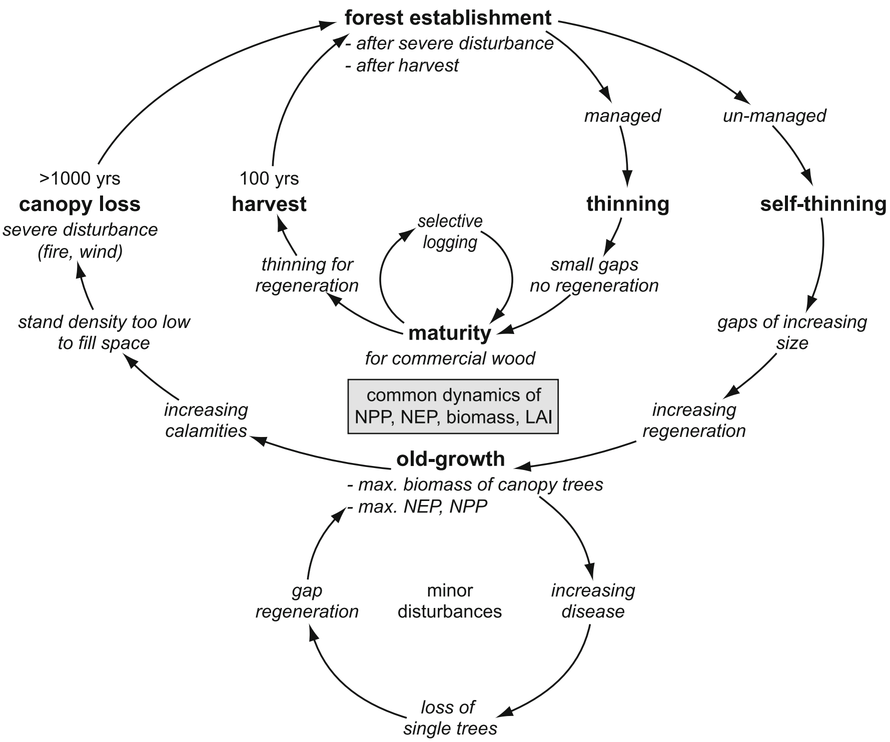

Fig. 15.6 Conceptual scheme of processes that affect biomass and turnover in managed and unmanaged forests

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

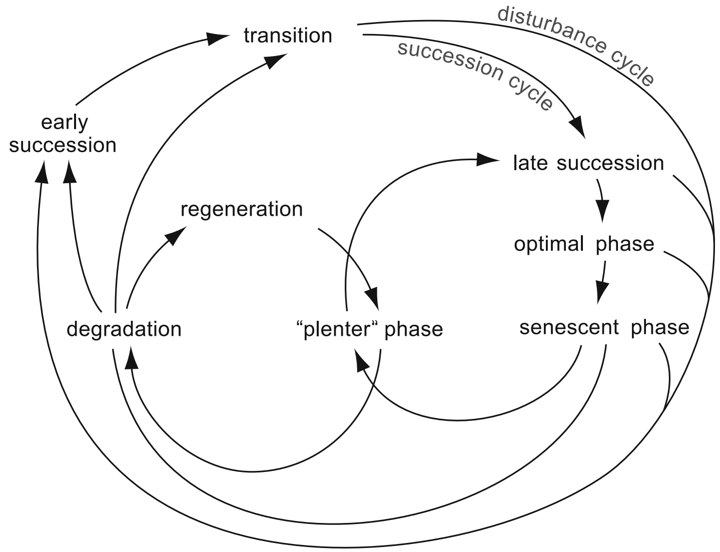

Fig. 15.7 Stages of natural forest succession in primary forests without and with disturbances (after Scherzinger 1996)

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

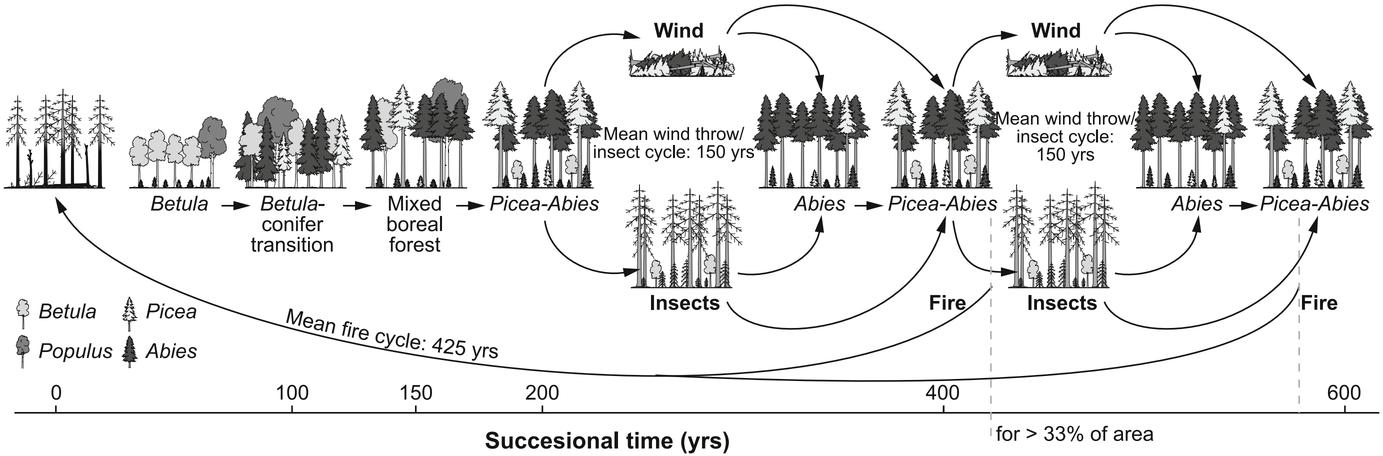

Fig. 15.8 Succession in a *Picea*- and *Abies*-dominated dark Taiga of central Siberia (Schulze et al. 2005b)

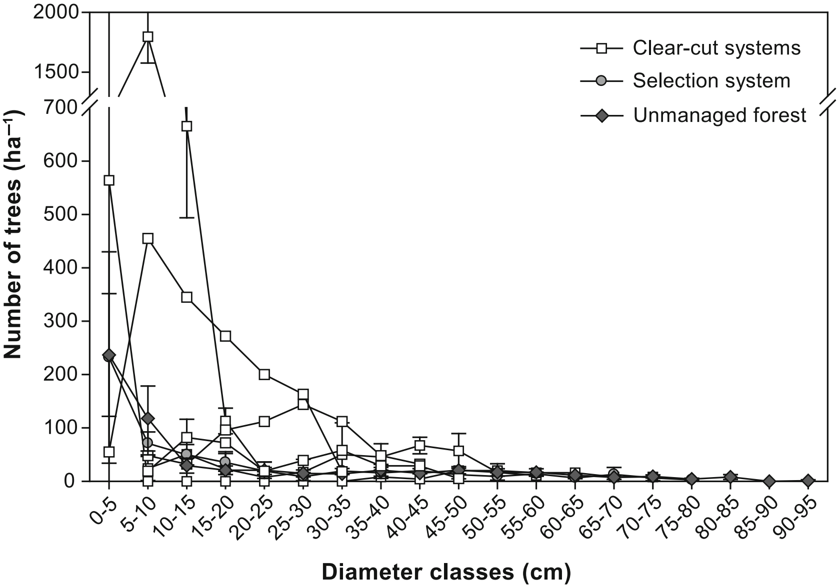

Fig. 15.9 Number of trees belonging to different breast height diameter classes in forests of different management. The unmanaged forest and the selection system contain all diameter classes within the same stand at almost equal numbers. In contrast, the shelterwood system exhibits cohorts of diameter 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 windthrow 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 ($497 \pm 16\ \mathrm{m}^3\ \mathrm{ha}^{-1}$) in the unmanaged Hainich NP forest than in selectively harvested forest ($409 \pm 21\ \mathrm{m}^3\ \mathrm{ha}^{-1}$) (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

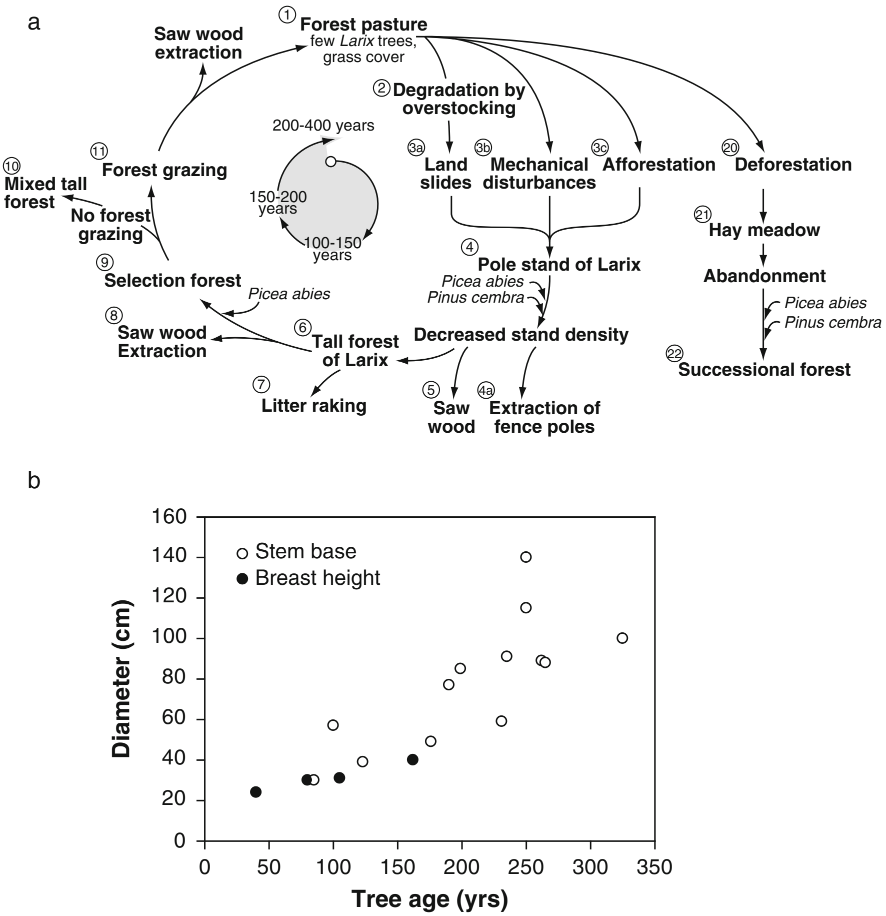

Fig. 15.10 **a** Succession and land use of *Larix*forests. The *numbers* refer to specific properties in the study region where these stages can be observed. **b** Diameter of trees as related to tree age during the course of a successional cycle (after Schulze et al. 2007)

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

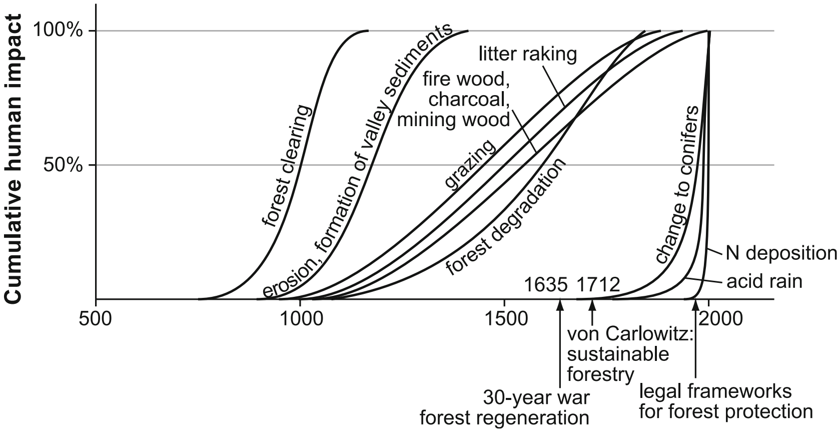

Fig. 15.11 Anthropogenic effects on forest ecosystems over time in Europe (after WBGU 1997). The *y*-axis scales the relative effect of each type of disturbance during the time it was operating, e.g. forest clearing terminated about in the year 1200. The change towards conifers started after 1700 and 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

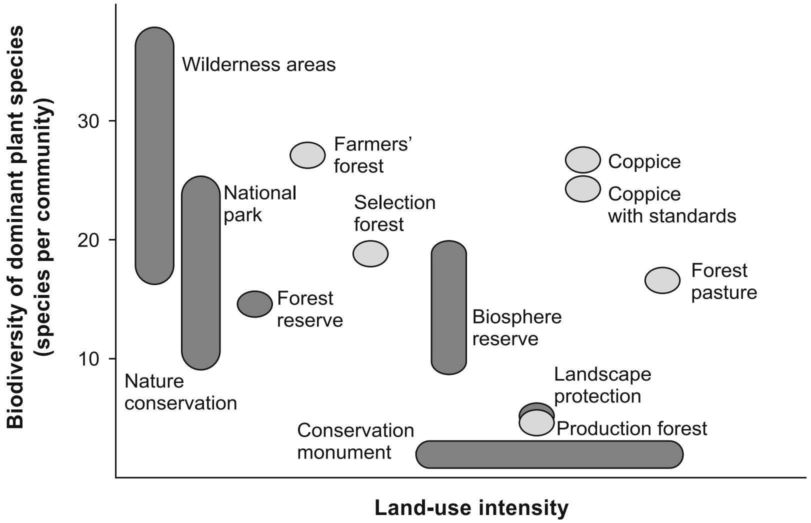

Fig. 15.12 Plant biodiversity of forest systems as related to management-intensity in central Europe. *Dark grey symbols* Forest types under nature conservation: *Wilderness areas* regions without management in historic times (only remnants exist, e.g. Rotwald in Austria); *Natural Parks* presently under 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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