

# Chapter 11

## Soil Carbon Accumulation in Old-Growth Forests

Gerd Gleixner, Cindy Tefs, Albrecht Jordan,  
Matthias Hammer, Christian Wirth, Angela Nueske,  
Alexander Telz, Uwe E. Schmidt, and Stephan Glatzel

### 11.1 Introduction

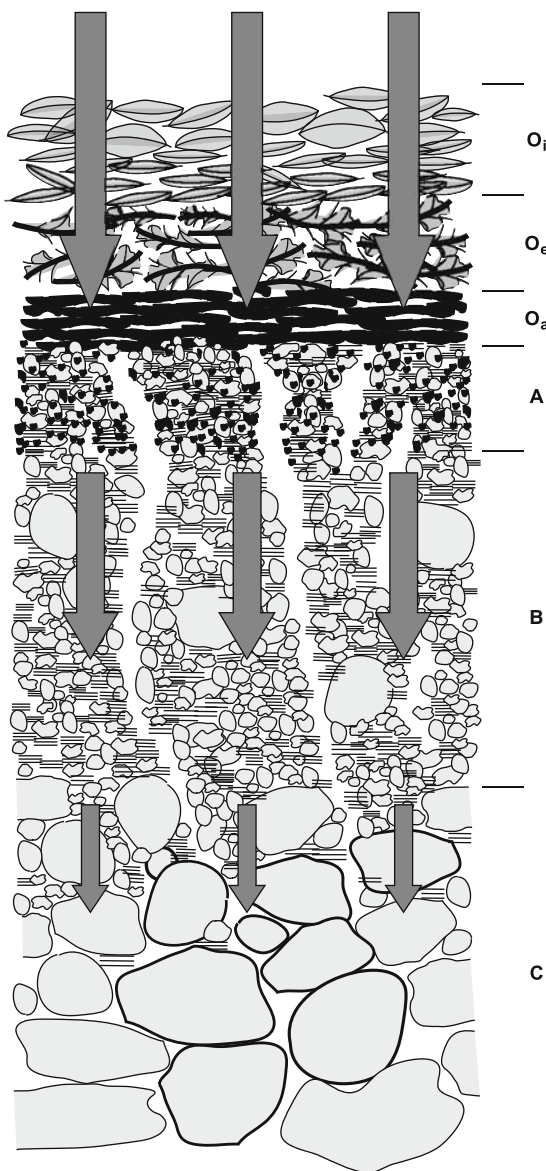
An area of 4.1 billion ha land is covered with boreal, temperate and tropical forest, together comprising up to 80% of the terrestrial aboveground carbon and 40% of total soil carbon (Dixon et al. 1994; Pregitzer and Euskirchen 2004). Forest ecosystems are well studied, mainly because of their importance 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

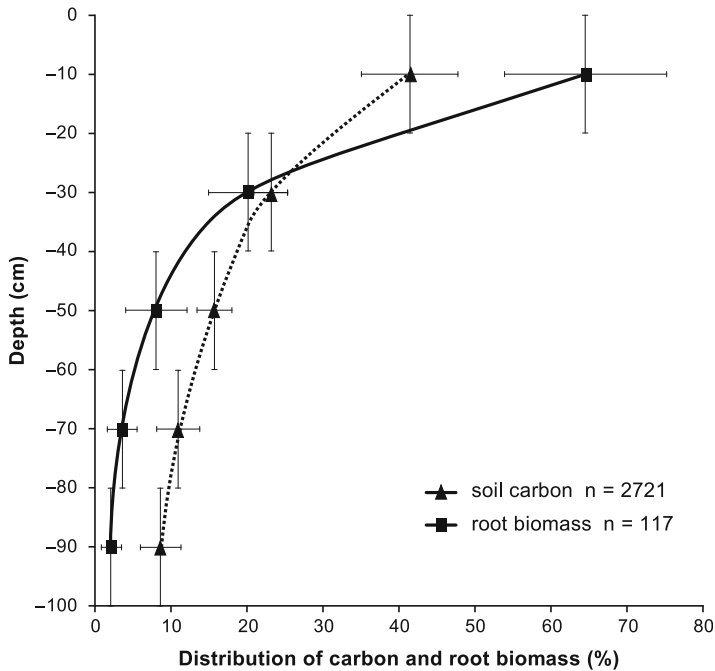
late Pleistocene, mainly lower plants such as lichens and mosses produce these reduced carbonaceous compounds and add them to the bare surface. As a consequence, surface rocks are biologically weathered and nutrients for plant growth are provided (Barker and Banfield 1996). First, soil organic matter (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



**Fig. 11.1** Terminology of soil horizons in a depth profile. *O<sub>i</sub>*, *O<sub>e</sub>* and *O<sub>a</sub>* 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<sub>2</sub>. 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.

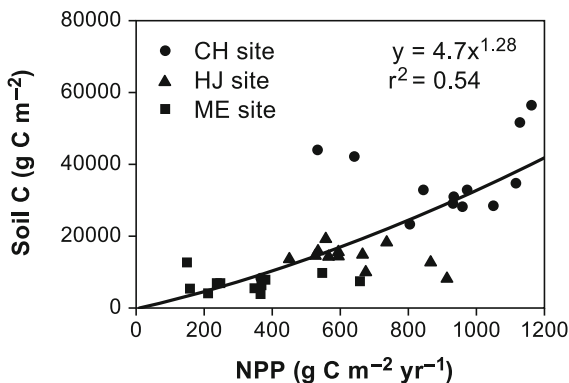
## 11.3 Soil Carbon Storage in Old-Growth Forests

### 11.3.1 Effects of Quantity and Quality of Input Material

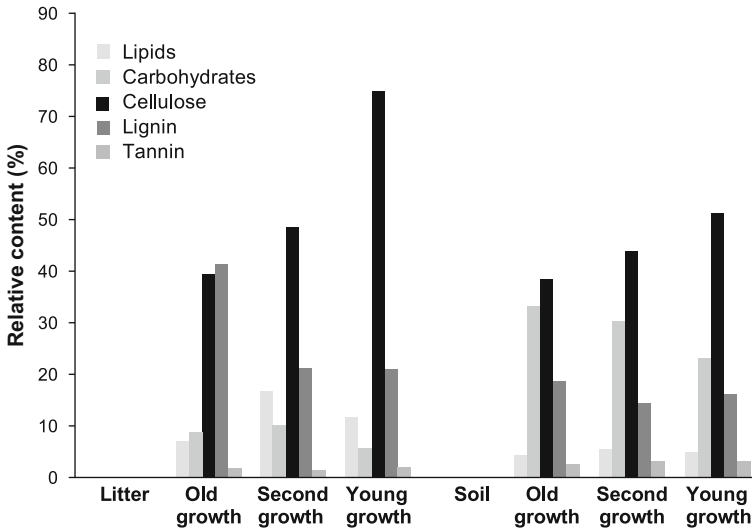
In general, the stock of carbon in soils is correlated to the mean annual temperature and the mean annual precipitation, and thus indirectly to net primary production (NPP) (Amundson 2001). Sun et al. (2004) analysed 36 forest stands from three

forest sites in Oregon with NPP ranging from 180 to 1,200 g C m<sup>-2</sup> year<sup>-1</sup>. 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 than 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<sup>-2</sup>, from a 20-year-old stand to an old-growth stand (Kloptek 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<sup>-2</sup> year<sup>-1</sup>. Ecosystems with high temperatures and high moisture availability like tropical rain forests have the highest rates, i.e. in the order of 2,000 ± 1,000 g C m<sup>-2</sup> year<sup>-1</sup> (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<sub>2</sub> efflux rates. Therefore, decomposition is higher at drier sites and carbon accumulation might occur at wetter sites.

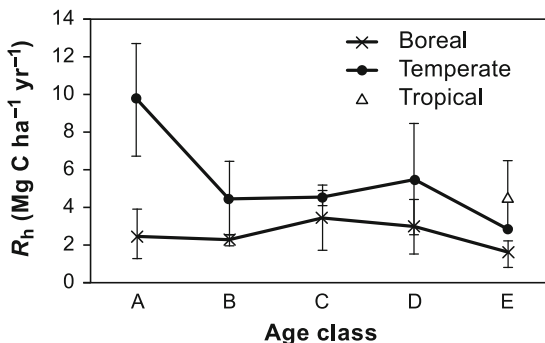
In temperate coniferous, broad-leaved and mixed forest, soil respiration seems to be driven primarily by the amount of fine roots of trees and understorey (M. Mund et al., manuscript in preparation). Although soil respiration near the trees is higher in young stands than in old stands, due to the higher 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<sup>-2</sup> year<sup>-1</sup>, 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 than 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 microorganisms (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  $7 \text{ g C m}^{-2} \text{ year}^{-1}$  2 years after afforestation to  $2 \text{ g C m}^{-2} \text{ year}^{-1}$  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  $10,000 \text{ g C m}^{-2}$ . 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<sup>-2</sup> 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<sup>-2</sup> were found in temperate deciduous forests; 9,961 (sd 8,614) g C m<sup>-2</sup> in temperate coniferous forests; and were highest, i.e. in the order of 13,420 (sd 4,366) g C m<sup>-2</sup>, 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 <sup>-2</sup> )	0–100 cm (g m <sup>-2</sup> )
<b>Boreal coniferous forest</b>					
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
	4	25	204	1,599	3,308
			383	797	1,649
			Mean	1,224	2,533
			14	1,779	3,681
			26	1,714	3,547
Van Cleve et al. 1983	1	20	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
			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			
Yermakov and Rothstein 2006	1	10	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
			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 <sup>-2</sup> )	0–100 cm (g m <sup>-2</sup> )
			Mean	2,267	9,935
Trumbore and Harden 1997	1	40	30	1,800	2,400
			90	2,900	3,867
	2	40	34	8,630	11,507
			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
<b>Temperate deciduous forest</b>					
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	5,600	7,670
			55	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
			Mean	4,322	9,853
	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
			123	3,440	7,842
			168	4,329	9,869
3	15	Mean	4,168	9,502	
		147	4,763	10,859	
		147	4,763	10,859	

(continued)

**Table 11.1** (Continued)

Reference	No.	Depth (cm)	Age (years)	SOC	
				Measured depth (g m <sup>-2</sup> )	0–100 cm (g m <sup>-2</sup> )
Gerighausen 2002	1	20	131	5,098	11,622
			153	4,510	10,282
			Mean	4,790	10,921
			22	3,155	6,074
			61	3,366	6,480
			170	3,682	7,089
			180	3,702	7,127
			Mean	3,476	6,693
			temperate broadleaf		
			Median	4,245	9,347
SD	1,733	2,652			
<b>Temperate coniferous forest</b>					
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
225	19,540	19,540			

(continued)

**Table 11.1** (Continued)

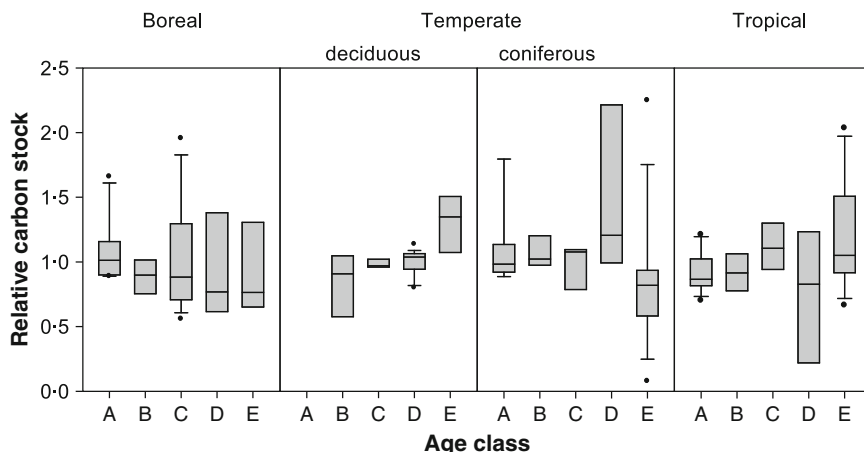
Reference	No.	Depth (cm)	Age (years)	SOC				
				Measured depth (g m <sup>-2</sup> )	0–100 cm (g m <sup>-2</sup> )			
Smithwick et al. 2002	2	100	400	3,670	3,670			
			750	1,160	1,160			
			455	12,250	12,250			
			Mean	14,634	14,634			
			300	26,260	26,260			
			470	10,900	10,900			
			500	5,990	5,990			
			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			
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			
			<b>Tropical evergreen broadleaf</b>					
			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	2,480	15,609				
		8	985	4,229				

(continued)

**Table 11.1** (Continued)

Reference	No.	Depth (cm)	Age (years)	SOC	
				Measured depth (g m <sup>-2</sup> )	0–100 cm (g m <sup>-2</sup> )
Street 1982	1	30	136	257	7,102
			22	6,990	14,982
			15	7,360	20,077
			Mean	3,614	12,400
			300	9,660	17,320
Brown and Lugo 1990	1	50	Mean	8,440	15,133
			23	9,000	12,317
			40	9,000	12,317
			40	11,000	15,054
			42.5	12,000	16,423
	1	50	55	14,500	19,844
			100	15,200	20,802
			300	13,000	17,791
			Mean	11,957	16,364
			2	25	35
Reiners et al. 1994	1	10	50	9,000	17,893
			300	4,500	8,947
			300	6,000	11,929
			Mean	6,750	13,420
			5	1,400	5,075
	1	10	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
	1	10	300	1,700	6,162
			300	2,800	10,150
			Mean	1,850	6,706
			23	11,700	26,566
			36	9,200	20,890
Smith et al. 1998	1	20	63	9,300	21,117
			36	9,500	21,571
			300	10,600	24,069
			Mean	10,060	22,843
			16	7,700	13,805
Guariguata et al. 1997	1	30	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	9,400	16,853
			tropical		
			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

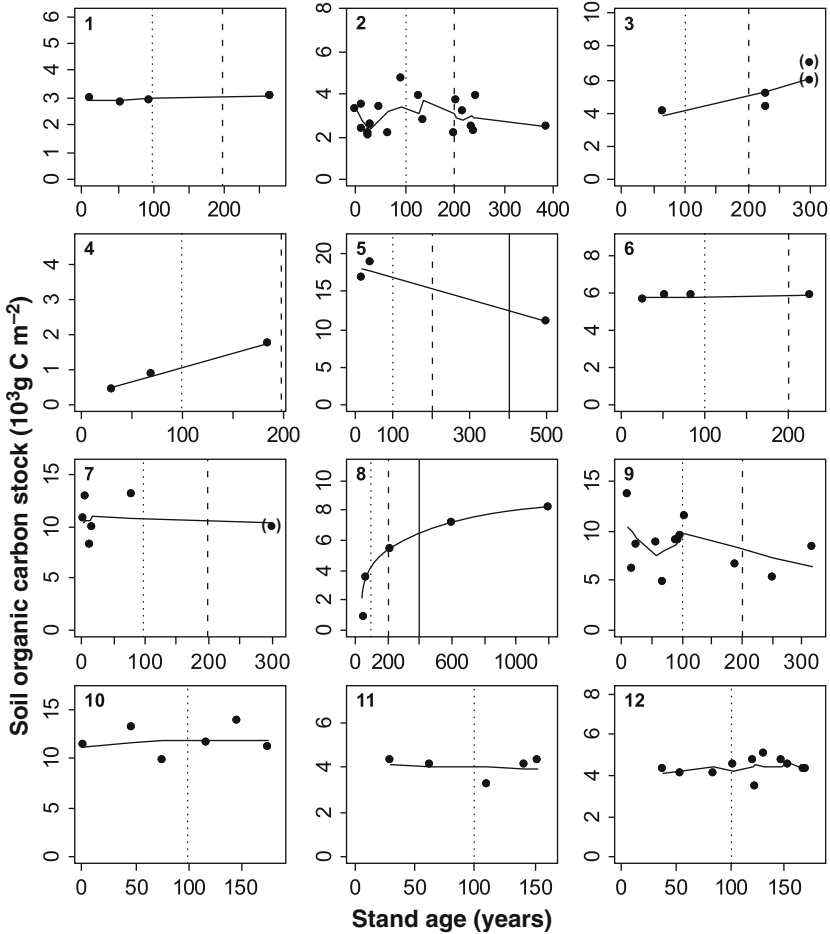
The high variability in rates of carbon stock changes ( $\Delta C_{SOM}$ ) was the most notable feature of the chronosequence data (Table 11.2, Fig. 11.7). Variability was most pronounced in the boreal and temperate coniferous sequences where both negative and positive rates were estimated for all developmental stages; values of  $\Delta C_{SOM}$  ranged from  $-14$  to  $+57$   $\text{g C m}^{-2} \text{ year}^{-1}$ . Mean values of  $\Delta C_{SOM}$  decreased with latitude from the boreal (between 1.4 and 2.5  $\text{g C m}^{-2} \text{ year}^{-1}$ ) 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.  $\Delta C$  Change in soil carbon stocks ( $\text{g C m}^{-2} \text{ year}^{-1}$ ), *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)	$\frac{\Delta C_{\text{SOM}}}{\text{Pioneer Transition}}$	$\frac{\Delta C_{\text{EOG}}}{\text{Transition}}$	$\frac{\Delta C_{\text{LOG}}}{\text{LOG}}$	Reference	
1	bc	Central Siberia	<i>Pinus sylvestris</i> , Vacc. type	25+	10.6	265	0.6	0.5	0.5	Wirth et al. 2002	
2	bc	Central Siberia	<i>Pinus sylvestris</i> , lichen type	25+	1	379	-0.8	-2.5	-3.1	Wirth et al. 2002	
3	bc	Central Siberia	<i>Abies sibirica</i> , <i>Picea obovata</i>	25+	67	320	4.5	9.5	8.3	C. Wirth, unpublished data	
4	tec	Oregon, USA	<i>Pseudotsuga menziesii</i>	10+	28.9	185	7.6	7.8	7.8	Entry and Enningham 1998	
5	tec	Washington, USA	<i>Pseudotsuga menziesii</i>	20+	21.4	400	-14.2	-14.1	-13.8	Klopatek 2002	
6	tec	Oregon, USA	<i>Tsuga heterophylla</i>	30+	24.4	223	-0.1	0.2	0.9	Boone et al. 1988	
7	tec	California, USA	Mixed conifer	20+	1	300 <sup>a</sup>	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	Sollins et al. 1983	
9	tec	Oregon, USA	<i>Pinus ponderosa</i>	100+	7.6	317	-8.5	-14.3	-14.2	Law et al. 2003	
10	tec	Fichtelgebirge, Germany	<i>Picea abies</i>	30	8	172	7.6	0.4	0.4	Mund 2004	
11	teb	Leinefelde, Germany	<i>Fagus sylvatica</i>	15	35	153	-0.6	-1.5	-1.5	Mund 2004	
12	teb	Hainich, Germany	<i>Fagus sylvatica</i>	15	43	170	-0.4	0.7	0.7	Mund 2004	
13	teb	Leinefelde, Germany	<i>Fagus sylvatica</i>	70+	29	179	4.5	4.2	4.2	Mund 2004	
14	teb	Patagonia, Chile	<i>Nothofagus pumilo</i>	30	31.44	300 <sup>a</sup>	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	5.9	Covington 1981	

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

<sup>a</sup>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  $\text{span} = 0.2$  and  $\text{bass} = 10$ ). 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  $17.6 \text{ g C m}^{-2} \text{ year}^{-1}$ ). Except in the tropics the overall magnitude of  $\Delta C_{\text{SOM}}$  was low. Using the biome-specific values of NPP from Luyssaert et al. (2007) for the four biomes (boreal coniferous:  $331 \text{ g C m}^{-2} \text{ year}^{-1}$ , temperate coniferous:  $355 \text{ g C m}^{-2} \text{ year}^{-1}$ , temperate broadleaved:  $738 \text{ g C m}^{-2} \text{ year}^{-1}$  and tropical evergreen:  $863 \text{ g C m}^{-2} \text{ year}^{-1}$ ), it becomes clear that only a small fraction

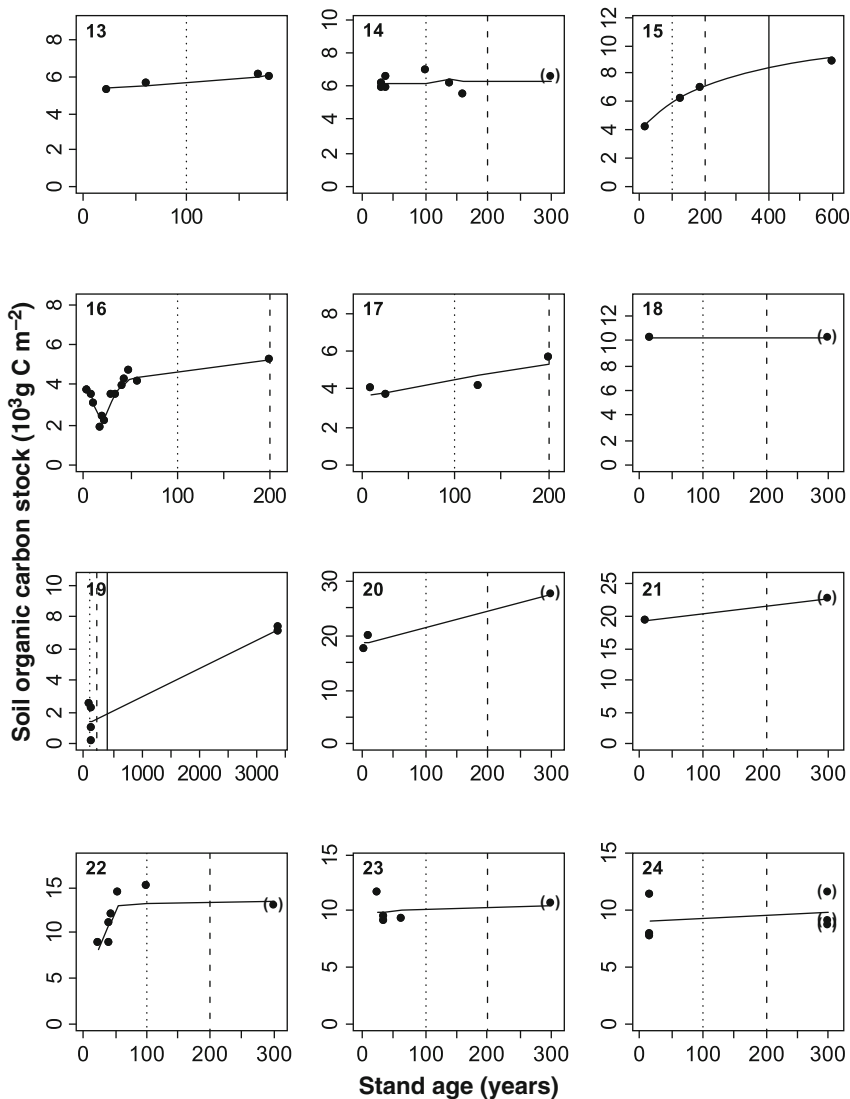


Fig. 11.7 (Continued)

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  $2 \text{ g C m}^{-2} \text{ year}^{-1}$  (boreal coniferous),  $3 \text{ g C m}^{-2} \text{ year}^{-1}$  (temperate broadleaved), and  $6 \text{ g C m}^{-2} \text{ year}^{-1}$  (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  $\Delta C_{\text{SOM}}$  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 ( $\Delta C_{\text{SOM}} = 7 \text{ g C m}^{-2} \text{ year}^{-1}$ ) to carbon losses ( $\Delta C_{\text{SOM}} = -4.5 \text{ g C m}^{-2} \text{ year}^{-1}$ ). In the tropical sequences,  $\Delta C_{\text{SOM}}$  dropped from 17.6 to 6.3  $\text{g C m}^{-2} \text{ year}^{-1}$  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  $\text{g C m}^{-2}$  (Mund 2004), coarse woody debris is 1,350  $\text{g m}^{-2}$  (Cotrufo et al. 2002), and litter production is, on average, 170  $\text{g m}^{-2} \text{ year}^{-1}$  (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  $\text{CO}_2$  efflux was determined from 79 collars in randomised locations using a double nested approach. The  $\text{CO}_2$  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  $\mu\text{m}$  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. Schrupf, 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  $125 \pm 31 \text{ g m}^{-2} \text{ year}^{-1}$  and for litter  $30 \text{ g m}^{-2} \text{ year}^{-1}$  (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  $68 \text{ g m}^{-2} \text{ year}^{-1}$  and increased 20 years after conversion up to  $120 \text{ g m}^{-2} \text{ year}^{-1}$ . Between 1950 and 1960, the increment of growth was harvested and  $254 \text{ g C m}^{-2} \text{ year}^{-1}$  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 ( $\text{g C m}^{-2} \text{ year}^{-1}$ )	Total C-export ( $\text{g C m}^{-2}$ )
1830–1920	Coppice-with-standards forest	$125 \pm 31$	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  $2 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ , which is equivalent to  $65 \text{ g m}^{-2} \text{ year}^{-1}$ . 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  $20,065 \text{ g C m}^{-2}$ , i.e. an average of  $110 \text{ g C m}^{-2} \text{ year}^{-1}$ , 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***

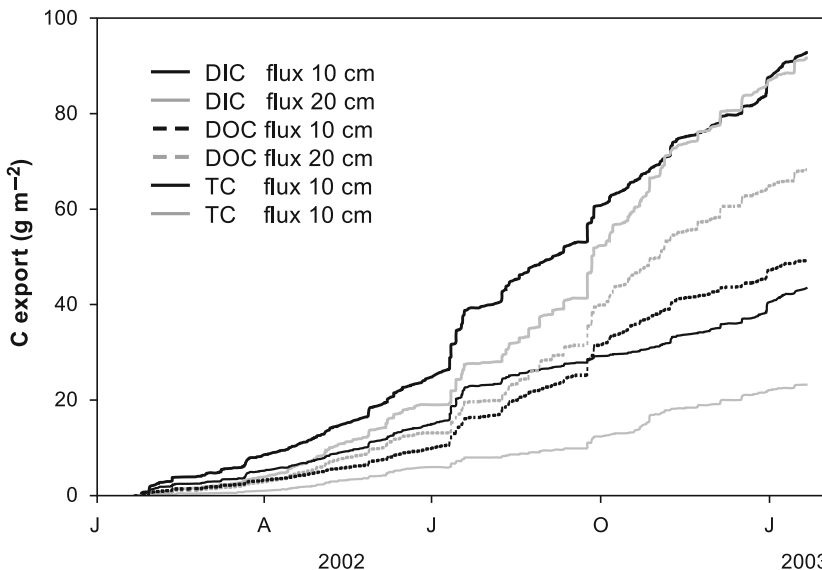
In 2006, mean and median  $\text{CO}_2$  efflux (mean from all collars and all measurements) was  $623$  and  $593 \text{ g m}^{-2} \text{ year}^{-1}$ . Rates from individual collars ranged from  $295$  to  $1,298 \text{ g m}^{-2} \text{ year}^{-1}$ . These rates are well within the range reported by 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  $0\text{--}30\%$  and  $3.6$  at  $30\text{--}60\%$  to  $2.3$  at  $60\text{--}90\%$  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  $45\text{--}50\%$  when soil temperature was low ( $0\text{--}12^\circ\text{C}$ ) and at  $35\%$  during times of high soil temperature ( $>12^\circ\text{C}$ ).

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.





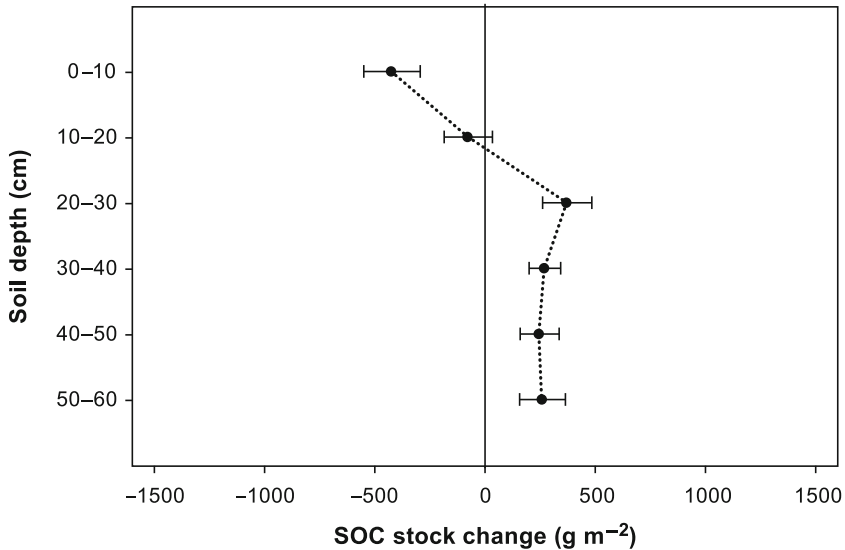
**Fig. 11.8** Export of dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and total carbon (TC) at 10 and 20 cm soil depth in 2002 at the water collection system within the study site ‘Weberstedter Holz’ in the Hainich National Park (NP), Germany

2004). The export of DOC at 10 cm soil depth reached 6.8 g m<sup>-2</sup> and at 20 cm, 5 g m<sup>-2</sup> (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<sup>-2</sup> at 10 cm to 4.3 g m<sup>-2</sup> at 20 cm. In total, the export of carbon was about 9 g m<sup>-2</sup> 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

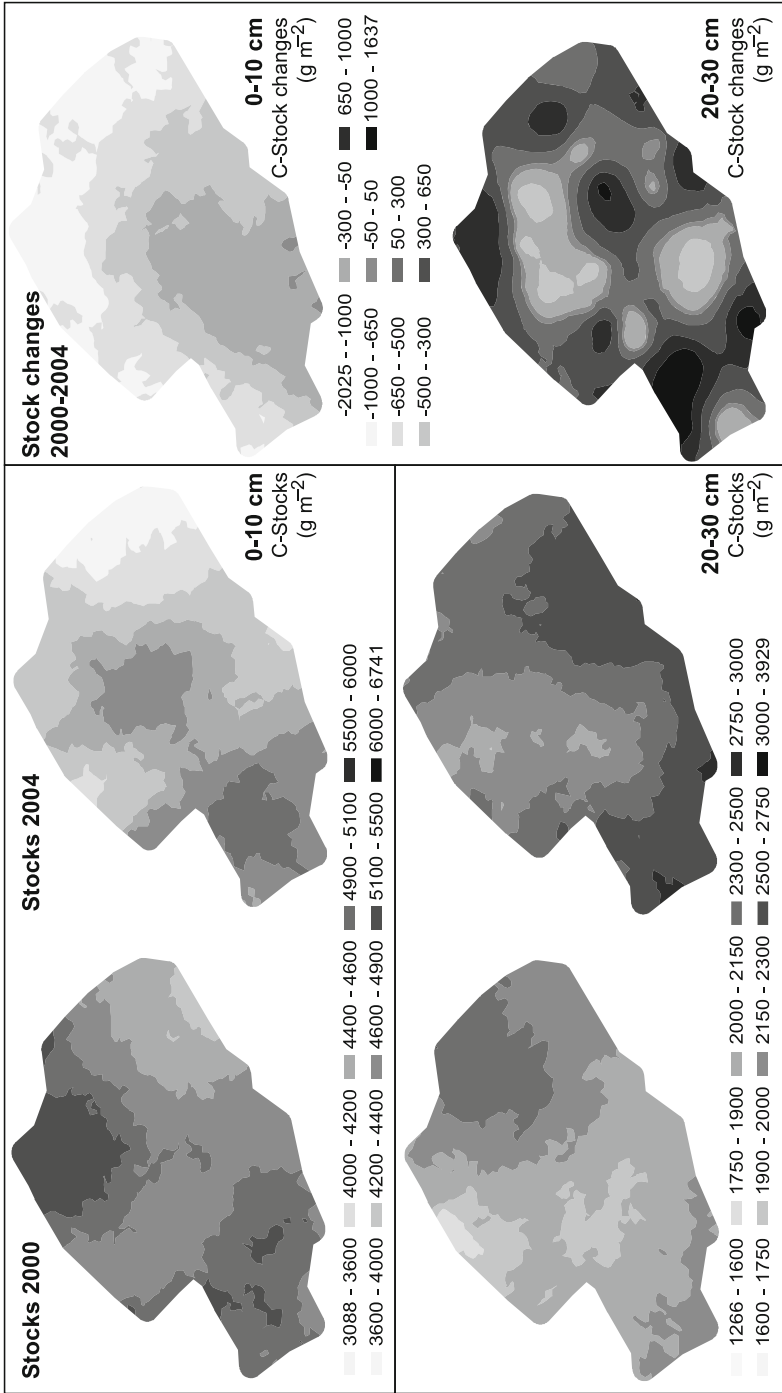
The concentration of soil organic carbon (SOC) measured for all 80 plots was distributed normally for all depths. The SOC concentration decreased continuously with increasing soil depth from 5,038 g m<sup>-2</sup> at 0–10 cm to 1,255 g m<sup>-2</sup> at 50–60 cm in 2000, and from 4,622 g m<sup>-2</sup> at 0–10 cm to 1,377 g m<sup>-2</sup> 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<sup>-2</sup> 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<sup>-2</sup> accumulated within 2000 and 2004. The greatest sequestration (270 g m<sup>-2</sup>) 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<sup>-2</sup> than in spring with 43 g m<sup>-2</sup> (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<sup>-2</sup> in 4 years, which is equivalent to 165 g SOC m<sup>-2</sup> year<sup>-1</sup>.

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<sup>-2</sup>), with fine roots decreasing continuously with increasing soil depth (20–30 cm, 50 g m<sup>-2</sup>; 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 Haimich 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 ( $\Delta C_{\text{SOM}}$ ) obtained from different regions and through different methods differ substantially (Table 11.4). It appears that chronosequence estimates (range:  $-4.5$  to  $17.6 \text{ g C m}^{-2} \text{ year}^{-1}$ ) are in the same range as estimates based on a carbon balance approach (range:  $-5$  to  $19 \text{ g C m}^{-2} \text{ year}^{-1}$ ), but are generally much lower than estimates based on repeated sampling (range:  $32$  to  $165 \text{ g C m}^{-2} \text{ year}^{-1}$ ). There were also pronounced differences between biomes but different methods yielded different rankings. Values of  $\Delta C_{\text{SOM}}$  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  $\Delta C_{\text{SOM}}$  within stages (across different methods) progressed 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  $6.9 \pm 19.7 \text{ g C m}^{-2} \text{ year}^{-1}$ . 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 that 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 <sup>a</sup>	Method <sup>b</sup>	Soil depth (cm) <sup>c</sup>	Carbon storage (g m <sup>-2</sup> year <sup>-1</sup> ) <sup>d</sup>
<b>Pioneer stage</b>				
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) <sup>e</sup>	Temp	PS	Var	24 ± 22
	Trop	PS	Var	69 ± 85
Pregitzer and Euskirchen (2004) <sup>f</sup>	Bor	C	Var	18.6
	Temp	C	Var	-5.5
	Trop	C	Var	76
Liski et al. (2002) <sup>g</sup>	Various	CB	N.I.	19 (0-107)
Median ± SD				14.8 ± 25.6
<b>Transition stage</b>				
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) <sup>f</sup>	Bor	C	Var	56
	Temp	C	Var	31
	Trop	C	Var	8
Homann et al. (2005) <sup>h</sup>	Temp-c	RS	0-15+	32
Trumbore and Harden (1997) <sup>i</sup>	Bor-c	CB	0-40+	-5 to 12
Median ± SD				8.4 ± 17.6
<b>Early old-growth stage</b>				
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) <sup>j</sup>	Temp-b	RS	0-15	76
Case study (Sect. 11.4)	Temp-b	RS	0-60	165
				21.0 ± 57.0
<b>Late old-growth stage</b>				
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 <sup>k</sup>	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

<sup>a</sup>Biome: *Bor-c* Boreal coniferous, *Temp-c* temperate coniferous, *Temp-b* temperate broadleaved, *Trop-b* tropical broadleaved

<sup>b</sup>Method: *RS* Repeated soil sampling, *C* chronosequence approach, *CB* carbon balance approach, *PS* paired sampling of forest and surrounding agricultural soil

<sup>c</sup>Abbreviations: *N.I.* not indicated, + including forest floor, *Var* variable

<sup>d</sup>Bootstrap medians were calculated as measures of central tendency for the chronosequence estimates of  $C_{\text{SOM}}$  as well as for all data in developmental phase

<sup>e</sup>Based on a meta-analysis of SOC accumulation during forest regrowth after agricultural abandonment. Accumulation rates were determined as the difference in  $C_{\text{SOM}}$  between forests and surrounding agricultural control sites

<sup>f</sup>Based on forest SOC stock observations arranged in chronosequences (see text)

<sup>g</sup>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

<sup>h</sup>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

<sup>i</sup>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

<sup>j</sup>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

<sup>k</sup>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

( $84 \pm 57 \text{ g C m}^{-2} \text{ year}^{-1}$ ). 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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