





Geoderma 137 (2007) 253-268

www.elsevier.com/locate/geoderma

Review

How strongly can forest management influence soil carbon sequestration?

Robert Jandl ^{a,*}, Marcus Lindner ^b, Lars Vesterdal ^c, Bram Bauwens ^d, Rainer Baritz ^e, Frank Hagedorn ^f, Dale W. Johnson ^g, Kari Minkkinen ^h, Kenneth A. Byrne ⁱ

^a BFW, Vienna, Austria
^b EFI, Joensuu, Finland
^c KVL, Hørsholm, Denmark
^d Wageningen Universiteit, Netherlands
^e Bundesanstalt für Geowissenschaften, Hannover, Germany
^f WSL, Birmensdorf, Switzerland
^g University of Reno, Nevada, USA
^h University of Helsinki, Finland
ⁱ University College Cork, Cork, Ireland

Received 14 August 2004; received in revised form 15 September 2006; accepted 18 September 2006 Available online 31 October 2006

Abstract

We reviewed the experimental evidence for long-term carbon (C) sequestration in soils as consequence of specific forest management strategies. Utilization of terrestrial C sinks alleviates the burden of countries which are committed to reducing their greenhouse gas emissions. Land-use changes such as those which result from afforestation and management of fast-growing tree species, have an immediate effect on the regional rate of C sequestration by incorporating carbon dioxide (CO₂) in plant biomass. The potential for such practices is limited in Europe by environmental and political constraints. The management of existing forests can also increase C sequestration, but earlier reviews found conflicting evidence regarding the effects of forest management on soil C pools. We analyzed the effects of harvesting, thinning, fertilization application, drainage, tree species selection, and control of natural disturbances on soil C dynamics. We focused on factors that affect the C input to the soil and the C release via decomposition of soil organic matter (SOM). The differentiation of SOM into labile and stable soil C fractions is important. There is ample evidence about the effects of management on the amount of C in the organic layers of the forest floor, but much less information about measurable effects of management on stable C pools in the mineral soil. The C storage capacity of the stable pool can be enhanced by increasing the productivity of the forest and thereby increasing the C input to the soil. Minimizing the disturbances in the stand structure and soil reduces the risk of unintended C losses. The establishment of mixed species forests increases the stability of the forest and can avoid high rates of SOM decomposition. The rate of C accumulation and its distribution within the soil profile differs between tree species. Differences in the stability of SOM as a direct species effect have not yet been reported.

Keywords: Soil C dynamics; Forest management; Natural disturbance; C sequestration

Contents

1.	Introduction	254
2.	The pool of soil organic carbon	254
	2.1. Factors influencing the soil C pool	254
	2.2. Stabilization of soil organic matter	255

E-mail addresses: robert.jandl@bfw.gv.at (R. Jandl), marcus.lindner@efi.fi (M. Lindner), lv@kvl.dk (L. Vesterdal), bram.bauwens@wur.nl (B. Bauwens), rainer.baritz@bgr.de (R. Baritz), frank.hagedorn@wsl.ch (F. Hagedorn), dwj@unr.edu (D.W. Johnson), kari.minkkinen@helsinki.fi (K. Minkkinen), k.byrne@ucc.ie (K.A. Byrne).

^{*} Corresponding author. Fax: +43 1 87838 1250.

3.	Affore	estation — Kyoto Protocol article 3.3	255
4.	Influe	ence of tree species	256
5.	Stand	management — Kyoto Protocol article 3.4	257
6.	Distur	rbances — fire, storm and pest infestation	259
7.	Impro	everent of site conditions	259
	7.1.	Nitrogen fertilization	259
		Natural aggradation of forests	
	7.3.	Liming	260
	7.4.	Water management — peatlands	260
	7.5.	Site preparation	261
8.	Discus	ssion	262
Refe	erences	1	263

1. Introduction

Forest ecosystems store more than 80% of all terrestrial aboveground C and more than 70% of all soil organic C (Batjes, 1996; Jobbágy and Jackson, 2000; Six et al., 2002a). The annual $\rm CO_2$ exchange between forests and the atmosphere via photosynthesis and respiration is ≈ 50 Pg C/yr, *i.e.* 7 times the anthropogenic C emission. An increase in soil respiration would increase the $\rm CO_2$ emissions from forest ecosystems. In order to mitigate climate change, more C should be sequestered in forest ecosystems and strategies for an adapted forest management are sought (Brown et al., 1996).

According to the Kyoto Protocol (KP), C sequestration in terrestrial sinks can be used to offset greenhouse gas emissions. Currently, European forests absorb 7 to 12% of European emissions with agricultural land being a source and forests a sink of CO₂ (Janssens et al., 2003). Several Europeans countries have so far failed to curtail their greenhouse gas emissions and may rely on the inclusion of terrestrial C sinks in order to meet their emission reduction targets. The Kyoto Protocol states in Article 3.3 that "net changes in greenhouse gas emissions by sources and removals by sinks resulting from direct human-induced land-use change and forestry activities, limited to afforestation, reforestation and deforestation since 1990, measured as verifiable changes in carbon stocks in each commitment period, shall be used to meet the commitments". However, the ability to utilize afforestation as a tool to offset carbon emissions is constrained by available land area. The upper limit for afforestation projects in Europe has been estimated to be 20% of the agricultural land area (Cannell, 1999a). In several countries (e.g. Austria, Finland, Sweden, Switzerland) the forest cover is already 50% and further increases are unlikely. In countries with a low forest cover (e.g. Ireland, Denmark, Mediterranean countries), however, an increase in the forested area is on the political agenda. KP Article 3.4 allows the use of forest management for C sequestration up to nationally applicable limits (United Nations Framework Convention on Climate Change, 2002; Cannell, 2003; ECCP-Working group on forest sinks, 2003).

National Forest Inventories are used to assess the C sequestration in the aboveground biomass in the context of national greenhouse gas emission reports (Löwe et al., 2000). Measuring changes in soil C is more difficult because its spatial

variability is high and soil C accumulation is a slow process (Conen et al., 2004). The rate of formation of stable SOM is between 2 and 12 kg C/ha/yr and much lower than the accumulation of C in the aboveground biomass of a moderately productive forest (Schlesinger et al., 2000). Experiments have found different effects of forest management activities on C sequestration (Johnson, 1992; Post and Kwon, 2000; Johnson and Curtis, 2001). Treatments such as thinning, harvesting, and fertilization modify soil C dynamics and different results can be explained by specific site and soil conditions. In this paper, we review the effects of forest management on C sequestration from the perspective of soil processes. We attempt to generalize about soil processes, that are affected by forest management, scrutinize forest management strategies with respect to their influence on soil C pools, and recommend activities that can lead to long-term C sequestration in forest soils.

2. The pool of soil organic carbon

2.1. Factors influencing the soil C pool

The soil C pool is determined by the balance between C input by litterfall and rhizodeposition on the one hand and the release of C during decomposition on the other side. The turnover of SOM depends on the chemical quality of the C compounds (labile or stable C), site conditions (climate), and soil properties (clay content, soil moisture, pH, nutrient status). Several of these factors are directly or indirectly influenced by forest management. The relative effect of temperature and chemical quality on the decomposition rate has received considerable attention (Trumbore et al., 1996; Liski et al., 1999; Giardina and Ryan, 2000; Knorr et al., 2005; Davidson and Janssens, 2006). The actual turnover rate differs between regions. In boreal peatland forests, excess soil moisture is a limiting factor; in both high elevation and boreal forests the short growing season limits the annual decomposition rate, whereas in mediterranean systems summer droughts inhibit the turnover of SOM.

In a warming world both the primary productivity and the decomposition of SOM accelerate and the soil C pool will move towards a new equilibrium. Forest soils respond more strongly than soils under other forms of land use (Schimel, 1995; Valentini et al., 2000; Rustad et al., 2001). A review of soil respiration experiments concluded that in the long run warming

will reduce the amount of SOM because soil respiration rates will be stimulated more than the productivity (Rustad et al., 2001). In cold regions the response is expected to be more pronounced (Cox et al., 2000; Kirschbaum, 2000). However, 10 years of experimental warming suggest that the loss of soil C is only a temporary effect, because only the labile soil C pool is exhausted (Jarvis and Linder, 2000; Melillo et al., 2002). The response of SOM to rising temperatures is still a subject of controversy, mainly owing to different assumptions on the heterogeneity of fractions of SOM (Kirschbaum, 2004; Powlson, 2005).

The chemical quality of SOM limits the rate of soil respiration (Giardina and Ryan, 2000; Liski et al., 2003). Labile C fractions are quickly mineralized when the temperature regime is appropriate, but the turnover of stable fractions of SOM such as organic compounds associated with the mineral soil is independent of the temperature (Trumbore et al., 1996; Hobbie et al., 2000). Soil microorganisms will acclimatize to changed conditions and the temperature sensitivity of soil respiration will decrease (Luo et al., 2001). Nevertheless, microbial processes are controlled by the quality and availability of substrate and by site properties such as nutrient availability and moisture supply. The substrate availability depends on litter input, the chemical bonding between SOM, and the mineral soil and the chemical structure of the organic compounds.

2.2. Stabilization of soil organic matter

The process of C stabilization is different from the process of accumulation. Accumulation is driven by site factors inhibiting soil respiration, such as excess soil moisture or low temperatures. For an increase of stable soil C pools it is necessary to identify sites where soil properties are conducive to C sequestration. An abundance of reactive surfaces of clay minerals and oxides, where C can form complexes with a low turnover rate, leads to the stabilization of C. The adsorption of organic matter at the mineral surface creates an intimate bond, which leads to an enduring stabilization (Torn et al., 1997; Torn et al., 2002; Hagedorn et al., 2003).

Processes that affect the aggregation of the soil also affect the C sequestration capacity. Stabilized SOM is found in microaggregates of the mineral soil. Stabilization of SOM can either be a consequence of the inherent recalcitrance of the molecules, bonding at oxide and clay mineral surfaces, or simply the inaccessibility of SOM for potential microbial grazers (Sollins et al., 1996; Six et al., 2002a,b). The surface accumulation of SOM is positively related to the C input. There are gradual differences between different clay minerals. The bonding of SOM to smectite is tighter than to kaolinite and its turnover time is twice as long (Wattel-Koekkoek et al., 2003). The chemical reaction is a surface condensation that forms stable bondings (Keil et al., 1994; Kennedy et al., 2002). Even over the longest available time series of soil data (150 years) from Russian grasslands, it was shown that the abundance of amorphous minerals was the single most important factor determining the size of the soil C pool. The decisive factor is the physical protection of C upon adsorption to the surface. Once C is stabilized, the C pool does not change, even when marked differences in land use and climate occur. A comparison of recent data with archived soil material from the Russian steppe shows minimal changes over a century. Despite cultivation and global warming the recalcitrant C stock remained unchanged (Torn et al., 2002).

Stabilization of soil C is not strongly related to site productivity. ¹³C tracer experiments have shown that the net accumulation of new tree-derived C can be greater in loamy soils with a low productivity than in fertile sandy soils with a high productivity (Hagedorn et al., 2003). This suggests that soil properties play a dominant role.

Soil C sequestration in peatlands is a special case of biochemical stabilization. Under anaerobic conditions the enzyme phenol oxidase is inactive, even when temperatures are rising (Freeman et al., 2001). Consequently, chemically labile SOM accumulates on this site. A change in land management, *e.g.*, the drainage of peatland, can lift this biological constraint and increase the mobilization of SOM. Global warming also promotes drying of peatland and will partially mobilize this huge C pool (Goulden et al., 1998).

3. Afforestation — Kyoto Protocol article 3.3

Forests have a higher C density than other types of ecosystems (Bolin et al., 2000). The terrestrial C pool has been greatly reduced by human activities such as conversion of forests into agricultural land and urban areas. Among the consequences was a reduction of the soil C pool. The currently observed carbon sink is a reversal of past carbon losses (Erb, 2004; Lal, 2004). The afforestation of former agricultural land increases the C pool in the aboveground biomass and replenishes the soil C pool. Accumulation occurs until the soil reaches a new equilibrium between C input (litterfall, rhizodeposition) and C output (respiration, leaching). Recent reviews report that the average rate of soil C sequestration was 0.3 t C ha⁻¹ yr⁻¹ (range 0–3 t C ha⁻¹ yr⁻¹) across different climatic zones (Post and Kwon, 2000). On average afforestation increases total C stocks by 18% over a variable number of years (Guo and Gifford, 2002). The initial C accumulation occurs in the forest floor. Its thickness and chemical properties vary with tree species (Vesterdal and Raulund-Rasmussen, 1998; Six et al., 2002a, see chapter 4).

Changes in soil C storage have been reported from a number of studies based on stand chronosequences, paired plots and repeated sampling. Results are quite diverse as soils may gain C, experience no change or even lose C following afforestation (Guo and Gifford, 2002; Vesterdal et al., 2002b). Carbon loss can occur in a brief period following afforestation, when there is an imbalance between C loss by soil microbial respiration and C gain by litterfall. Planting leads to soil disturbance and can stimulate the mineralization of SOM. These losses are not necessarily offset by the low C input by litterfall in a young plantation. Experimental evidence supports this theory. Carbon gains in the upper mineral soil of plantation forests can be offset by losses of old C from deeper parts of the soil (Bashkin and Binkley, 1998; Giardina and Ryan, 2002; Markewitz et al., 2002; Paul et al., 2002; Vesterdal et al., 2002a). In experiments in

South Carolina with Pinus taeda, 80% of the C accumulation occurred in the biomass, some accumulation was found in the forest floor and only a small amount ended up in the mineral soil (Richter et al., 1999). A synthesis of afforestation chronosequences in northwestern Europe suggested that soils can contribute about 30% of the total C sequestration in afforested ecosystems (Vesterdal et al., 2006). Mineral soils only sequestered C in two out of the six chronosequences. Radiocarbon analyses and ¹³C tracer experiments showed that litter-derived C was moved into the mineral soil, but it remained unstabilized and was lost rapidly by decomposition (Trumbore, 2000; Hagedorn et al., 2003). The available long-term experiments found that after several decades more C is moved to the mineral soil (Jenkinson, 1991; Compton et al., 1998; Richter et al., 1999; Gaudinski et al., 2000; Post and Kwon, 2000; Hooker and Compton, 2003; Johnson et al., 2003; Paul et al., 2003; DeGryze et al., 2004).

Following afforestations soils accumulate less C and at a slower rate than the aboveground biomass. Conditions that are not conducive to soil microbial processes, such as sandy texture, low nutrient availability and low pH, can lead to the formation of a thick forest floor layer (Staaf, 1987; Vesterdal et al., 1995; Vesterdal and Raulund-Rasmussen, 1998). It is less certain how C sequestration in the mineral soil is affected by the soil type. In some cases, fertile and clayey soils stored more C, because the production of above- and belowground litter is high and because the formation of organo-minerals complexes protects SOM from decomposition (van Veen and Kuikman, 1990; Liski, 1995; Vogt et al., 1995). In other cases, poor mineral soils were reported to store more C, which was attributed to the slow decomposition and complex formation between organic molecules and metal ions (Vesterdal et al., 2006). In an assessment of soil C stocks in pure Norway spruce and mixed spruce-broadleaved stands on poor soils the C stocks were positively related to soil aluminum pools in an area with relatively poor soils (Berger et al., 2002), because decomposition of SOM is slow in acidic soils. However, the question of how the C stock of different soil types responds to afforestation is not yet resolved (Vejre et al., 2003).

Previous land use affects the C sequestration potential of afforested sites. Pasture soils already have high C stocks and high root densities in the upper part of the mineral soil, so afforestation has a small effect (Guo and Gifford, 2002; Römkens et al., 1999; Murty et al., 2002). Chronosequence studies from New Zealand on former pastures, northern Spain on arable land, and northern England on peatland found that soils initially lost, but later gained C (Romanyá et al., 2000; Halliday et al., 2003; Zerva et al., 2005). In contrast, croplands are more depleted in soil C, and have a greater potential to sequester soil C.

In conclusion, the rate of soil C sequestration is slower than changes in the aboveground C, and it takes decades until net gains occur in former arable soils. Forest floors accumulate C quickly, but most of it in a labile form and for a limited time.

4. Influence of tree species

Despite much research on the role of vegetation in soil formation, a general understanding of the extent of the effect of

tree species across site types has not yet been reached (Stone, 1975; Augusto et al., 2002; Binkley and Menyailo, 2005). Tree species affect the C storage of the ecosystem in several ways. Shallow rooting coniferous species tend to accumulate SOM in the forest floor, but less in the mineral soil, compared with deciduous trees. At identical biomass volumes, trees with a high wood density (many deciduous tree species) accumulate more C than trees with light wood (many coniferous species) (Table 1). Late-successional trees tolerate a higher stem density than pioneer species. Species that occupy different ecological niches can complement each other so that the biomass production of a mixed stand is higher than that for pure stands (Resh et al., 2002; Pretzsch, 2005). For the productivity of a forest over the entire rotation period, its stability against disturbance is important. In Central Europe, mixtures of beech and spruce are the better option, even if pure spruce stands have a higher growth rate (Pretzsch, 2005).

Table 1 shows the differences in soil C pools under common European tree species. Pine forests have remarkably low soil C pools, whereas beech forests have the highest soil and total C pools. It must be kept in mind that mean values for different species also represent site conditions where the species are dominant. For instance, Scots pine forests often grow on shallow and dry soils, which have low C stocks, whereas beech is found on more fertile soils (Callesen et al., 2003, Table 1).

The influence of tree species was studied in common garden experiments with replicated stands of the same species (Fyles et al., 1994; Binkley, 1995; Prescott et al., 2000). In Denmark, a study of seven species replicated at seven different sites along a soil fertility gradient focused on the forest floor C stock (Vesterdal and Raulund-Rasmussen, 1998). Lodgepole pine (Pinus contorta), Sitka spruce (Picea sitchensis) and Norway spruce had much higher C stocks than European beech (Fagus sylvatica) and oak (Quercus robur). Similarly, a German experiment showed more C in the forest floor under pine than under beech. This was attributed to the slower decay of pine and spruce litter compared with the litter of deciduous trees (Vesterdal and Raulund-Rasmussen, 1998; Fischer et al., 2002). It should be noted that the effects on the mineral soil are variable. An Austrian study showed higher soil C stocks in pure Norway spruce stands than in mixed spruce-broadleaf stands (Berger et al., 2002). An interaction between tree species and soil type was shown. On poor soils the admixture of spruce increased the soil C pool to a larger extent than on fertile soils. There is insufficient evidence of a consistent effect of tree species on mineral soil C stocks, but the establishment of a spruce forest

Table 1 Wood density of European tree species and median of C pools in European forests (de Vries et al., 2003)

Species	Wood density [kg/m³]	Tree C [t/ha]	Soil C [t/ha]	∑C [t/ha]
Pinus sylvestris (Scots pine)	490	60	62	122
Picea abies (Norway spruce)	430	74	140	214
Abies alba (Silver fir)	410	100	128	228
Fagus sylvatica (beech)	680	119	147	266
Quercus sp. (oak)	660	83	102	185

after beech leads to the release of C from parts of the mineral soil that is no longer penetrated by roots (Kreutzer et al., 1986). The rooting depth is relevant for soil C because root growth is a most effective way of introducing C to the soil (Jobbágy and Jackson, 2000; Rothe et al., 2002; Vesterdal et al., 2002a).

The conversion of Central European secondary Norway spruce plantations to mixed species forests has been proposed (Spiecker et al., 2004). The primary objective is to reduce storm damages and increase the stability of forests in a changing environment (von Lüpke, 2004; Pretzsch, 2005). Spruce forests generate a higher revenue than mixed species forests or pure beech stands, even when the higher production risk of spruce is taken into account (Assmann, 1961; Dieter, 2001). According to models the long-term C sequestration in Douglas fir (Pseudotsuga menziesii) and beech stands is higher than in Norway spruce stands (Burschel et al., 1993; Schöne and Schulte, 1999). In pine stands that have been underplanted with beech, the depth gradient of soil C was changed. In mixed pine-beech stands more C accumulated in deeper parts of the mineral soil, because beech roots reached deeper into the mineral soil. It remains to be seen if this C will be shifted into a stable pool. Nevertheless, the total soil C gain after conversion from pine to beech was low (Fischer et al., 2002).

In conclusion, the effect of tree species on forest floor C stocks is rapid. For the permanence of C sequestration it is more relevant to select tree species that increase the pool of stabilized C in the mineral soil. The driving process is the production of belowground biomass. However, little evidence for the size of this effect is available.

5. Stand management — Kyoto Protocol article 3.4

The thinning regime, the length of the rotation period, specific harvesting techniques, uneven-aged forest management, and continuous-cover forestry are management options with tangible economical and ecological consequences.

Thinning interventions increase the radial growth of the remaining trees at the expense of the total biomass and are not primarily aimed at maximizing C sequestration (Assmann, 1961; Sobachkin et al., 2005). Thinning changes the microclimate. Decomposition of forest floor C is temporarily stimulated because soils become warmer and possibly wetter due to reduced evapotranspiration and the soil C pool decreases (Piene and van Cleve, 1978; Aussenac, 1987). The stand microclimate returns to previous conditions unless the thinning intervals are short and intensities are high. Apart from the changed microclimate, litterfall is temporarily lowered in heavily thinned stands. This reduces forest floor accumulation and contributes to lower soil C stocks. The input of thinning residues into the soil may compensate for losses (de Wit and Kvindesland, 1999). Forest floor C stocks decreased with increasing thinning intensity in field studies in New Zealand, Denmark and the USA (Wollum and Schubert, 1975; Carey et al., 1982; Vesterdal et al., 1995). In the Danish study, forest floor C stocks were inversely related to the basal area, but the change in the forest floor C pool was smaller than its variation between experimental sites with different soil types (Vesterdal et al., 1995).

Less experimental evidence is available for the effect of thinning on the C pool in the mineral soil. The balance in forest soil C depends on the extent of the soil disturbance, the input of thinning residues into the soil and the rate of the litterfall. In an Austrian experiment of a Norway spruce stand, all thinning intensities decreased the C storage (Fig. 1). A thinning intervention in an experimental site with flux measurements in Finland did not result in a net release of C from the ecosystem, because the enhanced growth of the ground vegetation compensated for the reduced C sequestration of the tree layer and the increase of heterotrophic soil respiration was balanced by a decrease in autotrophic respiration of similar magnitude (Suni et al., 2003). In a Korean study, neither soil CO₂ efflux nor litter decomposition was increased with increasing thinning intensity (Son et al., 2004). Any effects on soil respiration rates were apparently overruled by root respiration as indicated by a positive relationship between stand density and soil CO₂ efflux.

Harvesting removes biomass, disturbs the soil and changes the microclimate more than a thinning operation. In the years following harvesting and replanting, soil C losses may exceed C gains in the aboveground biomass. The long-term balance depends on the extent of soil disturbance. Harvesting influences soil carbon in two contrasting ways: harvest residues left on the soil surface increase the C stock of the forest floor and disturbance of the soil structure leads to soil C loss. In a comparative study, harvesting turned forests into a C source because soil respiration was stimulated, or reduced to a lesser extent, than photosynthesis (Kowalski et al., 2004). A scheme of C dynamics after harvest shows the almost immediate C loss that is followed by a slow recovery of the C pool Fig. 2.

A review of harvesting techniques suggested that the effect on soil C is rather small, on average, and depends on the harvesting type (Johnson and Curtis, 2001). Whole-tree harvesting caused a small decrease in A-horizon C stocks, whereas conventional harvesting, leaving the harvesting residues on the soil, resulted in a small increase. Although soil C changes were noted after harvesting, they diminished over time without a lasting effect. In general, different harvesting methods had a far greater effect on ecosystem C due to its effect on the biomass of the regenerating

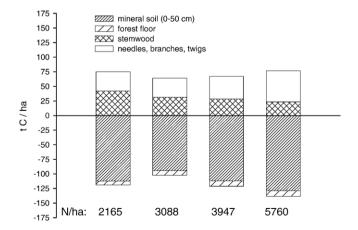


Fig. 1. Carbon in the aboveground biomass and the soil in a thinning experiment eight years after the intervention. "N" denotes the number of stems per ha (Hager, 1988).

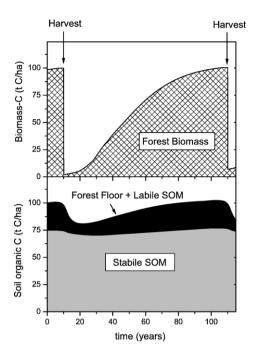


Fig. 2. Simulation of C dynamics in the aboveground biomass and the soil after harvesting. — Assumptions: Biomass-C stock typical for Central European Norway spruce forest; rotation period ≈ 100 years; 25% of SOM are labile, total SOM loss from literature (Olsson et al., 1996).

stand, and a weaker effect on soil C (Johnson and Curtis, 2001; Johnson et al., 2002).

Other researchers report large soil C losses after harvesting. Measurement of net ecosystem C exchange showed that for at least 14 years after logging, regenerating forests remained net sources of CO₂ owing to increased rates of soil respiration (Olsson et al., 1996; Schulze et al., 1999; Yanai et al., 2003). Reductions in soil C stocks over 20 years following clear cuts can range between 5 and 20 t C/ha and are therefore significant compared to the gain of C in biomass of the maturing forest (Pennock and van Kessel, 1997).

Continuous-cover forestry, including selective harvesting, resembles thinning with respect to its effect on the soil C pool, and is considered a possible measure to reduce soil C losses compared with clear-cut harvesting (ECCP-Working group on forest sinks, 2003).

An elongation of the *rotation period* has been proposed to foster C sequestration in forests. Old-growth forests have the

highest C density, whereas younger stands have a larger C sink capacity. After harvest operations, soil C pools in managed forests recover to the previous level. Short rotation lengths where the time of harvest is close to the age of maximum mean annual increment will maximize aboveground biomass production, but not C storage. Longer rotation periods imply that the disturbance frequency due to forest operations is reduced and soils can accumulate C (Schulze et al., 1999). Growth and yield tables suggest that stand productivity declines significantly in mature forest stands. However, even very old unmanaged forests can sequester large amounts of C. A 250-year old beech stand in the Hainich National Park (Central Germany) accumulated more than 4 t C/ha/yr (Knohl et al., 2003). A mature Siberian Scots pine forest and old-growth forests in the USA transferred a higher proportion of its C into the soil than in the early stages of the stand development and continuously increased the soil C stock (Harmon et al., 1990; Schulze et al., 2000). In Sitka spruce plantations in the UK all investigated C pools increased with a 20 year longer rotation, because the productivity of the forest remained very high (Kaipainen et al., 2004). The accumulation of C continues until the C gain from photosynthesis is larger than respiration losses. Late-successional species (e.g. beech, Norway spruce) are able to maintain high C sequestration rates for longer than pioneer tree species. Over-mature forest stands are not able to close canopy gaps created by natural mortality or thinning. Consequently the decomposition of SOM is enhanced and decreases the soil C pool.

Chronosequences of spruce in Norway and pine in Northern Germany showed an increase in the thickness of the forest floor layer with age, reaching a steady state after several decades (Sogn et al., 1999; Böttcher and Springob, 2001). No C changes with stand age were found in the mineral soil of the pine forest. A chronosequence of Norway spruce stands in Austria shows only a slight, statistically insignificant, C enrichment of the soil (Fig. 3).

Several modeling studies suggest that very long rotation lengths do not necessarily maximize the total C balance of managed forests (Cannell, 1999b; Liski et al., 2001; Harmon and Marks, 2002). In a simulation experiment of the effect of increased rotation length on C storage in Scots pine plantations in Finland, Germany, and Spain stand productivity declined, because the currently applied harvest age was already beyond the maximum annual increment. Soil C accumulated for several decades but leveled off. The main reason was the decline in

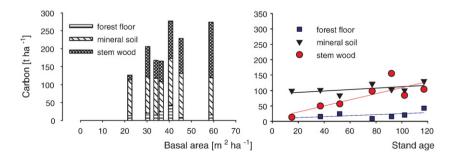


Fig. 3. Carbon pools a chronosequence of Norway spruce stands in Kobernauser Wald/Austria. (a) C pools versus stand basal area, and (b) temporal trend of C pools over stand age (Bauer, 1989).

aboveground litter production, which controlled the soil C pool (Kaipainen et al., 2004).

The elongation of the rotation period has consequences for the wood product market. Carbon that remains in the forest ecosystem cannot be built into wood products and cannot contribute to the substitution of fossil fuels (Schlamadinger and Marland, 1996). It therefore needs to be substantiated, in which types of forests are long rotation periods effective, and where greater volume growth rates in short- to medium-rotation length systems are a better choice.

We conclude that ageing of forests results in increasing C densities in management systems with longer rotation lengths, provided the harvest age is not beyond the age where the forest stand turns from a net sink to a source of C. The magnitude of the effect of increased rotation lengths depends on the current management practice. At the landscape level, longer rotation lengths with more old forests lead to higher C pools than short rotations with only young plantations. A conclusive summary of the long-term C accumulation in forests is still needed. Even when single old stands can sequester C at a high rate, it needs to be demonstrated that these forests are truly representative for the life time of the respective forest type within a given region. — Management interventions such as thinning add value to the stand, but remove biomass. The net effect for C is a loss. Nevertheless, thinning increases the stand stability and therefore offers an important control mechanism for the maintenance of C storage in ecosystems.

6. Disturbances — fire, storm and pest infestation

Recommendations for forest management need to consider the regional disturbance regime. Fire has always played an integral role in the structure and function of forest ecosystems, especially in seasonally dry forests (Fisher and Binkley, 2000). The policy of fire suppression can delay but cannot prevent wildfires over the long term. It leads to an apparent net C accumulation that in fact increases the risk of large C release during catastrophic fires. The role of fire in ecosystem C changes is not straightforward. Several experiments showed that wildfire had caused increases in soil C, which may be driven by the incorporation of charcoal into soils and new C inputs via post-fire N₂ fixation (Schulze et al., 1999; Hirsch et al., 2001; Johnson and Curtis, 2001; Johnson et al., 2004). However, N-fixing plants are not common to all fire-prone ecosystems.

In boreal and mediterranean forests wildfires impose natural limits on the rotation period. Owing to the fire cycle, Siberian forests which are younger than 40 years are a net C source because the rate of decay of forest floor material is larger than biomass accumulation. Forests between 40 and 100 years old are a strong net C sink (≈ 1 t C/ha/yr), older forests are a weak sink (≈ 0.2 t C/ha/yr) (Wirth et al., 2002). Wildfires in tropical forests are not common, but can have serious impacts on the global C cycle. Burning of forested peatlands of Indonesia in 2002 released an equivalent of 13 to 40% of the annual global C emissions from fossil fuels. No management options exist to affect the size of the C pool in tropical peatlands, but protection of these swamp–forest ecosystems is required (Page et al., 2002).

Climate change may increase the frequency and intensity of drought, especially in the Mediterranean and temperate zones. The impacts are site specific and difficult to predict. Water limitations will tend to affect tree growth negatively, but on the other hand the decomposition of soil C may be reduced (Hanson and Weltzin, 2000). Climate change also has an impact on forest pest infestations. A feedback mechanism between ozone, CO₂ and insect populations has been demonstrated in a FACE experiment in North America with aspen (*Populus tremuloides*) and mixed aspen-birch (Betula papyrifera) stands. Under changing conditions the population of insects and the frequency of diseases increased. Moreover, forests did not reach the anticipated productivity, either because of damage or the detrimental effect of ozone. The decreased biomass production lowered the rate of soil C formation significantly (Percy et al., 2002; Loya et al., 2003).

Storm damage may result in strongly increased amounts of coarse woody debris on the forest floor. Carbon dynamics after the disturbance are also affected by subsequent management decisions. In the case of a severe reduction in the value, the stand will be harvested and damaged timber will be salvaged. When only parts of the canopy are broken and the stand is already mature, it may be wise to continue the originally planned production cycle (Thürig et al., 2005). Uprooting of trees by windthrow destroys soil structure, which in turn makes protected C accessible for decomposers. Two years after a windthrow in European Russia, the whole ecosystem lost 2 t C/ha to the atmosphere over a 3-month summer period (Knohl et al., 2002).

In conclusion, disturbances consistently lead to the mobilization of C and present a potentially large C source. There are many interdependencies with management activities such as choice of tree species, regulation of stand structure, thinning intensity, and rotation length. Without forest management interventions, the importance of disturbances for C dynamics increases.

7. Improvement of site conditions

7.1. Nitrogen fertilization

Cycling of SOM is influenced by fertilization in contrasting ways. (1) Nitrogen fertilization stimulates tree growth, which potentially increases C inputs into soils through litterfall and rhizodeposition. Increases in tree growth and SOM content due to long-term N fertilization would support this assumption, but there are also reports about decreased root biomass under experimental N additions (Mäkipää, 1995; Eriksson et al., 1996; Andersson et al., 1998; Gundersen et al., 1998). (2) Fertilization increases the nutrient content of the litter material, which stimulates decomposition of SOM (Paul and Clark, 1989). In contrast there are indications that input of mineral N retards decomposition rates of old litter and recalcitrant SOM by suppression of ligninolytic enzymes of soil microbes and by chemical stabilization. Nitrogen stimulates the initial decomposition of fresh litter, but suppresses humus decay in later stages. Radiocarbon and 13C tracer experiments indicated that N additions increased the fraction of old and stable humus in soils, which may significantly affect soil C storage in the long run (Fog, 1988; Berg and Matzner, 1997; Magill and Aber, 1998; Berg and Meetemeyer, 2002; Neff et al., 2002; Franklin et al., 2003; Hagedorn et al., 2003).

A meta-analysis of 48 experiments from a wide geographical range reported the effects of N, both directly applied as mineral fertilizers and captured by N-fixing plants. A significant increase in soil C was found in the upper mineral soil and in the total soil C pool. A less consistent response was found in a N-fertilization experiment with *Pinus ponderosa* seedlings. The effect of ammonium sulphate on the soil C pool did not differ significantly from the control (Johnson et al., 2000; Johnson and Curtis, 2001).

The effects of N fertilization on the soil C pool vary widely and depend on subsequent soil processes. Often a decrease in the soil C:N ratio is observed, indicating that the N retention effect of the soils is stronger than the C sequestration (Johnson and Curtis, 2001; Jandl et al., 2003). By contrast, a Swedish fertilization experiment to a mature pine forest with very high N applications rates doubled the C pool of the forest floor within 20 years (+5 to 9 t C/ha). This response was interpreted as a consequence of the greatly accelerated growth rate, which in return led to a massive increase in the litter production but also to a decrease in the decomposition rate (Nohrstedt, 1990; Franklin et al., 2003).

Fertilization of forests can lead to the sequestration of larger amounts of soil C than is feasible by afforestation projects. However, the results are site specific and no general recommendation for greater regions can be derived (Canary et al., 2000; Chen et al., 2000).

Nitrogen fertilization stimulates biomass production, but the effect on the soil C pool is more complex. It stimulates the microbial decomposition of SOM, which can lead to a net C loss from the soil and can lead to the formation of nitrogen oxides. The effect of C sequestration in the aboveground biomass is then partly offset by the production of N_2O . This has been shown in agricultural as well as in forest ecosystems (Brumme and Beese, 1992; Mosier et al., 1998). It can be concluded that N fertilization has positive effects on ecosystem level C pools on nutrient-limited sites. However, widespread anthropogenic N deposition has greatly reduced the area of European forests with severe N deficiency. The effects on soil C sequestration are variable.

7.2. Natural aggradation of forests

Many European forests recover from exploitative uses such as litter raking, unregulated fellings, and coppicing (Farrell et al., 2000). Increasing the length of the growing season, N deposition, improved forest management, as well as the enrichment effect of CO₂ has all enhanced the growth rate. In many countries annual increment exceeds the harvest (Spiecker et al., 1996, Fig. 4). Gradually, old forests with a high standing biomass are becoming more common. The current conclusion is that N deposition exerts a fertilization effect on the aboveground biomass, but the effect on soil C is uncertain and at best weak (Nadelhoffer et al., 1999; Davidson and Hirsch, 2001; Oren et al., 2001; Schlesinger and Lichter, 2001; Pussinen et al., 2002).

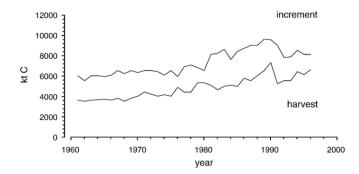


Fig. 4. The persistent difference between increment and harvest leads to C sequestration — example: Austrian forests. Sources: Austrian National Forest Inventory, Austrian Carbon Balance (Weiss et al., 2000).

The interaction between productivity, C sequestration and N availability was confirmed with pan-European data. The C sequestration potential closely follows a deposition gradient: in Northern Europe, where the rate of N deposition is small, C sequestration is also small. A large part of the N is retained in the vegetation and the productivity of the forests is increased. By contrast, both the C sequestration and the N deposition are high in Central and Eastern Europe. The increase in N availability leads to greater productivity and more C sequestration until future constraints to growth are imposed (de Vries et al., 2003). Insufficient water supply may become more common as a result of climate change. The shortage will be aggravated by the increasing water demand of forests, whose productivity will have changed by the increasing length of the growing season and the higher N availability.

7.3. Liming

In Central and Northern Europe many forest soils have been limed in the past in order to regulate soil and surface water chemistry, to protect the ecosystem from irreversible acidification and to mobilize recalcitrant forest floor material (Fiedler et al., 1973; von Wilpert and Schäffer, 2000). However, the target of mobilizing the forest floor is in conflict with the objective of C sequestration. A literature review showed that liming causes a net loss of C in temperate and boreal forests owing to increased microbial activity and DOC leaching (Brumme and Beese, 1992; Jandl et al., 2003; Lundström et al., 2003).

In two fertilizer experiments NPK was applied together with lime. The intention of this 'harmonized amelioration' was the mobilization of nutrients from the forest floor and the provision of readily available nutrients. The overall effect on C is a net loss from the soil (Fig. 5). In the experiment 'Dobrowa' the total soil C content was reduced, whereas in 'Altmanns' C was transferred from the previously inactive mor layer to the mineral soil. In both cases, SOM was mobilized.

7.4. Water management — peatlands

In peat soils, excess water suppresses the rate of decomposition of SOM and leads to C accumulation. It does not influence

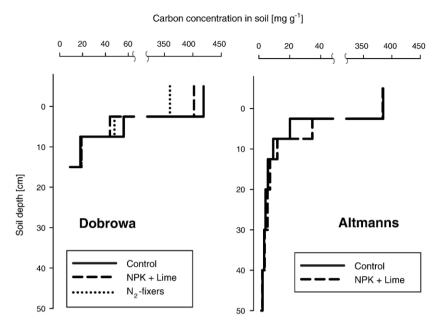


Fig. 5. Effect of NPK fertilization, liming and planting of N₂-fixers (*Lupinus heterophyllus*) on soil C in two Austrian amelioration experiments; Dobrowa (Jandl et al., 2003) and Altmanns (Jandl et al., 2002).

its stabilization. As a result of soil anoxia natural peatlands emit the greenhouse gas methane (CH₄) while nitrous oxide (N₂O) emissions from natural mires are insignificant (Martikainen et al., 1993). In the Nordic countries, approximately 15 million ha peatland have been drained for forestry (Paavilainen and Päivänen, 1995). Drainage stimulates the productivity of forested peatlands and enables the establishment of a forest in otherwise treeless peatlands. Global warming and drainage would result in peatlands becoming drier and the increased microbial activity could turn boreal mires from C sinks to C sources (Moore and Dalva, 1993; Silvola et al., 1996). On the other hand CH₄ emissions would decrease for the same reasons (Nykänen et al., 1998). The increased decomposition of organic matter following drainage is at least partly compensated by the higher inflow of C into the system through increases in plant biomass and primary production and decreases in soil temperature, soil pH and litter decomposability (Minkkinen et al., 1999; Laiho et al., 2003). Leaching of dissolved organic C (DOC) increases immediately after digging the drainage network, but returns to pre-drainage levels later on (Ahtiainen, 1988; Sallantaus, 1994). Direct measurements of soil C balances in peatlands are rare, but both decreases and increases following drainage have been reported (Braekke and Finer, 1991; Sakovets and Germanova, 1992; Minkkinen and Laine, 1998; Minkkinen et al., 1999; Gustafsson, 2001; Hargreaves et al., 2003; Byrne and Farrell, 2005). As C stores in vegetation nearly always increase following forestry drainage, peatlands may remain C sinks despite C losses from the soil (Minkkinen et al., 2002; Hargreaves et al., 2003; Laiho et al., 2003). To conclude, forest drainage decreases CH₄ emissions, increases N₂O and CO₂ emissions from peat, but increases C sequestration in the vegetation. Simulations using data from Finnish peatlands indicated that the radiative forcing of forest drainage may even be negative, i.e. drainage may have a "cooling" effect on the global

climate during the first centuries (Laine et al., 1996; Minkkinen et al., 2002).

7.5. Site preparation

Site preparation promotes rapid establishment, early growth and good survival of seedlings. Techniques include manual, mechanical, chemical methods and prescribed burning, most of which include the exposure of the mineral soil by removal or mixing of the organic layer. The soil disturbance changes the microclimate and stimulates the decomposition of SOM, thereby releasing nutrients (Palmgren, 1984; Johansson, 1994). Another effect is improved water infiltration into the soil and better root development. The recent trend towards nature-oriented forest management reduces the importance of site preparation. A review on the effects of site preparation showed a net loss of soil C and an increase in productivity (Johnson, 1992). The effects varied with site and treatment. Several studies that compared different site preparation methods found that the loss of soil C increased with the intensity of the soil disturbance (Johansson, 1994; Örlander et al., 1996; Schmidt et al., 1996; Mallik and Hu, 1997). At scarified sites, organic matter in logging residues and humus, mixed with or buried beneath the mineral soil, is exposed to different conditions for decomposition and mineralization compared with conditions existing on the soil surface of clearcut areas. The soil moisture status of a site has great importance for the response to soil scarification. The increase in decomposition was more pronounced at poor, coarsely textured dry sites than on richer, moist to wet sites (Johansson, 1994). Sandy soils are particularly sensitive to management practices, which result in significant losses of C and N (Carlyle, 1993). Intensive site preparation methods might result in increased nutrient losses and decreased long-term productivity (Lundmark, 1988). In most of the reviewed studies biomass production was favored by site

preparation and this effect may balance or even outweigh the loss of soil C in the total ecosystem response. In conclusion, there is in general a net loss of soil C with site preparation, which increases with the degree of disturbance. The chosen technique of site preparation is important and will determine if the net C effect of the activity is positive or negative.

8. Discussion

Forest soils are considered to have a considerable potential as C sinks (Frolking et al., 1996; Perruchoud et al., 1999; Halliday et al., 2003). Modeling studies suggest that European forest soils are currently sequestering 26 Tg C yr⁻¹, i.e. 30-50% of the estimated C sink in the forest biomass (Liski et al., 2002). However, modeled accumulation rates of soil C have so far not been detected in nature. Field and process-based studies conclude that the rate of soil C accumulation is small, compared with the C accretion in the aboveground biomass, because only a small proportion of plant-derived C becomes stabilized in the mineral soil (Martin and Haider, 1986; Mayer, 1994; Richter et al., 1999; Kaiser and Guggenberger, 2003; Giardina et al., 2005). Either the understanding of the geochemical C fluxes is still incomplete, or the accumulation occurs, but much slower than predicted, or the changes are not detectable owing to the spatial and temporal variability of soil C.

Efforts to increase soil C storage should ideally increase the pool of recalcitrant C. Nevertheless, an increase in less stable pools is also relevant when these pools are sustained by a continuous input of organic matter. The recovery of degraded forest ecosystems and the afforestation of land after agricultural use are cases, that affect mostly the C pool in the forest floor, which is not stabilized by the formation of organo-mineral complexes.

In regions where exploitative historic land-use practices have reduced the soil C pool, one option is to foster the restoration of the previous forest type. This can be achieved by ameliorations, such as underplanting, liming, and fertilizer application, or through a natural aggradation process, which is supported by anthropogenic N deposition and climatic change (Jandl et al., 2002). The response of the aboveground biomass is often an increase in productivity. A temporary soil C sink exists, where intensive litter raking has greatly depleted the soil C pool, and where the previous level can be re-established. At other sites, the nutrient export has created unfavorable conditions for soil microorganisms and biologically inactive mor humus layers have formed. Their mobilization leads to the formation of more favorable humus forms (Jandl et al., 2003). There, site recovery leads to a reduction of the C pool in the forest floor. The C losses may or may not be offset by C gains in the mineral soil and the aboveground biomass. Forest floor C is physically and chemically less stable than C in the mineral soil and can be respired within a few decades under changed site conditions (Covington, 1981; Hamilton et al., 2002). Its mineralization can very quickly turn forest soils from a C sink into a C source.

Afforestation affects the C pool in the forest floor more strongly than in the mineral soil. The accumulation of a forest floor layer in, *e.g.*, a conifer forest is a C sink. The forest floor should not be discounted with regard to C sequestration, al-

though this C pool is more volatile than mineral soil C and can be lost upon changing site conditions. A long-term consequence of afforestation is the gradual incorporation of C in the mineral-associated soil C pool. This effect is by no means intermediate (DeGryze et al., 2004).

Forest management can stimulate the decomposition of the forest floor and can modify its quality by the tree species selection (quantity and chemical quality of litter, rooting depth) and the thinning regime (microclimate). Several studies have stressed the negative impacts of intensive site preparation on the C balance (Johnson, 1992; Schmidt et al., 1996; Mallik and Hu, 1997). Critical situations are after thinning interventions and the end of the rotation period. Frequent thinning of stands throughout the rotation increases their stability. The lightest thinning operation removes at least those trees which would fall victim to natural mortality (Assmann, 1961). Maintaining a high stand density would maximize the C pool, but would also bear a considerable risk of disturbance. A lower stand density increases the stability of individual trees and thus reduces the risk of C losses

Table 2

Summary of the effects of specific forest management actions on ecosystem C stocks ('+'...increases C stock, '-'...decreases C stock; ' \pm ' neutral with respect to C stock)

Afforestation

- + Accumulation of aboveground biomass formation of a C-rich litter layer and slow build-up of the C pool in the mineral soil
- ± Stand stability depends on the mixture of tree species
- -Monotone landscape, in the case of even-aged mono-species plantations

Tree species

- +Affects stand stability and resilience against disturbances; effect applies for entire rotation period; positive side-effect on landscape diversity, when mixed species stands are established
- -Effect on C storage in stable soil pools controversial and so far insufficiently proven

Stand management

- +Long rotation period ensures less disturbance due to harvesting, many forest operations aim at increased stand stability, every measure that increases ecosystem stability against disturbance
- \pm Different conclusions on the effect of harvesting, depending if harvest residues are counted as a C loss or a C input to the soil
- Forests are already C-rich ecosystems small increase in C possible;
 thinning increases stand stability at the expense of the C pool size; harvesting invariably exports C

Disturbance

- + Effects such as pest infestation and fire can be controlled to a certain extent
- ± Low intensity fires limit the risk of catastrophic events
- Catastrophic (singular) events cannot be controlled; probability of disturbance can rise under changed climatic conditions, when stands are poorly adapted

Site improvement

- +N fertilization affects aboveground biomass; effect on soil C depends on interaction of litter production by trees and carbon use efficiency of soil microbes
- \pm Drainage of peatland enables the establishment of forests (increased C storage in the biomass) and decreases CH_4 emissions from soil, but is linked to the increased release of CO_2 and N_2O from the soil
- -Liming and site preparation always stimulate soil microbial activity. The intended effect of activating the nutrient cycle is adverse to C sequestration; N fertilization leads to emission of potent greenhouse gases from soils

due to disturbance. The presence of biomass residues left on site after thinning plays a role in evaluating C pools. Our view is that this pool of thinning residues is not relevant for C sequestration. Nevertheless, we are aware that thinning residues are a C pool that is not clearly represented, because it neither counts as forest floor material nor as wood product.

A trend towards nature-oriented silviculture and continuous-cover forestry will reduce the relevance of site preparations and clear cuts (Pommerening and Murphy, 2004). The effect of continuous-cover forestry is difficult to assess at the present time, because the long-term impacts have not yet been measured. It is characterized by the avoidance of large canopy openings. The forest floor layer will therefore be less exposed to decomposition and will be rather stable in time, but effects on the recalcitrant C pool as a direct result of management specific processes in the mineral soil are not expected. A relevant factor may be the slow formation of organo-mineral complexes in the undisturbed soil (DeGryze et al., 2004).

The relevance of tree species for the objective of C sequestration in Central Europe invariably leads to a weighing of the benefits and peculiarities of Norway spruce versus beech. On most acidic to neutral sites, spruce produces more stem volume. Consequently, many mixed species stands in Central Europe have been converted to "secondary spruce forests". For the objective of C sequestration, the relevant characteristic is total biomass production. The higher C density of beech wood and the higher production of non-stem aboveground biomass mean, that the total aboveground accumulation of C of the two species is not far apart. Moreover, beech develops a deep rooting system which increases the C pool in the mineral soil (Kreutzer et al., 1986), allowing longer rotation periods than spruce, and increasing the stability of mixed stands (Pretzsch, 2005). Mixed species stands are also less susceptible to pest infestations, whereas secondary spruce forests are notorious for extensive bark beetle damage (Baier et al., 2000). Considering these factors we conclude, that mixtures of beech and spruce are a better forest management option than pure spruce stands, when terrestrial C sinks need to be optimized.

Even though single old-growth forests can have impressive rates of C sequestration (Schulze et al., 2000; Knohl et al., 2003), we are skeptical with respect to the role of the elongation of the rotation period of forests. Forests beyond a certain age are susceptible to disturbances. The aboveground productivity declines with age (Ryan et al., 2004). Openings in the canopy are closed more slowly than in younger stands and old stands are therefore more vulnerable to windthrow. Limits in the expectable life span of forests are evident from records of long-term experimental plots. Only a few of these studies can be continued over decades, whereas most stands disintegrate when they reach maturity (Johann, 2000). Recommendations for the elongation of the rotation period need to be based on experimental evidence obtained from a representative set of stands. These trials still await implementation.

This evaluation of forest management activities indicates that few practices are clearly good or bad with respect to C sequestration (Table 2). Productive forests with a high rate of aboveground and belowground litterfall circulate a large amount

of C and are a precondition for efficient C sequestration. Their overall impact depends on the degree of soil disturbance in the course of harvesting or thinning operations and the degree of stability against disintegration of the stand structure. Two governing processes are the quantity and quality of the litter (C input) and the decomposition of SOM (C output). Optimized forest management with regard to soil C sequestration should aim to secure a high productivity of the forest on the input side, and avoid soil disturbances as much as possible on the output side. Our review shows that forest management directly influences the C flow into the soil. The pathways are both aboveand belowground C fluxes. The subsequent stabilization of SOM in the soil partly depends on soil properties which cannot be influenced by stand management. What is beyond dispute is that the formation of a stable soil C pool requires time. Avoiding soil disturbances is important for the formation of stable organomineral complexes which in turn are crucial elements in the process of C soil sequestration.

References

Ahtiainen, M., 1988. Effects of clear-cutting and forestry drainage on water quality in the Nurmes-study. Proceedings International Symposium on the Hydrology of Wetlands in Temperate and Cold Regions. Joensuu, Finland, pp. 206–219.

Andersson, F., Brække, F.N., Hallbäcken, L., 1998. Nutrition and growth of Norway spruce forests in a Nordic climatic and deposition gradient. Tech. Rep. Tema Nord, vol. 566. Nordic Council of Ministers, København, Denmark.

Assmann, E., 1961. Waldertragskunde — Organische Produktion, Struktur, Zuwachs und Ertrag von Waldbeständen. BLV Verlagsgesellschaft, München.

Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of tree species on soil solutions in acidic conditions. Annals of Forest Science 59, 233–253.

Aussenac, G., 1987. Effets de l'èclaircie sur l'écophysiologie des peuplements forestiers. Schweizerische Zeitschrift fur Forstwesen 138, 685–700.

Baier, P., Führer, E., Kirisits, T., Rosner, S., 2000. Comparison of the resistance of Norway spruce (*Picea abies* [L.] Karst.) in secondary pure spruce and mixed species stands against bark beetles (Coleoptera, Scolytidae) and the associated blue stain fungus *Ceratocystis polonica* (Siem.) C. Moreau. In: Hasenauer, H. (Ed.), Forest Ecosystem Restoration — Ecological and Economical Impacts of Restoration. Processes in Secondary Coniferous Forests. Universität für Bodenkultur, Institute of Forest Growth Research, Vienna.

Bashkin, M.A., Binkley, D., 1998. Changes in soil carbon following afforestation in Hawaii. Ecology 79, 828–833.

Batjes, N., 1996. Total carbon and nitrogen in the soils of the world. European Journal of Soil Science 47, 151–163.

Bauer, H. 1989. Nährstoffvorräte von Fichtenbeständen auf einer Standortseinheit des Kobernausser Waldes. Master's thesis, Universität für Bodenkultur.

Berg, B., Matzner, E., 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environmental Reviews 5, 1–25.

Berg, B., Meetemeyer, V., 2002. Litter quality in a north European transect versus carbon storage potential. Plant and Soil 242, 83–92.

Berger, T., Neubauer, C., Glatzel, G., 2002. Factors controlling soil carbon and nitrogen stores in pure stands of Norway spruce (*Picea abies*) and mixed species stands in Austria. Forest Ecology and Management 159, 3–14.

Binkley, D., 1995. The influence of tree species on forest soils: processes and patterns. In: Mead, D., Comfort, I. (Eds.), Proceedings of the Trees and Soil Workshop. Agronomy Society of New Zealand, Lincoln University Press, Canterbury, pp. 1–33.

Binkley, D., Menyailo, O., 2005. Gaining insights on the effects of trees on soils. In: Binkley, D., Menyailo, O. (Eds.), Tree Species Effects on Soils: Implications for Global Change. Springer, New York, pp. 1–16. NATO Science Series.

- Bolin, B., Sukumar, R., Ciais, P., Cramer, W., Jarvis, P., Kheshgi, H., Nobre, C., Semonov, S., Steffen, W., 2000. Global perspective. In: Watson, R., Noble, I., Bolin, B., Ravindranath, N., D.J., V., Dokken, D. (Eds.), Land Use, Land-Use Change, and Forestry. Cambridge University Press, Cambridge, pp. 23–52.
- Böttcher, J., Springob, G., 2001. A carbon balance model for organic layers of acid forest soils. Journal for Plant Nutrition and Soil Science 164, 399–405.
- Braekke, F., Finer, L., 1991. Fertilization effects on surface peat of pine bogs. Scandinavian Journal of Forest Research 6, 433–449.
- Brown, S., Sathaye, J., Cannell, M., 1996. Management of forests for mitigation of greenhouse gas emissions. In: Watson, R., Zinyowera, M., Moss, R. (Eds.), Climate Change 1995. Impacts, Adaptation and Mitigation of Climate Change: Scientific—Technical Analyses. Contribution of WG II to the Second Assessment Report of the IPCC. Cambridge University Press, Cambridge, pp. 773–797.
- Brumme, R., Beese, F., 1992. Effects of liming and nitrogen fertilization on emissions of CO₂ and N₂O from a temperate forest. Journal of Geophysical Research 97, 12851–12858.
- Burschel, P., Kuersten, E., Larson, B., Weber, M., 1993. Present role of German forests and forestry in the national carbon budget and options to its increase. Water, Air, and Soil Pollution 325–340.
- Byrne, K.A., Farrell, E.P., 2005. The effect of afforestation on soil carbon dioxide emissions in blanket peatland in Ireland. Forestry 78, 217–227.
- Callesen, I., Liski, J., Raulund-Rasmussen, K., Olsson, M.T., Tau-Strand, L., Vesterdal, L., Westman, C.J., 2003. Soil carbon stores in Nordic welldrained forest soils relationships with climate and texture class. Global Change Biology 9, 358–370.
- Canary, J., Harrison, R., Compton, J., Chappell, H., 2000. Additional carbon sequestration following repeated urea fertilization of second-growth Douglas-fir stands in western Washington. Forest Ecology and Management 138, 225–232.
- Cannell, M.G., 1999a. Environmental impacts of forest monocultures: water use, acidification, wildlife conservation, and carbon storage. New Forests 17, 239–262.
- Cannell, M.G., 1999b. Growing trees to sequester carbon in the UK: answers to some common questions. Forestry 72, 237–247.
- Cannell, M.G., 2003. Carbon sequestration and biomass energy offset: theoretical, potential and achievable capacities globally, in Europe and the UK. Biomass and Bioenergy 24, 97–116.
- Carey, M., Hunter, I., Andrew, I., 1982. *Pinus radiata* forest floors: factors affecting organic matter and nutrient dynamics. New Zealand Journal of Forest Science 12, 36–48.
- Carlyle, J., 1993. Organic carbon in forested sandy soils: properties, processes, and the impact of forest management. New Zealand Journal Forest Science 23, 390–402.
- Chen, W., Chen, J.M., Price, D.T., Cihlar, J., Liu, J., 2000. Carbon offset potentials of four alternative forest management strategies in Canada: a simulation study. Mitigation and Adaptation Strategies for Global Change 5, 143–169
- Compton, J.E., Boone, R.D., Motzkin, G., Foster, D.R., 1998. Soil carbon and nitrogen in a pine-oak sand plain in central Massachusetts: role of vegetation and land-use history. Oecologia 116, 536-542.
- Conen, F., Zerva, A., Arrouays, D., Jolivet, C., Jarvis, P., Grace, J., Mencuccini, M., 2004. The carbon balance of forest soils: detectability of changes in soil carbon stocks in temperate and boreal forests. In: Griffiths, H., Jarvis, P. (Eds.), The Carbon Balance of Forest Biomes, vol. 9. Garland Science/BIOS Scientific Publishers, Southampton, UK, pp. 233–247. chap. 11.
- Covington, W.W., 1981. Changes in forest floor organic mater and nutrient content following clear cutting in northern hardwoods. Ecology 62, 41–48.
- Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187.
- Davidson, E.A., Hirsch, A.I., 2001. Carbon cycle fertile forest experiments. Nature 411, 431–433.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.
- de Vries, W., Reinds, G.J., Posch, M., Sanz, M., Krause, G., Calatyud, V., Dupouey, J., Sterba, H., Gundersen, P., Voogd, J., Vel, E., 2003. Intensive

- Monitoring of Forest Ecosystems in Europe. Tech. Rep., EC. UN/ECE, Brussels.
- de Wit, H., Kvindesland, S., 1999. Carbon Stocks in Norwegian Forest Soils and Effects of Forest Management on Carbon Storage. Rapport fra skogforskningen — Supplement. Forest Research Institute, Ås, Norway.
- DeGryze, S., Six, J., Paustian, K., Morris, S.J., Paul, E.A., Merckx, R., 2004. Soil organic carbon pool changes following land-use conversions. Global Change Biology 10, 1120–1132.
- Dieter, M., 2001. Land expectation values for spruce and beech calculated with Monte Carlo modelling techniques. Forest Policy and Economics 2, 157–166.
- ECCP-Working group on forest sinks, 2003. Conclusions and Recommendations Regarding Forest Related Sinks and Climate Change Mitigation. Tech. Rep., EC-DG Environment http://www.europa.eu.int/comm/environment/climat/forestrelatedsinks.htm.
- Erb, K.-H., 2004. Land-use related changes in aboveground carbon stocks of Austrias terrestrial ecosystems. Ecosystems 7, 563–572.
- Eriksson, H., Berdén, M., Rosén, K., Nilsson, S., 1996. Nutrient distribution in an Norway spruce stand after long-term application of ammonium nitrate and superphosphate. Water, Air, and Soil Pollution 92, 451–467.
- Farrell, E.P., Führer, E., Ryan, D., Andersson, F., Hüttl, R., Piussi, P., 2000. European forest ecosystems: building the future on the legacy of the past. Forest Ecology and Management 132, 5–20.
- Fiedler, H.J., Nebe, W., Hoffmann, F., 1973. Forstliche Pflanzenernährung und Düngung. G. Fischer Verlag, Stuttgart.
- Fischer, H., Bens, O., Hüttl, R., 2002. Veränderung von Humusform, -vorrat und -verteilung im Zuge von Waldumbau-Massnahmen im nordostdeutschen Tiefland. Forstwissenschaftliches Centralblatt 121, 322–334.
- Fisher, R.F., Binkley, D., 2000. Ecology and Management of Forest Soils, third ed. John Wiley & Sons, Inc., New York.
- Fog, K., 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biological Reviews 63, 433–462.
- Franklin, O., Högberg, P., Ekblad, A., Ågren, G.I., 2003. Pine forest floor carbon and accumulation in response to N and PK additions: bomb ¹⁴C modelling and respiration studies. Ecosystems 6, 644–658.
- Freeman, C., Ostle, N., Kang, H., 2001. An enzymatic latch on a global carbon store. Nature 409, 149.
- Frolking, S., Goulden, M., Wofsy, S., Fan, S., Sutton, D., Munger, J., Bazzaz, A., Daube, B., Grill, P., Aber, J., Band, L., Wang, X., Savage, K., Moore, T., Harriss, R., 1996. Modelling temporal variability in the carbon balance of a spruce/moss boreal forest. Global Change Biology 2, 343–366.
- Fyles, J., Coté, B., Courchesne, F., Hendershot, W., Savoie, S., 1994. Effects of base cation fertilization on soil and foliage nutrient concentrations, and litterfall and throughfall nutrient fluxes in a sugar maple forest. Canadian Journal of Forest Research 24, 542–549.
- Gaudinski, J.B., Trumbore, S.E., Davidson, E.A., Zheng, S., 2000. Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. Biogeochemistry 51, 33–69.
- Giardina, C.P., Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404, 858–561.
- Giardina, C.P., Ryan, M.G., 2002. Total belowground carbon allocation in a fast-growing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems 5, 487–499.
- Giardina, C.P., Coleman, M.D., Hancock, J.E., King, J.S., Lilleskov, E.A., Loya, W.M., Pregitzer, K.S., Ryan, M.G., Trettin, C.C., 2005. The response of belowground carbon allocation in forests to global change. In: Binkley, D., Menyailo, O. (Eds.), Tree Species Effects on Soils: Implications for Global Change. Springer, New York, pp. 119–154. NATO Science Series.
- Goulden, M., Wofsy, S., Harden, J., Trumbore, S., Crill, P., Gower, T., Fries, T., Daube, B., Fan, S., Sutton, D., Bazzaz, A., Munger, J., 1998. Sensitivity of boreal forest carbon balance to soil thaw. Science 279, 214–217.
- Gundersen, P., Emmett, B., Kjønaas, O., Koopmans, C., Tietema, A., 1998. Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. Forest Ecology and Management 101, 37–55.
- Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. Global Change Biology 8, 345–360.
- Gustafsson, M., 2001. Carbon loss after forest drainage of three peatlands in southern Sweden. Master's thesis, Department of Forest Soils SLU, Uppsala Sweden.

- Hagedorn, F., Spinnler, D., Bundt, M., Blaser, P., Siegwolf, R., 2003. The input and fate of new C in two forest soils under elevated CO₂. Global Change Biology 9, 862–872.
- Hager, H., 1988. Stammzahlreduktion Die Auswirkungen auf Wasser-, Energie- und N\u00e4hrstoffhaushalt von Fichtenjungw\u00fcchsen. Forstliche Schriftenreihe der Universit\u00e4t f\u00fcr Bodenkultur 1, 1-189.
- Halliday, J.C., Tate, K.R., McMurtrie, R.E., Scott, N.A., 2003. Mechanisms for changes in soil carbon storage with pasture to *Pinus radiata* land-use change. Global Change Biology 4, 1294–1308.
- Hamilton, J.G., DeLucia, E.H., George, K., Naidu, S.L., Finzi, A.C., Schlesinger, W.H., 2002. Forest carbon balance under elevated CO₂. Oecologia 131, 250–260.
- Hanson, P., Weltzin, J., 2000. Drought disturbance from climate change: response of United States forests. The Science of the Total Environment 262, 205–220.
- Hargreaves, K., Milne, R., Cannell, M., 2003. Carbon balance of afforested peatland in Scotland. Forestry 76, 299–317.
- Harmon, M.E., Marks, B., 2002. Effects of silvicultural practices on carbon stores in Douglas-fir — western hemlock forests in the Pacific Northwest, U.S.A.: results from a simulation model. Canadian Journal of Forest Research 32, 863–877.
- Harmon, M.E., Ferrell, W.K., Franklin, J.F., 1990. Effects of carbon storage of conversion of old-growth forests to young stands. Science 247, 699–702.
- Hirsch, K., Kafka, C., Tymstra, R., McAlpine, B., Hawkes, H., Stegehuis, S., Quintilio, S., Gauthier, S., Peck, K., 2001. FireSmart forest management: a pragmatic approach to sustainable forest management in fire-dominated ecosystems. Forest Chronicle 77, 357–363.
- Hobbie, S.E., Schimel, J.P., Trumbore, S., Randerson, J.R., 2000. Controls over carbon storage and turnover in high-latitude soils. Global Change Biology 6, 196–210.
- Hooker, T.D., Compton, J.E., 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecological Applications 13, 299–313.
- Jandl, R., Kopeszki, H., Bruckner, A., Hager, H., 2003. Forest soil chemistry and mesofauna 20 years after an amelioration fertilization. Restoration Ecology 11, 239–246.
- Jandl, R., Starlinger, F., Englisch, M., Herzberger, E., Johann, E., 2002. Long-term effect of a forest amelioration experiment. Canadian Journal of Forest Research 32, 120–128.
- Janssens, I.A., Freibauer, A., Ciais, P., Smith, P., Nabuurs, G.-J., Folberth, G., Schlamadinger, B., Hutjes, R.W.A., Ceulemans, R., Schulze, E.-D., Valentini, R., Dolman, A.J., 2003. Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO₂ emissions. Science 300, 1538–1542.
- Jarvis, P., Linder, S., 2000. Constraints to growth of boreal forests. Nature 405,
- Jenkinson, D., 1991. The Rothamsted long-term experiments: are they still of use? Agronomy Journal 83, 2–10.
- Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10, 423–436.
- Johann, K., 2000. Ergebnisse von Düngungsversuchen nach 30 Jahren ertragskundlicher Beobachtung. Berichte der FBVA 114, 1–93.
- Johansson, M.-B., 1994. The influence of soil scarification on the turn-over rate of slash needles and nutrient release. Scandinavian Journal of Forest Research 9, 170–179.
- Johnson, D.W., 1992. Effects of forest management on soil carbon storage. Water, Air, and Soil Pollution 83–121.
- Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. Forest Ecology and Management 140, 227–238.
- Johnson, D.W., Cheng, W., Ball, J., 2000. Effects of [CO₂] and nitrogen fertilization on soils planted with ponderosa pine. Plant and Soil 224, 99–113.
- Johnson, D., Knoepp, J., Swank, W., Shan, J., Morris, L., van Lear, D., Kapeluck, P., 2002. Effects of forest management on soil carbon: results of some long-term resampling studies. Environmental Pollution 116, 201–208.
- Johnson, D., Todd, D., Tolbert, V., 2003. Change in ecosystem carbon and nitrogen in a Loblolly pine plantation over the first 18 years. Soil Science Society America Journal 67, 1594–1601.

- Johnson, D., Susfalk, R., Caldwell, T., Murphy, J., Mille, W., Walker, R., 2004.
 Fire effects on carbon and nitrogen budgets in forests. Water, Air, and Soil Pollution: Focus 4, 263–275.
- Kaipainen, T., Liski, J., Pussinen, A., Karjalainen, T., 2004. Managing carbon sinks by changing rotation length in European forests. Environmental Science and Policy 7, 205–219.
- Kaiser, K., Guggenberger, G., 2003. Mineral surfaces and soil organic matter. European Journal of Soil Science 54, 219–236.
- Keil, R.G., Muntlucon, D.B., Prahl, F.G., Hedges, J.I., 1994. Sorptive preservation of labile organic matter in marine sediments. Nature 370, 549–552.
- Kennedy, M.J., Pevear, D.R., Hill, R.J., 2002. Mineral surface control of organic carbon in black shale. Science 295, 657–660.
- Kirschbaum, M.U., 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? Biogeochemistry 48, 21–51.
- Kirschbaum, M.U., 2004. Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? Global Change Biology 10, 1870–1877.
- Knohl, A., Kolle, O., Minayeva, T., Milyukova, I.M., Vygodskaya, N., Fokens, T., Schulze, E.D., 2002. Carbon dioxide exchange of a Russian boreal forest after disturbance by wind throw. Global Change Biology 8, 231–246.
- Knohl, A., Schulze, E.-D., Kolle, O., Buchmann, N., 2003. Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. Agricultural and Forest Meteorology 118, 151–167.
- Knorr, W., Prentice, I., House, J., Holland, E., 2005. Long-term sensitivity of soil carbon turnover to warming. Nature 433, 298–301.
- Kowalski, A.S., Loustau, D., Berbigier, P., Manca, G., Tedeschi, V., Borghetti, M., Valentini, R., Kolari, P., Berninger, F., Rannik, Ü., Hari, P., Rayment, M., Mencuccini, M., Moncrieff, J., Grace, J., 2004. Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe. Global Change Biology 10, 1707–1723.
- Kreutzer, K., Deschu, E., Hösl, G., 1986. Vergleichende Untersuchungen uber den Ein-fluβ von Fichte (*Picea abies* [L.] Karst.) und Buche (*Fagus sylvatica* L.) auf die Sickerwasserqualität. Forstwissenschaftliches Central-blatt 105, 364–371.
- Laiho, R., Vasander, H., Penttilä, T., Laine, J., 2003. Dynamics of plant-mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands. Global Biogeochemical Cycles 17. doi:10.1029/(2002)GB002015.
- Laine, J., Silvola, J., Tolonen, K., Alm, J., Nykänen, H., Vasander, H., Sallantaus, T., Savolainen, I., Sinisalo, J., Martikainen, P.J., 1996. Effect of water level drawdown in northern peatlands on the global climatic warming. Ambio 25, 179–184.
- Lal, R., 2004. Soil carbon sequestration impacts on climate change and food security. Science 304, 1623–1627.
- Liski, J., 1995. Variation in soil organic carbon and thickness of soil horizons within a boreal forest stand — effect of trees and implications for sampling. Silva Fennica 29, 255–266.
- Liski, J., Ilvesniemi, H., Mäkelä, A., Westman, C.J., 1999. CO₂ emissions from soil in response to climatic warming are overestimated—the decomposition of old soil organic matter is tolerant to temperature. Ambio 28, 171–174.
- Liski, J., Pussinen, A., Pingoud, K., Mäkipää, R., Karjalainen, T., 2001. Which rotation length is favourable to carbon sequestration? Canadian Journal of Forest Research 31, 2004–2013.
- Liski, J., Perruchoud, D., Karjalainen, T., 2002. Increasing carbon stocks in the forest soils of western Europe. Forest Ecology and Management 169, 159–175
- Liski, J., Nissinen, A., Erhard, M., Taskinen, O., 2003. Climate effects on litter decomposition from arctic tundra to tropical rainforest. Global Change Biology 9, 575–584.
- Löwe, H., Seufert, H., Raes, F., 2000. Comparison of methods used within member states for estimating CO₂ emissions and sinks according to UNFCCC and EU monitoring mechanism: forest and other wooded land. Biotechnology, Agronomy, Society and Environment 4, 315–319.
- Loya, W.M., Pregitzer, K.S., Karberg, N.J., King, J.S., Giardina, C.P., 2003. Reduction of soil carbon formation by tropospheric ozone under increased carbon dioxide levels. Nature 425, 705–707.
- Lundmark, J., 1988. Skogsmarkens Ekologi, del II, tillämpning (The Forest Soil's Ecology, Part II, Application). Skogsstyrelsen, Jönköping.

- Lundström, U., Bain, D., Taylor, A., van Hees, P., 2003. Effects of acidification and its mitigation with lime and wood ash on forest soil processes: a review. Water, Air, and Soil Pollution, Focus 3, 5–28.
- Luo, Y., Wan, S., Hui, D., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413, 622–625.
- Magill, A.H., Aber, J.D., 1998. Long-term effects of experimental nitrogen additions on foliar litter decay and humus formation in forest ecosystems. Plant and Soil 203, 301–311.
- Mäkipää, R., 1995. Effect of nitrogen input on carbon accumulation of boreal forest soils and ground vegetation. Forest Ecology and Management 79, 217–226.
- Mallik, A., Hu, D., 1997. Soil respiration following site preparation treatments in boreal mixedwood forest. Forest Ecology and Management 97, 265–275.
- Markewitz, D., Sartori, F., Craft, C., 2002. Soil change and carbon storage in longleaf pine stands planted on marginal agricultural lands. Ecological Applications 12, 1276–1285.
- Martikainen, P., Nykänen, H., Crill, P., Silvola, J., 1993. Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. Nature 366, 51–53
- Martin, J.P., Haider, K., 1986. Influence of mineral colloids on turnover rates of soil organic carbon. Interactions of Soil Minerals with Natural Organics and Microbes. Soil Science Society of America, pp. 283–304. chap. 9.
- Mayer, L.M., 1994. Relationships between mineral surfaces and organic carbon concentrations in soils and sediments. Chemical Geology 114, 347–363.
- Melillo, J., Steudler, P., Aber, J., Newkirk, K., Lux, H., Bowles, F., Catricala, C., Magill, A., Ahrens, T., Morrisseau, S., 2002. Soil warming and carboncycle. Feedbacks to the climate system. Science 298, 2173–2176.
- Minkkinen, K., Laine, J., 1998. Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland. Canadian Journal of Forest Research 28, 1267–1275.
- Minkkinen, K., Vasander, H., Jauhiainen, S., Karsisto, M., Laine, J., 1999. Post-drainage changes in vegetation composition and carbon balance in Lakkasuo mire Central Finland. Plant and Soil 207, 107–120.
- Minkkinen, K., Korhonen, R., Savolainen, T., Laine, J., 2002. Carbon balance and radiative forcing of Finnish peatlands 1900–2100 — the impact of forestry drainage. Global Change Biology 8, 785–799.
- Moore, T., Dalva, M., 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. Journal of Soil Science 44, 651–664.
- Mosier, A., Kroeze, C., Nevison, C., Oenema, O., Seitzinger, S., van Cleemput, O., 1998. Closing the global N2O budget: nitrous oxide emissions through the agricultural nitrogen cycle. Nutrient Cycling in Agroecosystems 52, 225–248.
- Murty, D., Kirschbaum, M., McMurtrie, R., McGilvray, H., 2002. Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. Global Change Biology 8, 105–123.
- Nadelhoffer, K.J., Emmett, B.A., Gundersen, P., Kjønaas, O.J., Koopmans, C.J., Schleppi, P., Tietema, A., Wright, R.F., 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398, 145–148.
- Neff, J.C., Townsend, A.R., Gleixner, G., Lehman, S.J., Turnbull, J., Bowman, W.D., 2002. Variable effects of nitrogen additions on the stability and turnover of soil carbon. Nature 419, 915–917.
- Nohrstedt, H.-O., 1990. Effects of repeated nitrogen fertilization with different doses on soil properties in a *Pinus sylvestris* stand. Scandinavian Journal of Forest Research 5, 3–15.
- Nykänen, H., Alm, J., Silvola, J., Tolonen, K., Martikainen, P., 1998. Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. Global Biogeochemical Cycles 12, 53–69.
- Olsson, B., Staaf, H., Lundkvist, H., Bengtsson, H., Rosén, J., 1996. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. Forest Ecology and Management 82, 19–32.
- Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schäfer, K.V., McCarthy, H., Hendrey, G., McNulty, S.G., Katul, G.G., 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. Nature 411, 469–472.
- Örlander, G., Egnell, G., Albrektsson, A., 1996. Long-term effects of site preparation on growth in Scots pine. Forest Ecology and Management 86, 27–37.

- Paavilainen, E., Päivänen, J., 1995. Peatland Forestry Ecology and Principles. Ecological Studies, vol. 111. Springer, Berlin.
- Page, S.E., Siegert, F., Rieley, J.O., Boehm, H.-D.V., Jaya, A., Limin, S., 2002. The amount of carbon released from peat and forest fires in Indonesia during 1997. Nature 420, 61–65.
- Palmgren, K., 1984. Microbiological changes in soil following soil preparation and liming (in Finnish, English abstract). Folia Forestalia 603, 1–27.
- Paul, E., Clark, F., 1989. Soil Microbiology and Biochemistry. Academic Press, San Diego.
- Paul, K., Polglase, P., Nyakuengama, J., Khanna, P., 2002. Change in soil carbon following afforestation. Forest Ecology and Management 168, 241–257.
- Paul, K.I., Polglase, P.J., Richards, G.P., 2003. Predicted change in soil carbon following afforestation or reforestation, and analysis of controlling factors by linking a c accounting model (CAMFor) to models of forest growth (3PG), litter decomposition (GENDEC) and soil C turnover (RothC). Forest Ecology and Management 177, 485–501.
- Pennock, D., van Kessel, C., 1997. Clear-cut forest harvest impacts on soil quality indicators in the mixedwood forest of Saskatchewan, Canada. Geoderma 75, 13–32.
- Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., Karnosky, D.F., 2002. Altered performance of forest pests under atmospheres enriched by CO₂ and O₃. Nature 420, 403–407.
- Perruchoud, D., Joos, F., Fischlin, A., Hajdas, I., Bonani, G., 1999. Evaluating timescales of carbon turnover in temperate forest soils with radiocarbon data. Global Biogeochemical Cycles 13, 555–573.
- Piene, H., van Cleve, K., 1978. Weight loss of litter and cellulose bags in a thinned white spruce forest in interior Alaska. Canadian Journal of Forest Research 8, 42–46.
- Pommerening, A., Murphy, S., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77, 27–44.
- Post, W., Kwon, K., 2000. Soil carbon sequestration and land-use change: processes and potential. Global Change Biology 6, 317–328.
- Powlson, D., 2005. Will soil amplify climate change? Nature 433, 204–205.
- Prescott, C., Vesterdal, L., Pratt, J., Venner, K., de Montigny, L., Trofymow, J., 2000. Nutrient concentrations and nitrogen mineralization in forest floors of single species conifer plantations in coastal British Columbia. Canadian Journal of Forest Research 30, 1341–1352.
- Pretzsch, H., 2005. Diversity and productivity in forests: evidence from long-term experimental plots. In: Scherer-Lorenzen, M., Körner, C., Schulze, E. (Eds.), Forest Diversity and Function: Temperate and Boreal Systems. Springer Verlag, Berlin, pp. 41–64. chap. 3.
- Pussinen, A., Karjalainen, T., Mäkipää, R., Valsta, L., Kellomäki, S., 2002. Forest carbon sequestration and harvests in Scots pine stand under different climate and nitrogen deposition scenarios. Forest Ecology and Management 158, 103–115.
- Resh, S.C., Binkley, D., Parrotta, J.A., 2002. Greater soil carbon sequestration under nitrogen-fixing trees compared with eucalyptus species. Ecosystems 5, 217–231.
- Richter, D.D., Markewitz, D., Trumbore, S.E., Wells, C.G., 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. Nature 400, 56–58.
- Romanyá, J., Cortina, J., Falloon, P., Coleman, K., Smith, P., 2000. Modelling changes in soil organic matter after planting fast-growing *Pinus radiata* on mediterranean agricultural soils. European Journal of Soil Science 51, 627–641.
- Römkens, P., van der Pflicht, J., Hassink, J., 1999. Soil organic matter dynamics after the conversion of arable land to pasture. Biology and Fertility of Soils 28, 277–284.
- Rothe, A., Kreutzer, K., Küchenhoff, H., 2002. Influence of tree species composition on soil and soil solution properties in two mixed spruce-beech stands with contrasting history in southern Germany. Plant and Soil 240, 47–56.
- Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.

- Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., Senock, R.S., 2004. An experimental test of the causes of forest growth decline with stand age. Ecological Monographs 74, 393–414.
- Sakovets, V., Germanova, N., 1992. Changes in the carbon balance of forested mires in Karelia due to drainage. Suo 43, 249–252.
- Sallantaus, T., 1994. Response of leaching from mire ecosystems to changing climate. In: Kanninen, M., Heikinheimo, P. (Eds.), The Finnish Research Programme on Climate Change, pp. 291–296. The Academy of Finland, Helsinki, second progress report ed.
- Schimel, D.S., 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1, 77–91.
- Schlamadinger, B., Marland, G., 1996. The role of forest and bioenergy strategies in the global carbon cycle. Biomass and Bioenergy 10, 275–300.
- Schlesinger, W.H., Lichter, J., 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. Nature 411, 466–469.
- Schlesinger, W.H., Palmer Winkler, J., Megonigal, J.P., 2000. Soils and the global carbon cycle. In: Wigley, T., Schimel, D. (Eds.), The Carbon Cycle. Ecological Studies, vol. 142. Cambridge University Press, Cambridge, pp. 93–101. chap. 6.
- Schmidt, M., Macdonald, S., Rothwell, R., 1996. Impacts of harvesting and mechanical site preparation on soil chemical properties of mixed-wood boreal forest sites in Alberta. Canadian Journal of Soil Science 76, 531–540.
- Schöne, D., Schulte, A., 1999. Forstwirtschaft nach Kyoto: Ansätze zur Quantifizierung und betrieblichen Nutzung von Kohlenstoffsenken. Forstarchiv 70, 167–176.
- Schulze, E.D., Lloyd, J., Kelliher, F.M., Wirth, C., Rebmann, C., Lühker, B., Mund, M., Knohl, A., Milyukova, I.M., Schulze, W., Ziegler, W., Varlagin, A., Sogachev, A.F., Valentini, R., Dore, S., Grigoriev, S., Kolle, O., Panfyorov, M.I., Tchebakova, N., Vygodskaya, N., 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink a synthesis. Global Change Biology 5, 703–722.
- Schulze, E.-D., Wirth, C., Heimann, M., 2000. Managing forests after Kyoto. Science 289, 2058–2059.
- Silvola, J., Alm, J., Ahlholm, U., Nykänen, H., Martikainen, P., 1996. CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. Journal of Ecology 84, 219–228.
- Six, J., Callewaert, P., Lenders, S., Gryze, S.D., Morris, S.J., Gregorich, E.G., Paul, E.A., Paustian, K., 2002a. Measuring and understanding carbon storage in afforested soils by physical fractionation. Soil Science Society America Journal 66, 1981–1987.
- Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002b. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant and Soil 241, 155–176.
- Sobachkin, R., Sobachkin, D., Buzkykin, A., 2005. The influence of stand density on growth of three conifer species. In: Binkley, D., Menyailo, O. (Eds.), Tree Species Effects on Soils: Implications for Global Change. Springer, New York, pp. 247–255. NATO Science Series.
- Sogn, T.A., Stuanes, A., Abrahamsen, G., 1999. The capacity of forest soils to adsorb anthropogenic N. Ambio 28, 346–349.
- Sollins, P., Homann, P., Caldwell, B., 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74, 65–105.
- Son, Y., Jun, Y., Lee, Y., Kim, R., Yang, S., 2004. Soil carbon dioxide evolution, litter decomposition, and nitrogen availability four years after thinning in a Japanese larch plantation. Communications in Soil Science and Plant Analysis 35, 1111–1122.
- Spiecker, H., Mielikäinen, K., Köhl, M., Skovsgaard, J., 1996. Growth Trends in Europe Studies from 12 Countries. EFI Research Reports, vol. 5. Springer, Heidelberg.
- Spiecker, H., Hansen, J., Klimo, E., Skovsgaard, J., Sterba, H., von Teuffel, K., 2004. Norway Spruce Conversion — Options and Consequences. Research Report, vol. 18. EFI, Brill, Leiden, Boston, Köln.
- Staaf, H., 1987. Foliage litter turnover and earthworm populations in three beech forests of contrasting soil and vegetation types. Oecologia 72, 58–64.
- Stone, E.L., 1975. Effects of species on nutrient cycles and soil change. Philosophical Transactions of the Royal Society of London. B 271, 149–162.
- Suni, T., Vesala, T., Rannik, Ü., Keronen, P., Markkanen, T., Sevanto, S., Grönholm, T., Smolander, S., Kulmala, M., Ojansuu, R., Ilvesniemi, H.,

- Uotila, A., Mäkelä, A., Pumpanen, J., Kolari, P., Berninger, F., Nikinmaa, E., Al, A., 2003. Trace gas fluxes in a boreal forest remain unaltered after thinning. http://www.boku.ac.at/formod/Monday/T_Suni.ppt.
- Thürig, E., Palosuo, T., Bucher, J., Kaufmann, E., 2005. The impact of windthrow on carbon sequestration in Switzerland: a model-based assessment. Forest Ecology and Management 210, 337–350.
- Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. Nature 389, 170–173.
- Torn, M.S., Lapenis, A.G., Timofeev, A., Fischer, M.L., Babikov, B.V., Harden, J.W., 2002. Organic carbon and carbon isotopes in modern and 100-year-old-soil archives of the Russian steppe. Global Change Biology 8, 941–953.
- Trumbore, S., 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. Ecological Applications 10, 399–410.
- Trumbore, S.E., Chadwick, O.A., Amundson, R., 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science 272.
- United Nations Framework Convention on Climate Change, 2002. Report of the Conference of the Parties on its Seventh Session, held at Marrakesh from 29 October to 10 November 2001. Addendum. Part Two: Action Taken by the Conference of the Parties, p. 77. FCCC/CP/2001/13/Add.3, http://unfccc.int/ resource/docs/cop7/13a03.pdf, UNFCCC.
- Valentini, R., Matteucci, G., Dolman, A., Schulze, E.-D., Rebmann, C., Moors, E., Granier, A., Gross, P., Jensen, N., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guõmundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861–865.
- van Veen, J., Kuikman, P., 1990. Soil structural aspects of decomposition of organic matter by micro-organisms. Biogeochemistry 11, 213–233.
- Vejre, H., Callesen, I., Vesterdal, L., Raulund-Rasmussen, K., 2003. Carbon and nitrogen in Danish forest soils — contents and distribution determined by soil order. Soil Science Society America Journal 67, 335–343.
- Vesterdal, L., Raulund-Rasmussen, K., 1998. Forest floor chemistry under seven tree species along a soil fertility gradient. Canadian Journal of Forest Research 28, 1636–1647.
- Vesterdal, L., Dalsgaard, M., Felby, C., Raulund-Rasmussen, K., Jørgensen, B., 1995. Effects of thinning and soil properties on accumulation of carbon, nitrogen and phosphorus in the forest floor of Norway spruce stands. Forest Ecology and Management 77, 1–10.
- Vesterdal, L., Ritter, E., Gundersen, P., 2002a. Change in soil organic carbon following afforestation of former arable land. Forest Ecology and Management 169, 137–147.
- Vesterdal, L., Rosenqvist, L., Johansson, M.-B., 2002b. Effect of afforestation on carbon sequestration in soil and biomass. In: Hansen, K. (Ed.), Planning Afforestation on Previously Managed Arable Land — Influence on Deposition, Nitrate Leaching, and Carbon Sequestration, pp. 63–88. http://www.fsl.dk/afforest.
- Vesterdal, L., Rosenqvist, L., van der Salm, C., Groenenberg, B.-J., Johansson, M.-B., Hansen, K., 2006. Carbon sequestration in soil and biomass following afforestation: experiences from oak and Norway spruce chronosequences in Denmark, Sweden, and the Netherlands. In: Heil, G., Muys, B., Hansen, K. (Eds.), Environmental Effects of Afforestation. Field Observations, Modelling and Spatial Decision Support. Springer, Berlin, p. 999–999.
- Vogt, K., Vogt, D., Brown, S., Tilley, J., Edmonds, R., Silver, W., Siccama, T., 1995. Dynamics of forest floor and soil organic matter accumulation in boreal, temperate, and tropical forests. In: Lal, R., Kimble, J., Levine, E., Stewart, B. (Eds.), Soil Management and Greenhouse Effect, Advances in Soil Science. CRC Press, Boca Raton, Florida, pp. 159–178.
- von Lüpke, B., 2004. Risikominderung durch mischwälder und naturnaher waldbau: ein spannungsfeld. Forstarchiv 75, 43–50.
- von Wilpert, K., Schäffer, J., 2000. Bodenschutzkalkung im Wald. Tech. Rep. 50, FVA Baden-Württemberg, Freiburg/Br.
- Wattel-Koekkoek, E., Buurman, P., van der Plicht, J., Wattel, E., van Breemen, N., 2003. Mean residence time of soil organic matter associated with kaolinite and smectite. European Journal of Soil Science 54, 269–278.

- Weiss, P., Schieler, K., Schadauer, K., Radunsky, K., Englisch, M., 2000. Die Kohlenstoffbilanz des österreichischen Waldes und Betrachtungen zum Kyoto-Protokoll. Monographien, vol. 106. FBVA Umweltbundesamt.
- Wirth, C., Schulze, E.-D., Lühker, B., Grigoriev, S., Siry, M., Hardes, G., Ziegler, W., Backor, M., Bauer, G., Vygodskaya, N., 2002. Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. Plant and Soil 242, 41–63.
- Wollum, A., Schubert, G., 1975. Effect of thinning on the foliage and forest floor properties of ponderosa pine stands. Soil Science Society America Journal 39, 968–972.
- Yanai, R.D., Currie, W.S., Goodale, C.L., 2003. Soil carbon dynamics after forest harvest: an ecosystem paradigm reconsidered. Ecosystems 6, 197–212.
- Zerva, A., Ball, T., Smith, K.A., Mencuccini, M., 2005. Soil carbon dynamics in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) chronosequence on a peaty gley. Forest Ecology and Management 205, 227–240.