

Carbon dynamics in successional and afforested spruce stands in Thuringia and the Alps

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Abstract

Changes in the carbon stocks of stem biomass, organic layers and the upper 50 cm of the mineral soil during succession and afforestation of spruce (*Picea abies*) on former grassland were examined along six chronosequences in Thuringia and the Alps. Three chronosequences were established on calcareous and three on acidic bedrocks. Stand elevation and mean annual precipitation of the chronosequences were different. Maximum stand age was 93 years on acid and 112 years on calcareous bedrocks. Stem biomass increased with stand age and reached values of 250–400 t C ha⁻¹ in the oldest successional stands. On acidic bedrocks, the organic layers accumulated linearly during forest succession at a rate of 0.34 t C ha⁻¹ yr⁻¹. On calcareous bedrocks, a maximum carbon stock in the humus layers was reached at an age of 60 years.

Total carbon stocks in stem biomass, organic layers and the mineral soil increased during forest development from 75 t C ha⁻¹ in the meadows to 350 t C ha⁻¹ in the oldest successional forest stands (2.75 t C ha⁻¹ yr⁻¹). Carbon sequestration occurred in stem biomass and in the organic layers (0.34 t C ha⁻¹ yr⁻¹ on acid bedrock), while mineral soil carbon stocks declined.

Mineral soil carbon stocks were larger in areas with higher precipitation. During forest succession, mineral soil carbon stocks of the upper 50 cm decreased until they reached approximately 80% of the meadow level and increased slightly thereafter. Carbon dynamics in soil layers were examined by a process model. Results showed that sustained input of meadow fine roots is the factor, which most likely reduces carbon losses in the upper 10 cm. Carbon losses in 10–20 cm depth were lower on acidic than on calcareous bedrocks. In this depth, continuous dissolved organic carbon inputs and low soil respiration rates could promote carbon sequestration following initial carbon loss.

At least 80 years are necessary to regain former stock levels in the mineral soil. Despite the comparatively larger amount of carbon stored in the regrowing vegetation, afforestation projects under the Kyoto protocol should also aim at the preservation or increase of carbon in the mineral soil regarding its greater stability of compared with stocks in biomass and humus layers. If grassland afforestation is planned, suitable management options and a sufficient rotation length should be chosen to achieve these objectives. Maintenance of grass cover reduces the initial loss.

Keywords: afforestation, carbon sequestration, carbon stocks, chronosequence, forest, litter input, organic layer, soil organic carbon, spruce, succession

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Introduction

Human land-use determines the land surface of the Earth in the 21st century. By agricultural land-use, forestry and building of infrastructure, humans inter-

fered with natural or seminatural ecosystems. While tropical deforestation continues and even accelerates in some regions (Laurence *et al.*, 2004), more and more agricultural land in Europe (Rabbinge & van Diepen, 2000) and North America (Foster & Motzkin, 2003) is set aside and becomes afforested. Both types of land-use changes have consequences not only for biodiversity, human nutrition, or the availability of clean water, but

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also strongly affect the carbon pools in soils and vegetation. Despite carbon losses because of fossil fuel emissions and deforestation, the Earth's land surface also offers a great potential for carbon sequestration.

Concerns about climatic change caused by elevated CO₂ have led to the Kyoto protocol. Besides a reduction in the use of fossil fuels, the Kyoto protocol allows for accounting of emission reductions by afforestation (planting of trees on former arable land or grassland) or reforestation (planting or natural regeneration of trees on arable land or grassland, which had been forest before cultivation by humans). Currently, forest carbon sinks are the only accountable biological sinks, and therefore, receive considerable attention. Afforestation and forest regeneration clearly increase the amount of carbon stored in vegetation biomass. Less known and still under debate are changes in soil carbon: in recent years, several studies on the development of soil carbon stocks after afforestation of former arable land (ploughed to grow cereals, vegetables, etc.) mainly in the US have shown losses (Hamburg, 1984; Richter *et al.*, 1999), gains (Schiffman & Johnson, 1989; Huntington, 1995; Hooker & Compton, 2003) or initial losses followed by slight increases in later stages of forest development (Johnston *et al.*, 1996). Most studies on the afforestation of former meadows and pastures (semi-natural grassland created by humans and used as hayfields or grazing areas for cattle) have been carried out in the Pacific region. They show mainly losses under the newly established plantations or forests as compared with the grassland (Giddens *et al.*, 1997; Ross *et al.*, 1999; Scott *et al.*, 1999; Turner & Lambert, 2000; Mendham *et al.*, 2003). For Europe, there are only a few studies on the changes of carbon stocks after afforestation, most of them covering periods of about 30 years or less (Harkness & Harrison, 1989; Muys *et al.*, 1992; Jug *et al.*, 1999; Vesterdal *et al.*, 2002).

Concerning mitigation of climate change, it is an important question if a longer lasting mineral soil carbon sequestration or loss takes place besides the short-term sequestration in plant tissue. It is still unclear which mechanisms determine an increase or decline in mineral soil carbon stocks. Only some climatic factors like precipitation have been examined concerning their influence on mineral soil carbon stocks (Guo & Gifford, 2002; Jackson *et al.*, 2002), whereas soil immanent parameters like parent material, particle size distribution, or root turnover have not been investigated in the past.

As a consequence of industrial development, traditional agropastoral systems in the Alps collapsed, leading to the abandonment of remote or unproductive areas (Laiolo *et al.*, 2004). Depopulation in these rural areas as well as reductions in cattle stocking levels are

long-term trends which peaked after the Second World War and are still omnipresent (Dirnböck *et al.*, 2003). Many of the nowadays abandoned meadows and pastures undergo natural successions towards woody vegetation or are afforested on purpose. One of the important successional species especially in later stages is spruce (*Picea abies*). Spruce forests on former grassland in the Alps provide ideal conditions for studying changes in carbon stocks during forest succession or reforestation because stands of various ages can be found close to each other.

Based on the results of a preliminary study on spruce afforestations in the Southern Alps (Thuille *et al.*, 2000), it was hypothesized that carbon stocks in the organic layers increase during forest development, whereas mineral soil carbon declines initially before a new stock level develops. The aim of the present study was to verify these results by the investigation of a broad range of spruce chronosequences on different bedrocks and in different climatic regions covering a period of approximately 100 years. A second aim was to understand the mechanisms, which can explain eventual increases or declines of carbon stocks in the organic layers and the mineral soil.

Materials and methods

Site description

In order to be able to characterize the dynamics of carbon stocks in spruce (*P. abies*) successions, a variety of chronosequences on different bedrocks and in different climatic regions was chosen (Table 1). Five of them were located in the southern, central, and northern part of the Alps, where spruce belongs to the natural vegetation. In many parts of the Alps, humans created meadows and pastures by clear-cutting or burning of the native coniferous forests since the 16th century (Dullinger *et al.*, 2003). In a preliminary study of one of the chronosequences (Valsorda), charcoal founds were dated to the beginning of the 18th century, meaning that there had been grasslands for at least 200 years (Thuille *et al.*, 2000). Temperature and precipitation are well within the ideal range for Norway spruce (Schmidt-Vogt, 1987). Stands at high elevation experience a shorter growing season than the other stands. In Thuringia, beech forests would be the natural vegetation in most of the area, whereas growth conditions are not optimal for spruce, because of low precipitation values during the growing season. A chronosequence was also chosen within this area.

Chronosequences are false time series, which integrate independent forest stands with their distinct history into one unit, thus, substituting space for time.

Table 1 Coordinates, altitude, climatic, and edaphic parameters of the different chronosequences

Chronosequence	Geographical position			Climatic parameters		Edaphic parameters	
	Longitude (°E)	Latitude (°N)	Altitude (m a.s.l.)	Precipitation (mm yr ⁻¹)	Temperature (°C)	Bedrock	Soil type
Eichsfeld	10°20'	51°18'	380–410	661	7.5	Calcareous rock	Rendzina, luvisol, cambisol
Vilstal	10°30'	47°35'	1000–1175	1370	6.8	Flysch	Cambisol
Aiarei	11°53'	46°48'	1700–1775	970	4.1	Calcareous rock	Cambisol, luvisol
Kienberg	11°51'	46°47'	1150–1200	815	5.8	Quartzphyllite	Cambisol
Val Canali	11°50'	46°12'	1250–1400	1466	6.2	Calcareous rock	Cambisol
Valsorda	11°42'	46°13'	1200–1390	1350	5.9	Quartzphyllite	Cambisol

Coordinates were taken from the following topographical maps: Eichsfeld: Thüringer Landesvermessungsamt (1998a–c). Valsorda: Geografica (1984). For the remaining areas geological maps were used. Geological data were taken from the following maps: Eichsfeld: Thüringer Landesanstalt für Geologie (1853a–c), Vilstal: Zacher (1963, 1966), Aiarei: Istituto Poligrafico e Zecco dello Stato (1992a), Kienberg: Istituto Poligrafico e Zecco dello Stato (1969), Val Canali und Valsorda: Istituto Poligrafico e Zecco dello Stato (1992b). Altitude was determined with an altimeter or taken from topographical maps. Climatic parameters are mean annual values for 1961–1990 of station Leinefelde (Eichsfeld), 1961–1990 of station Schwangau-Horn (Vilstal), 1991–2000 of station Toblach (Kienberg), 1985–1995 of station Ritten (Aiarei), of station San Martino di Castrozza (Val Canali, precipitation), data from Zunica (1981) (Valsorda, precipitation) and own measurements over a period of 3 years (Valsorda und Val Canali, temperature).

In order to minimize the resulting variability, stands within one chronosequence should be as identical as possible in their stand characteristics. They should have experienced equal environmental conditions (Cole & van Miegroet, 1989; Klinger & Short, 1996). Therefore, neighbouring stands in the same altitude, on the same bedrock and with a similar topography were selected. Nevertheless, also these stands experienced a change in CO₂ and N emissions at different ages and may have been undergone distinct soil forming processes. Each chronosequence represented a broad age range, started with a meadow (mown once or twice per year) and was compared with a continuously forested control stand that had not been used as grassland before, but experienced different degrees of forest management.

Table 2 shows the age range and some stand characteristics of the six chronosequences under study. In the Alps, spruce stands regenerated naturally on abandoned grasslands (exception: 34- and 56-year-old stands in Vilstal), while all Thuringian stands were planted. Most of the younger stands had not been thinned until the study was carried out. In contrast, older stands in the Alps and all stands in Thuringia have been thinned or single stems have been harvested (see Table 2 for details). The 57- and 86-year-old Thuringian stands were affected by wind breaks, whereas the stands in the Alps were healthy and well growing. Understorey was missing in most stands with the exception of the continuously forested control plots in Aiarei, Kienberg, Val Canali, and Valsorda where large

patches of *Vaccinium myrtillus* and *V. vitis-idaea* were present. The 14-year-old stand in Aiarei was characterized by a dense grass cover (*Calamagrostis* ssp.) between the young trees.

Methods

Carbon stocks in stem biomass were determined on plots of 100–1000 m² depending on the height of the trees. Trees were counted and carbon stocks were calculated from stem heights and diameters at breast height. Wood density of spruce was assumed to be 377.1 kg m⁻³ (Burschel *et al.*, 1993) and a carbon concentration of 50% of dry weight was used to calculate stocks. Canopy litterfall was measured in a young, a middle-aged, and an old forest stand as well as in the continuously forested control stand (exception Vilstal: no litterfall determined in middle-aged stand). Litter was collected in five littertraps with an area of a quarter of a square metre in the young and middle-aged stands and in three littertraps of a square metre in the old successional and the continuously forested stands over a period of 2–3 years. Mesh size was 0.3 mm. The collected litter was dried at 70 °C, ground to fine powder and carbon and nitrogen content was determined via a CN-analyser (Vario EL II, Elementar Analysensysteme GmbH, Hanau, Germany). Litter collected during the first year after installation of the traps was sorted into needles, leaves, twigs, cones and seeds, and lichens.

Table 2 Geographical location of the chronosequences, their age range, and stand properties

Name	Region	Chronosequence	Control	Stand origin	Stand management	Special features
		stand ages	stand age			
		(a)	(a)			
Eichsfeld	Thuringia, Germany	0, 15, 30, 57, 70, 86	100	All planted	All thinned	Wind throw in 57 and 86
Vilstal	Northern Alps, Germany	0, 14, 34, 56, 82	146	Natural, planted (34, 56)	Thinned: 34, 56, single stem: 82, 146	Snow damage in 34
Aiarei	Central Alps, Italy	0, 14, 37, 54, 78, 112	212	All natural	Single stem: 87, 112, 212	Organic fertilizer in 78
Kienberg	Central Alps, Italy	0, 24, 60, 93	114	All natural	All thinned except 24	
Val Canali	Southern Alps, Italy	0, 15, 33, 46, 60, 100	140	All natural	Single stem: 60, 100, 140	Long snow cover in spring in 46
Valsorda	Southern Alps, Italy	0, 15, 25, 33, 47, 62	130	All natural	Single stem: 130	

Chronosequence age gives the age of the successional forest stands only; the continuously forested control stand is shown in a separate column. Meadow plots are assigned the age '0'. Stand origin shows if forest stands regenerated naturally on former grassland or if they were planted, stand management indicates if stands are thinned or if single stems are used. Use of single stems means that in different time intervals some of the biggest stems are harvested while the rest of the respective forest stand remains untouched. Harvest intensity is lower during under regular thinning activities. Stands not mentioned in the column 'stand management' are completely unmanaged. The stands with organic fertilizer addition and prolonged snow cover in spring were excluded from the analysis of changes in soil carbon stocks during forest succession.

Litter decomposition was measured in the same stands where litter was collected. Ten grams of needle litter was buried in the uppermost humus layer in nylon meshbags of $15 \times 15 \text{ cm}^2$ with a mesh size of 0.25 mm. In each stand, 15 meshbags were laid out in September 1999. Five of these bags were collected in March 2000, November 2000, and November 2001, respectively. Analyses for carbon and nitrogen were performed as described above.

Soil samples were taken in each of the 39 selected study sites according to the following procedure: a ditch of 2 m length and a maximum depth of 70 cm was excavated in order to get an average of soil layer thickness. At the upper end of the ditch a square of 30 cm side length was marked. Within this square, litter and organic layers were collected separately. Soil was harvested on an area of $30 \times 30 \text{ cm}^2$ in layers of 5 cm depth. From 20 to 50 cm soil depth, layer thickness was 10 cm. Minimum depth in shallow and stony plots on calcareous soil was 20 cm. In each stand, the organic layer and the topmost 5 cm of mineral soil were harvested in three replicates, whereas deeper soil layers were only harvested in one pitch. The harvested area of $30 \times 30 \text{ cm}^2$ covers the small-scale variability. Although more replicates would have been desirable, the chosen method did not allow for them within a reasonable timeframe. It was our aim to examine several chronosequences in order to find common processes taking place during forest succession, thus, a reduction of

stand number in favour of more replicates would not have been useful.

As sampling depth was not correlated with mineral soil carbon stocks on calcareous soils, carbon stocks over the entire sampled profile were used in the following. Subsamples of the weighed and homogenized soil were taken to the laboratory, dried, ground, and analysed for carbon and nitrogen via a CN-analyser (Vario EL II, Elementar Analysensysteme GmbH). Bulk density was calculated from the volume and weight of the separately harvested litter and soil layers and used to determine carbon stocks per hectare. For all soil samples, pH values in water and NH_4Cl as well as cation exchange capacity in NH_4Cl or NH_4 acetate according to the method developed by Luer & Böhmer (2000) were measured. This analysis provided data on the amounts of exchangeable calcium, magnesium, potassium, sodium, iron, manganese, and aluminium. Particle size distribution was analysed by wet sieving of sand fraction and the use of a laser particle counter by Shimadzu (Duisburg, Germany) to determine silt and clay fraction; samples with high clay contents were analysed according to Deutsches Institut für Normung (1973).

A process model to explain changes in carbon stocks

A process model was developed in order to simulate the observed carbon stock changes in organic layers and the upper 20 cm of the mineral soil. The model contains two

separate parts: The first part simulates the changes in the organic layers during forest development by balancing carbon inputs via litterfall and carbon outputs because of litter decomposition. The second part models stock changes in the mineral soil. Data on fine root input, heterotrophic soil respiration, fluxes of dissolved organic carbon (DOC) and bioturbation were taken from literature.

Organic layers

Litterfall ($\text{tC ha}^{-1}\text{yr}^{-1}$) in all chronosequences increased with stand age and was described most accurately by a logarithmic equation. 'Age' indicates stand age in years.

$$\text{Litterfall} = -0.32 + 0.67 \ln(\text{age}), \quad r^2 = 0.73, P < 0.01.$$

An equation for litter decomposition in initial phases was calculated from own data determined by litterbags. The remaining litter fraction decreased according to an exponential decay function:

$$\text{Remaining litter fraction (\%)} = 12.19 \times e^{\frac{-3268}{\text{age}+1556}},$$

$$r^2 = 0.98, P < 0.01,$$

where age indicates age of decomposing litter in days.

As litter decay was only measured over a period of 2 years, a model developed by Berg *et al.* (1995, 1996) was used for later stages of litter decomposition. The proposed limit value of 68% for spruce needles was modified to 75% in order to adjust for more favourable climatic conditions in central European as compared with Scandinavian forests with average annual temperatures of only 3.4 °C. Decay constant k was calculated as 0.0011 from own data (r^2 of regression: 0.98, $P < 0.01$) (Berg *et al.*, 1995, 1996).

$$\text{Remaining litter fraction (\%)} = 100 - 75 \left(1 - e^{\frac{-0.0011 \times \text{age}}{75}} \right),$$

where age indicates age of decomposing litter in years.

Fine roots and their turnover rate were derived from literature values: fine root biomass was assumed to be 2% of stem biomass (Perruchoud *et al.*, 1999). Fourty percent of fine root biomass was taken as annual turnover entering organic layer carbon stock (Schulze & Zimmermann, 2003). Given these assumptions, fine root inputs with increasing stand age differed between stands on calcareous and acidic soils. While fine root input increased in a logarithmic mode on calcareous soils, input grew more rapidly on acid bedrock and reached higher maximum values. Therefore, two different equations were used to simulate fine root input

Acidic soils:

$$\text{Fine root turnover } [\text{tC ha}^{-1}\text{yr}^{-1}] = \frac{1.06}{1 + e^{-\text{age}-58.93/13.83}},$$

$$r^2 = 0.74, P < 0.01.$$

Calcareous soils:

$$\text{Fine root turnover } [\text{tC ha}^{-1}\text{yr}^{-1}] = -0.35 + 0.14 \ln(\text{age}),$$

$$r^2 = 0.46, P < 0.01.$$

where age indicates stand age in years.

Fine root decomposition was calculated as an approximation with the same rate as needle litter decay. This seems to be justified by a study on the decomposition of spruce fine roots, which yielded a decay of 25% of the initial biomass in the first year (Ivask *et al.*, 1991), a value that matches the initial decay of needles determined in this study.

Carbon input from decaying meadow vegetation was taken as $0.4 \text{ tC ha}^{-1}\text{yr}^{-1}$ in the first 5 years (Nöllert, 2003). Thereafter, inputs were reduced continuously until they ceased after 15 years. At this age, no grass vegetation was present in the studied stands with the exception of Aiarei.

On acid bedrock, a DOC flux of $0.2 \text{ tC ha}^{-1}\text{yr}^{-1}$ was used for model calculation, according to data measured in Norwegian spruce stands (Michalzik *et al.*, 2001). Minimal DOC losses of $0.01 \text{ tC ha}^{-1}\text{yr}^{-1}$ were used for stands on calcareous bedrocks.

As anecic earthworms (*Lumbricus spec.*) were present in the studied soil (although their numbers or biomass were not measured), the process of bioturbation was included into model. Mixing of organic materials into the soil by earthworms was quantified for orchards with around $1 \text{ tC ha}^{-1}\text{yr}^{-1}$ (Edwards & Lofty, 1977). In spruce forests, earthworm abundance is much lower than in meadows (Satchell, 1983). Thus, in stands younger than 20 years on calcareous bedrock, a mixing rate of one-fifth (Satchell, 1983; Lee, 1985) of the value for orchards (i.e., $0.2 \text{ tC ha}^{-1}\text{yr}^{-1}$) was used, referring to the activity of anecic lumbricids. No earthworm activity was assumed for vigorously growing middle-aged stands according to the results of Ponge (2003). On acid bedrocks, rates of bioturbation were reduced to $0.1 \text{ tC ha}^{-1}\text{yr}^{-1}$ because of the lesser activity and presence of earthworms at low pH values (Shakir & Dindal, 1997; Saetre, 1998). The model decreased carbon stocks in the organic layer and increased them in the mineral soil according to these rates.

Mineral soil

Fine root input to mountainous meadow soils is about $3\text{--}4 \text{ tC ha}^{-1}\text{yr}^{-1}$ (Kleber, 1997; Nöllert, 2003).

Seventy-five percent of this input enters the upper 10 cm of the mineral soil, the remainder the layer from 10 to 20 cm depth. Fine root input from forest was determined as for organic layers: 2% of stem biomass was assumed to be fine root biomass, and 40% of this biomass is turned over each year. Fine root distribution in the soil profile was calculated from own observations. Data were best met by simple linear regressions:

0–10 cm soil depth:

$$\text{Fine root turnover [tC ha}^{-1}\text{yr}^{-1}] = -0.15 + 0.13 \times \text{age,} \\ r^2 = 0.65, P < 0.01.$$

10–20 cm soil depth:

$$\text{Fine root turnover [tC ha}^{-1}\text{yr}^{-1}] \\ = -0.03 + 0.0023 \times \text{age,} \\ r^2 = 0.63, P < 0.01.$$

where age indicates stand age in years.

Soil respiration under the initial grassland was assumed to be $4 \text{ tC ha}^{-1} \text{ yr}^{-1}$ (Kleber, 1997). Two-thirds of this value were supposed to occur in the upper 10 cm, according to depth distribution of soil respiration rates given by Perrsson *et al.* (2000). Soil respiration rates in forests were determined according to data of Perrsson *et al.* (2000). They found higher values of soil respiration both in younger forests and in the upper compared with the lower soil layers. Considering this results, respiration rates in the upper 10 cm in forests younger than 40 years were assumed to be $0.95 \text{ tC ha}^{-1} \text{ yr}^{-1}$, in older forest stands $0.35 \text{ tC ha}^{-1} \text{ yr}^{-1}$. From 10–20 cm depth rates of 0.35 and $0.15 \text{ tC ha}^{-1} \text{ yr}^{-1}$ were used for young and old forests, respectively.

DOC data were taken from Michalzik *et al.* (2001). On acid soils, input from the organic layer to the upper 10 cm was estimated at $0.36 \text{ tC ha}^{-1} \text{ yr}^{-1}$, output to the next 10 cm at $0.17 \text{ tC ha}^{-1} \text{ yr}^{-1}$. Output from the 10–20 cm layer was assumed to be $0.06 \text{ tC ha}^{-1} \text{ yr}^{-1}$. For calcareous soils input to the upper 10 cm was determined to be $0.15 \text{ tC ha}^{-1} \text{ yr}^{-1}$, output from the upper 10 cm to the next layer $0.1 \text{ tC ha}^{-1} \text{ yr}^{-1}$, and losses from the 10–20 cm layer $0.07 \text{ tC ha}^{-1} \text{ yr}^{-1}$.

According to the observed data, two different model subtypes were developed for the upper 10 cm of the mineral soil, representing the increasing and the decreasing carbon stocks, respectively.

Statistical analyses

Data analyses were performed using the programme SPSS, version 11 (SPSS Inc., Chicago, IL, USA). In order to test data sets for significant differences, an analysis of variance (ANOVA) followed by a Student–Newman–

Keuls test was performed. ANOVA were applied for comparing C/N and pH values of litter or mineral soil as well as for detecting trends in mineral soil carbon stocks during forest succession. Despite analysing time series of successional forests, we chose not to use linear regression to verify stock changes because the changes in mineral soil carbon stocks during forest succession do not follow a linear pattern. Instead, stands were grouped into age classes and subsequently analysed via ANOVA.

Regression lines included in several figures were created with SigmaPlot, versions 7.0 and 8.0 (SPSS Inc.).

Results

Carbon stocks in different compartments

Figure 1 provides an overview of the development of carbon stocks in different compartments during spruce growth on former grassland plots. Stem biomass (Fig. 1a) increased exponentially without showing a consistent trend of reduced growth in older stands. The variation in old and continuously forested control stands is attributed to site-specific conditions of sub-optimal precipitation during the growing season (in Thuringia) and high altitude (in Aiarei), in contrast to optimal growth conditions in Val Canali and Kienberg.

Organic layers started to build up with stand establishment in all successional forest stands (Fig. 1b). In most chronosequences though, thickness and carbon stocks of the organic layers remained lower than in the continuously forested control stands. There was no significant difference concerning the amount of carbon stored in the organic layers of stands on acid or calcareous stands, but shapes of the increase and the amounts stored in the continuously forested control stands differed significantly. On acid soil, carbon stocks in the organic layer increased linearly at a rate of $0.34 \text{ tC ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.88$) to a value of approximately 40 tC ha^{-1} at a stand age of 93 years. In contrast, on calcareous soils the increase of the organic layers ceased in stands older than 60 years ($r^2 = 0.73$). Carbon stocks of the continuously forested control stands were especially high in stands where *Vaccinium* was present.

Contrary to carbon stocks in the organic layers, carbon stocks in the mineral soil decreased following grassland afforestation (Fig. 1c). Carbon stocks up to 50 cm depth reached a minimum 15–60 years after the onset of forest development. Thereafter, a new stock level was attained which remained lower than that of the original meadow with the exception of the Valsorda chronosequence. Here, mineral soil carbon stocks of the oldest successional forest stand reached those of the original meadow.

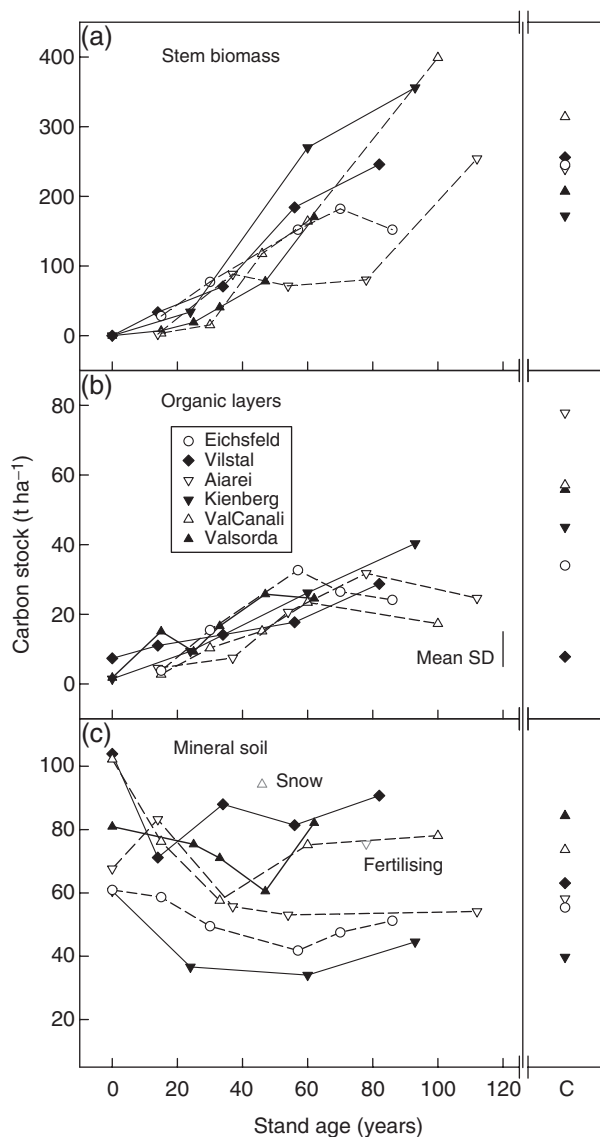


Fig. 1 Changes of carbon stocks in (a) stem biomass, (b) organic layers and (c) mineral soil to a maximum depth of 0.5 m with increasing stand age. C; continuously forested forest stands. Black symbols and solid lines represent forest stands on acid bedrocks, white symbols and dashed lines stands on calcareous bedrocks. Two stands were excluded from mineral soil carbon stock analysis – the 46-year-old stand in Val Canali because of its prolonged snow cover and the 78-year-old stand because of an unknown amount of organic fertilizer. They are shown in grey symbols. The vertical bar in plate b) shows the mean standard deviation of carbon stocks in the organic layers, derived from three replicates (10 t ha^{-1}). Mean standard deviation for carbon stocks in the upper 5 cm of the mineral soil was 3 t ha^{-1} or 20% of the respective stock.

Whole ecosystem carbon stocks (stem biomass, organic layer, mineral soil up to 50 cm depth) increased during from around 75 t C ha^{-1} in the original meadows

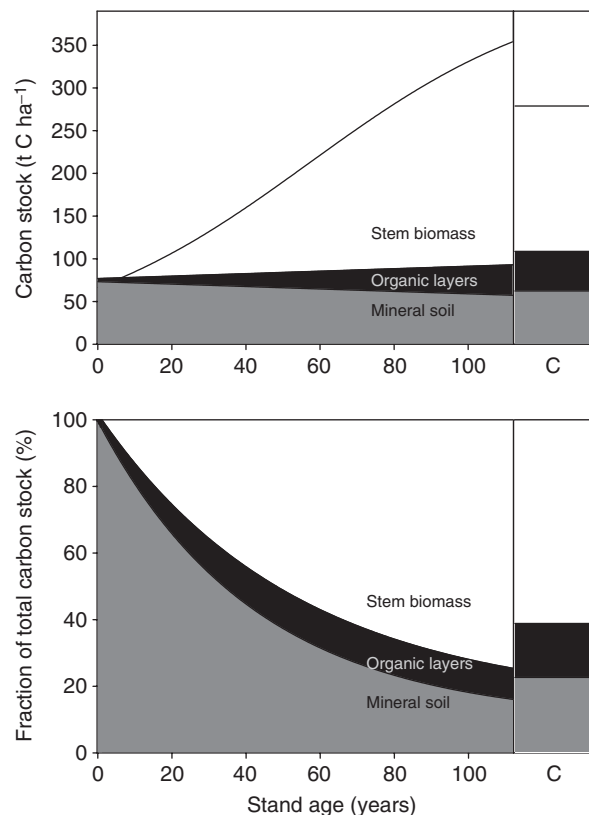


Fig. 2 Changes of carbon stocks in stem biomass, organic layers, and mineral soil up to 50 cm depth. Upper panel: changes of absolute carbon stocks during forest succession, averaged over all chronosequences. Lower panel: changes in the relative contributions of stem biomass, organic layers, and mineral soil to ecosystem carbon stocks. C; continuously forested control stands.

to 350 t C ha^{-1} in the older successional forest stands independent from bedrock type. This increase was mainly because of growing stem biomass, whereas mineral soil carbon stock decreased (Fig. 2). As root biomass was not measured, these values slightly underestimate total ecosystem carbon stocks.

Processes influencing the build-up of the organic layers

Litterfall in the 19 selected stands varied between 1 and $3 \text{ t C ha}^{-1} \text{ yr}^{-1}$. Despite climatic and geographic variation, chronosequences did not differ significantly in their amount of litterfall. Litterfall increased with growing stand age but remained low in the continuously forested stands in Vilstal and Eichsfeld (Fig. 3a). With increasing stand age, composition of the litter changed. In meadows and young forest stands, a greater percentage of the annual litter was represented by herbaceous tissues, whereas in older stands, fractions of twigs and branches increased (Fig. 3b), causing significantly

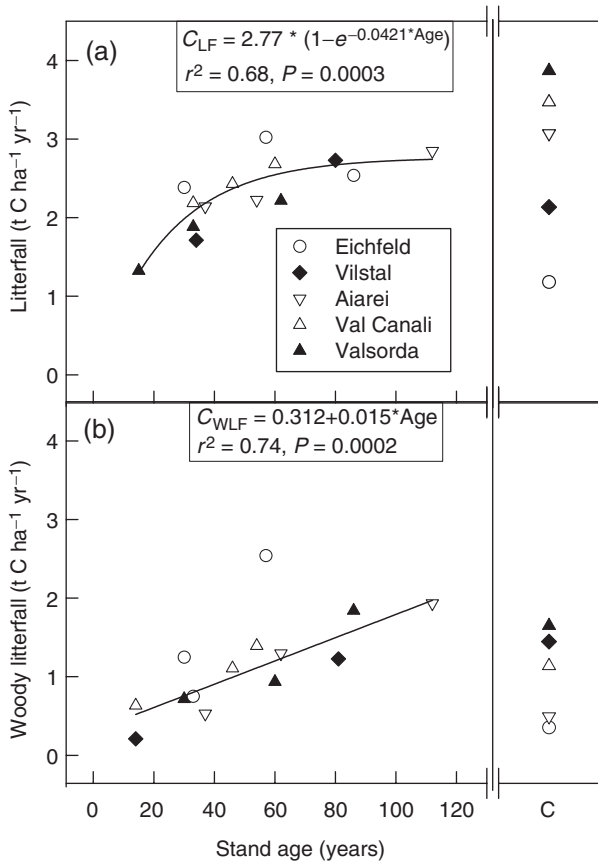


Fig. 3 (a) Increase of total litterfall (including needles, leaves, and woody litter) with growing stand age, LF, litterfall. (b) Increasing amount of woody litter (including branches, twigs, cones, pieces of bark etc.) with growing stand age, WLF, woody litterfall. Black symbols represent forest stands on acid bedrocks, white symbols stands on calcareous bedrocks, C, continuously forested stands.

Table 3 C/N values of different litter fractions

Litter fraction	C/N value	SD	n
Grasses	23.5a	4.8	7
Mosses	26.5a	3.9	9
<i>Vaccinium</i> spp.	38.6b	7.9	6
Young needles	40.3b	1.3	16
Seeds	42.0b	18.9	5
Twigs	59.6c	10.9	5
Old needles	59.9c	5.8	12

Different letters indicate significant differences ($\alpha = 0.05$). SD, standard deviation; n, number of measurements.

higher C/N values (Table 3). Therefore, decomposability of the material decreased. Growing amounts of less degradable litter are one of several factors correlated with the increasing stock of carbon in the organic layers

Table 4 pH values of meadow and forest litter as well as pH values of the upper 5 cm of meadow and forest soils

Compartment	pH	SD
Meadow litter	5.53a	0.47
Forest litter	4.87b	0.42
Meadow soil 0–5 cm	5.32a	1.05
Forest soil 0–5 cm	4.55b	0.75

A *t*-test was performed to test for differences. Different letters indicate significant differences at $\alpha = 0.05$.

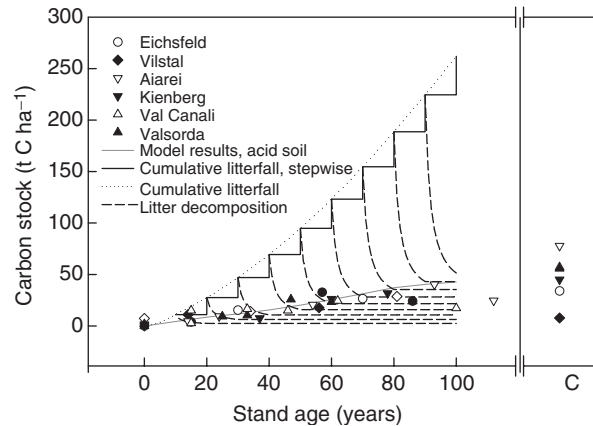


Fig. 4 Overview of the processes influencing carbon stocks in the organic layers. Cumulative litterfall and litter decomposition calculated according to measured data, model of Berg *et al.* (1995, 1996) used for later stages of litter decomposition. Black symbols represent forest stands on acid bedrocks, white symbols stands on calcareous bedrocks. C, continuously forested control plots.

during forest development. Additionally, pH value of both the litter and the upper soil horizon were significantly lower in forest than in meadow plots ($\alpha = 0.05$; Table 4), leading to less favourable conditions for biological decomposition of the litter.

Figure 4 combines the measured litterfall values with the decomposition rates obtained by the litterbags. After 100 years, cumulative litterfall would lead to an organic layer of 250 t C ha⁻¹, if no decomposition was assumed. Higher total amounts of litterfall in the older forests accelerated the process of litter accumulation with increasing stand age. Decomposition resulted in a 50% reduction of litter within the first 2 years after the onset of the litterbag experiments. As explained in the description of the process model (see 'Methods'), litter was decomposed exponentially until a limit of 25% of the original litter amount was reached. Carbon stocks of the organic layers as a result of litter input and litter decay increased linearly during forest succession.

Stock changes in the mineral soil

There was a significant positive correlation between annual precipitation and mean mineral soil carbon stock of the chronosequences (mean mineral soil carbon stock describes the average mineral soil carbon stock of the grassland and all forest stands of a chronosequence; Fig. 5): carbon stocks in the mineral soil increased with increasing rainfall whereas no correlation with mean annual temperature was detected.

For purposes of better comparison of the different chronosequences, Fig. 6 shows changes in mineral soil carbon stocks as percentages of the original meadow mineral soil carbon stocks. Losses of carbon were greatest in Kienberg and Val Canali. In four chronosequences the mineral soil carbon stock of the oldest successional forest stand was higher than that of the preceding one, whereas in Aiarei no increase was visible and in Val Canali the apparent initial gain between ages 30 and 60 slowed down considerably until age 100. An ANOVA was conducted to test if an increase of mineral soil carbon stocks in later stages of forest development could be expected. Stands were grouped into four age classes, consisting of the meadow, stands younger than 30 years, stands from 30 to 60 years and stands older than 60 years, respectively (Table 5). No significant differences between forest stands of different ages could be detected, but all forest stands had significantly lower mineral soil carbon stocks than the original grassland. If stands with minimum mineral soil carbon stocks of each chronosequence were compared with stocks of the oldest successional plot by a paired *t*-test, a significant difference between these pairs existed ($T = -9.2$, $P < 0.01$). Thus, mineral soil carbon stocks recover at

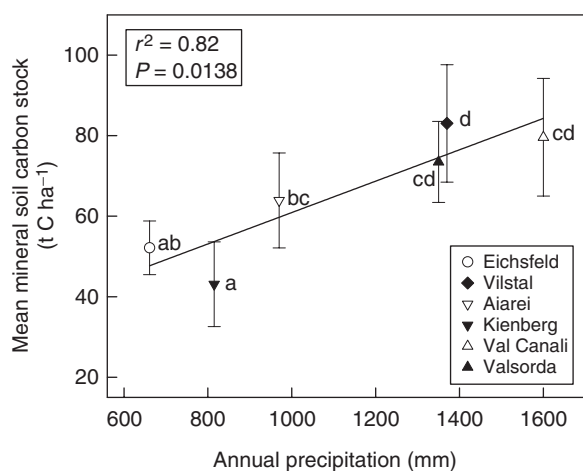


Fig. 5 Mean mineral soil carbon stocks of the entire chronosequences (including meadows and continuously forested stands) in relation to mean annual precipitation. Different letters indicate significant differences between means ($\alpha = 0.05$).

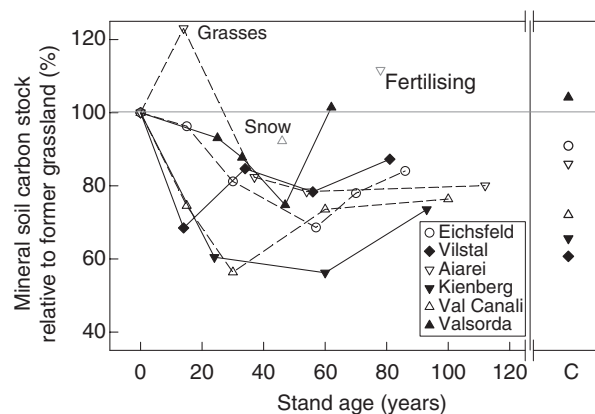


Fig. 6 Mineral soil carbon stocks over the entire profile relative to the former grassland. C, continuously forested stands. Black symbols and solid lines represent forest stands on acid bedrocks, white symbols and dashed lines stands on calcareous bedrocks. Two stands were excluded from mineral soil carbon stock analysis – the 46-year-old stand in Val Canali because of its prolonged snow cover and the 78-year-old stand because of an unknown amount of organic fertilizer. They are shown in grey symbols.

Table 5 Analysis of variance for the soil carbon stocks expressed as percentage of the original meadow stock in forest stands of different age

Group	Fraction of original meadow carbon stock (%)	Standard deviation
Meadows	100a	0
Stands 1–30 years	79b	14
Stands 31–60 years	74b	11
Stands older than 60 years	83b	9
Control stands	80b	17

Different letters indicate significant differences according to the Student–Newman–Keuls-test with $\alpha = 0.05$.

least partly from their initial losses, but no continuous increase during forest development occurred, if stocks over the entire profile were taken into account. It seems unlikely, however, that initial mineral soil carbon stocks over the whole soil profile will generally be reached during forest development, because also the continuously forested control stands show significantly lower mineral soil carbon stocks than the meadows.

Stand age was not the only factor correlated with changes in mineral soil carbon stocks after afforestation of grasslands. Among the physical and chemical soil parameters analysed, silt content and exchangeable manganese showed weak correlations with carbon dynamics: carbon losses were lower at higher silt contents and higher at increasing amounts of exchangeable

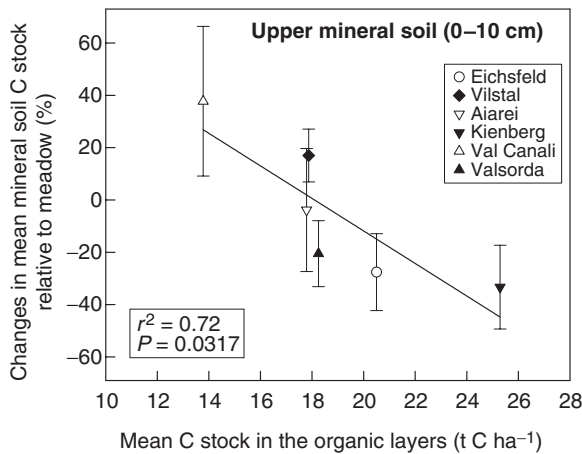


Fig. 7 Changes in the upper mineral soil related to carbon stocks in the organic layers. Average organic layer carbon stocks and average relative stock changes in the upper 10 cm of the mineral soil for the whole chronosequences are given. Black symbols represent forest stands on acid bedrocks, white symbols stands on calcareous bedrocks.

manganese (data not shown). Both regressions were only significant at $\alpha = 0.1$. In contrast, carbon losses in the uppermost 10 cm of the mineral soil were significantly higher at higher mean carbon stocks in the organic layers (Fig. 7). Thus, build-up of an organic layer in growing spruce forests seemed to be related to diminishing carbon stocks in the upper mineral soil.

Modelling carbon gains and losses in separate soil layers

Increasing amounts of carbon in organic layers are the result of a positive balance between carbon inputs in the form of litter, fine roots and DOC and carbon losses because of litter decay and DOC losses. These processes were used for modeling carbon stocks in the organic layers, the uppermost 10 cm of mineral soil and mineral soil from 10 to 20 cm depth.

In grasslands, fine root turnover dominates carbon input, whereas aboveground litter only adds minor amounts. In mountain meadows, input of fine roots amounts to $3\text{--}4\text{ t C ha}^{-1}\text{ yr}^{-1}$, while aboveground litter adds around $0.4\text{ t C ha}^{-1}\text{ yr}^{-1}$ (Nöllert, 2003). The major part of organic carbon is, therefore, directly incorporated into the mineral soil, the remainder entered by an active soil fauna. Soil respiration rates are $4\text{ t C ha}^{-1}\text{ yr}^{-1}$ on average (Kleber, 1997).

After the onset of forest regrowth, fine root and litter input from grassland vegetation cease, while forest litter and fine roots add continuously higher amounts of carbon to the soil. Soil respiration rates decline. For European spruce forests, average respiration rates in the upper 10 cm of mineral soil are $0.95\text{ t C ha}^{-1}\text{ yr}^{-1}$ in

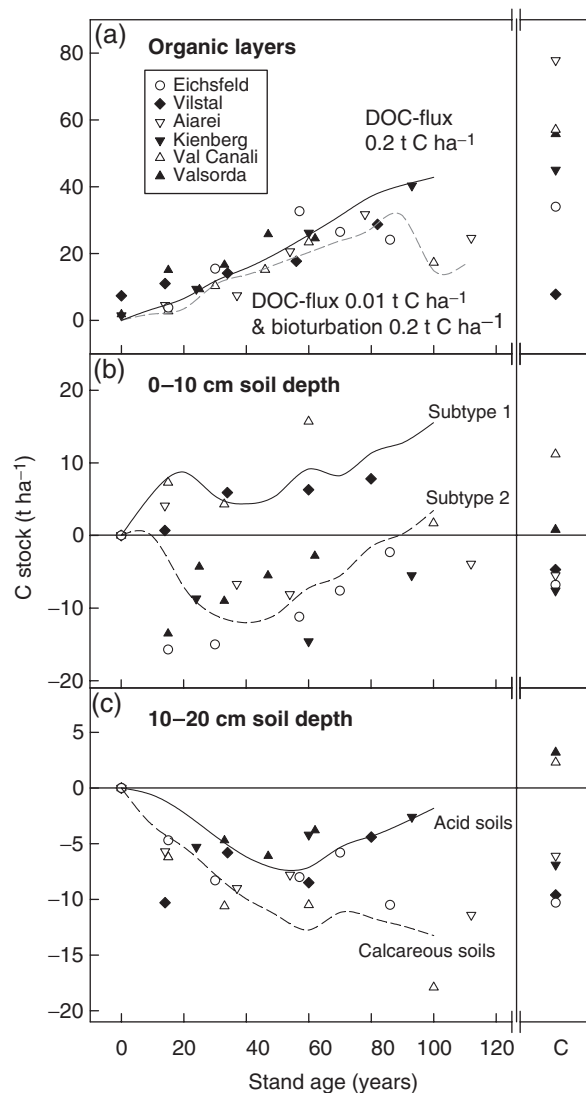


Fig. 8 Conceptual model results for the development of carbon stocks and mineral soil during forest succession. Different model results for acid and calcareous soils are given for organic layers (a) and 10–20 cm soil depth (c). For the uppermost 10 cm, two different model runs for increasing stocks and stocks decreasing before rising again are represented (b). Details are described in the text. All symbols represent measured data. Black symbols represent forest stands on acid bedrocks, white symbols stands on calcareous bedrocks. C, continuously forested plot.

young and $0.35\text{ t C ha}^{-1}\text{ yr}^{-1}$ in mature forests. At a depth of 10–20 cm they reach only 0.35 and $0.15\text{ t C ha}^{-1}\text{ yr}^{-1}$ in young and mature forests, respectively (Perrson *et al.*, 2000).

Figure 8 shows the development of carbon stocks on the organic layers and the upper mineral soil according to data and model calculations. The model matches the observation for the organic layers quite well (Fig. 8a) despite slightly higher carbon stocks in forest stands of

less than 20 years on acid soils, where a thick cover of grass roots contributes to a higher carbon stock.

For the uppermost 10 cm of mineral soil, measured data reveal several distinct patterns of stock development. Some forest stands show growing amounts of carbon after forest establishment, whereas most other stands exhibit a decrease in carbon stocks to varying degrees. Two different model subtypes were calculated for this horizon (Fig. 8b), representing stands with increasing carbon stocks (subtype 1) and stands, which experience an initial loss in mineral soil carbon stocks after the onset of forest succession. The input parameters for the two subtypes differed concerning the decline of grassland fine root input, respiration rates and bioturbation in the early stages of forest development. Different forest fine root input rates according to the differences between acidic and calcareous bedrock were used for forest stands older than 15 years (confer model description). The two resulting model outcomes represent growing, as well as, declining carbon stocks after forest establishment. Increasing carbon stocks as represented by subtype 1 can be expected if fine root input of grassland vegetation is sustained over an extended period and if respiration rates decrease relatively fast after the onset of forest development.

In 10–20 cm soil depth, measured carbon stocks behave differently in acid and calcareous soils (Fig. 8c). In acid soils, carbon stocks increase again after an initial decline, whereas in calcareous soils, the decline in carbon stocks continues. Differences between the two soil types consist mainly in the slowly as compared with rapidly ceasing fine root inputs from grasses and higher respiration rates on calcareous bedrock. On calcareous bedrock, DOC inputs are assumed to be lower than on acid bedrock. Higher respiration rates in calcareous soils can be explained by a higher microbial activity at higher pH values (Webster *et al.*, 2000).

Sensitivity of the model to several input parameters was tested for the upper mineral soil (0–10 cm depth, Fig. 9). For this purpose, subtype 2 of the model was modified concerning fine root input, heterotrophic respiration, and earthworm activity. If the lower meadow respiration rates of subtype 1 were applied to subtype 2, carbon stocks decreased less. An even more pronounced effect was achieved by using the higher meadow fine root inputs of type 1 for subtype 2. In contrast, lower carbon stocks were calculated, if no earthworm activity was assumed. Particularly severe decreases in soil carbon stocks were the result of the complete absence of fine root input from the meadow immediately after forest establishment. Although the variation of input parameters only concerned the first 15–20 years after forest establishment, the different shapes of stock development only levelled off after 70–80 years.

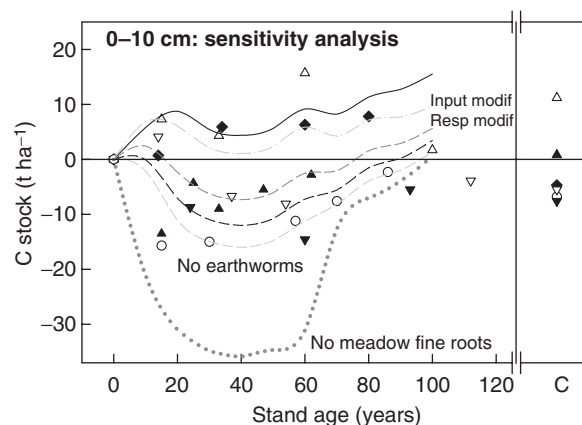


Fig. 9 Sensitivity analysis shown for the 0–10 cm layer. Black lines represent model subtypes 1 and 2. Model subtype 2 was modified concerning several parameters: replacing the original values for fine root input by grassland vegetation (grey line, dash-dot) or for meadow respiration rates (dark grey line, short dash) resulted in increased stock levels. In contrast, the absence of earthworm activity (grey line, short dash) or the absence of meadow fine root input (dark grey dots) caused reduced stock levels.

Discussion

Forest succession on former grasslands in the Alps and Thuringia caused increasing ecosystem carbon stocks mainly because of the stock development in the tree stems. Losses of carbon in the mineral soil are partially compensated for by the increasing carbon stock in the organic layers. Thus, the distribution of carbon within the ecosystem changes such that the vegetation is replacing the mineral soil as the largest carbon reservoir.

In the following, the processes leading to changed carbon stocks in the organic layers and the mineral soil are discussed in more detail, because soil carbon stocks play a vital role as long-term carbon stocks given that they are generally regarded as more stable (Garten & Ashwood, 2002) than carbon stored in organic layers or vegetation which can easily be destroyed or harvested.

Organic layers

The build-up of organic layers above the mineral soil surface is influenced the humus type (Burschel *et al.*, 1993), nutrient availability (Vesterdal *et al.*, 1995), forest type and understorey vegetation (Schulze *et al.*, 1995), as well as, stand age and development stage (Grier & McColl, 1971; Turner & Long, 1975; Grier *et al.*, 1981; Boone *et al.*, 1988; Thuille *et al.*, 2000).

During forest regeneration on former agricultural land carbon accumulation in the organic layers can

Table 6 Changes of organic layer carbon stocks during afforestation according to several studies

Study region	Tree species	Time (years)	Accumulation rate (t C ha ⁻¹ yr ⁻¹)	Source
Italy, Germany (calcareous soil)	Spruce	112	0.24	This study
Italy, Germany (acid soil)	Spruce	93	0.34	This study
Germany (north-east)	Pine	120	0.25	Heinsdorf (1994)
Denmark	Spruce	30	0.36	Vesterdal <i>et al.</i> (2002)
USA	Pine	114	0.37	Hooker & Compton (2003)
USA	Broad leafed	65	0.55	Hamburg (1984)

Time gives the period elapsed since onset of forest development. All forests developed on former arable land or pastures.

occur at different rates, depending on site properties and tree species. The carbon accumulation rates of 0.34 t C ha⁻¹ yr⁻¹ on acid soils and of 0.24 t C ha⁻¹ yr⁻¹ on calcareous soils confirm the value of 0.36 t C ha⁻¹ yr⁻¹ obtained in an earlier study on acid bedrock (Thuille *et al.*, 2000). Accumulation rates as determined in this study compare well with literature results, ranging from 0.25 t C ha⁻¹ yr⁻¹ under pine forests in Germany to 0.55 t C ha⁻¹ yr⁻¹ under broad-leafed trees in the US (Table 6).

What are the causes for the buildup of an organic layer, and why do organic layers on acid and calcareous soils differ in later stages of forest succession?

Aggrading forest stands alter the microclimate at the forest floor. The closed spruce canopy alleviates temperature extremes and lowers summer surface temperatures. Compared with open areas, surface soils get drier because of the greater amounts of water used by the trees. Both processes influence litter decomposition: numerous studies show temperature dependence of litter decomposition (Armson, 1979; Mathes & Schriefer, 1985; Oades, 1988; Naganawa *et al.*, 1989; Hobbie, 1996; Berg *et al.*, 1998; Buchmann, 2000). Moreover, in the growing forests, the amount of litter produced was higher than on the former meadows (compare (Harkness & Harrison, 1989; Muys *et al.*, 1992) and its C/N ratio increased, indicating a lower degradability. During forest development, plants with ectomycorrhiza or ericoid mycorrhiza replace plants with arbuscular mycorrhiza. Plants with these types of mycorrhiza are known for their slowly decaying litter (Cornelissen *et al.*, 2001). Coniferous forests show lower soil respiration rates under identical temperature and moisture conditions compared with broad-leafed forests (Flanagan & Van Cleve, 1983). Mature forests seem to produce substances like polyphenoles which make litter more resistant to decomposition (Minderman, 1968). The results of this study showed lower pH values in forest litter compared with grass litter. This is in concordance with studies describing soil acidification during development of coniferous forest stands (Miles, 1985; Richter *et al.*,

1994; Parfitt *et al.*, 1997; Ritter *et al.*, 2003). Whereas, the previous cultivation of the land as extensive hayfields or pastures favoured the development of earthworm populations, acid litter and forest soils developing during the forest establishment deteriorate conditions for litter decaying macrofauna, especially lumbricids (Judas *et al.*, 1997); a study in the French Alps showed declining earthworm biomass following afforestation of former meadows (Grossi & Brun, 1997). Earthworm numbers were not quantified in this study, but considerably fewer individuals (*Lumbricus* spec.) were observed in forest than in meadow plots. Saetre (1998) showed that spruce litter needs to contain at least 25% of better decomposable birch leaves in order to be a suitable habitat for earthworms in Scandinavian forests (Saetre, 1998). This is in agreement with results of Muys *et al.* (1992), indicating the development of organic layers during afforestation because of the lack of mixing of litter and mineral soil. Others even claim a global trend of declining earthworm biomass during the phase of intensive forest growth (Ponge, 2003), which in turn leads to a reduced mixing of organic layer and mineral soil (Jongmans *et al.*, 2003). Other soil organisms like collembolae, larvae of diptera and coleoptera also occur at low densities in acid forest soils, while microbial activity remains rather low (Saetre *et al.*, 1998). The results of these studies support the hypothesis that less degradable litter together with reduced activity of macro and microfauna because of altered microclimate caused the accumulation of organic layers on acid soils.

In agreement with results in deciduous forests (Hughes & Fahey, 1994), litter accumulation on calcareous soils ceased at a stand age of 60 years. Studies in the French Alps on the development of the organic layers in various stages of forest development showed increasing organic layers during intense growth phases because of the lack of earthworms but partial mixing of the organic layers into the soil as re-establishment of earthworm populations occurred in later stages of forest development (Bernier *et al.*, 1993; Bernier & Ponge, 1994; Ponge, 2003). Similar processes might cause the cessa-

Table 7 Changes of mineral soil carbon stocks during afforestation according to several studies

Study region	Former land use	Tree species	Time (years)	Study results concerning carbon stock	Source
(#)	Pasture	Coniferous		10% loss, especially at > 1500 mm ns	Guo & Gifford (2002)
Temperate region	Pasture	Coniferous	40	Losses; 3.46% yr ⁻¹ in the initial 10 years, >30 years: surface soil like arable land, 0.5%–0.86% increase in subsoil	Paul <i>et al.</i> (2002)
Australia	Pasture	Eucalypt	7–10	No major changes, only reallocation	Mendham <i>et al.</i> (2003)
New Zealand	Pasture	Pine		Under pine 17%–40% less C than under pasture in 0–10 cm depth	Scott <i>et al.</i> (1999)
New Zealand	Pasture	Pine	12	In 0–20 cm depth less C	Ross <i>et al.</i> (1999)
New Zealand	Pasture	Pine	20	No net accumulation in the upper 10 cm in 20 years, decrease during the initial 12 years	Turner & Lambert (2000)
New Zealand	Pasture	Pine	17–30	No change in carbon concentration, losses in the upper 10 cm in 60% of studied sites	Giddens <i>et al.</i> (1997)
Brazil, Amazon	Degraded pasture	Secondary forest	16	Minor changes, short residence time for carbon	de Camargo <i>et al.</i> (1999)
(~)	Grassland	Several species	30–100	–61 + 13 tC ha ⁻¹ , losses especially on wet sites	Jackson <i>et al.</i> (2002)
Great Britain	Grassland	Spruce	0–15	Losses due to mechanical soil preparation	Harkness & Harrison (1989)
			15–30	Constant stock, but higher turnover of carbon	
Belgium	Grassland	Deciduous	20	Diminution of A horizon due to lack of mixing	Muys <i>et al.</i> (1992)
Denmark	Arable land	Spruce; oak	29	No overall changes, increase in 0–5, decrease in 5–25 cm depth	Vesterdal <i>et al.</i> (2002)
USA, North	Arable land		40	Decrease in 0–10 cm depth immediately after abandonment, thereafter increase	Johnston <i>et al.</i> (1996)
USA, Northeast	Arable land	Pine; oak	40–60	31% less than in natural forest in 0–15 cm depth	Compton <i>et al.</i> (1998)
USA, Northeast	Arable land	Pine	115	No changes in 0–20 cm depth, increase in 20–70 cm depth, overall increase 6%	Hooker & Compton (2003)
USA, Southeast	Arable land	Pine; deciduous		34%–103% increase, after preceding losses upon cultivation	Huntington (1995)
USA, Southeast	Arable land	Deciduous	70	Decrease in plough layer, no changes in subsoil	Hamburg (1984)
USA, Southeast	Arable land	Pine	50	Increase in the upper soil from 9 to 18.5 tC ha ⁻¹ , overall increase from 55 to 67 tC ha ⁻¹	Schiffman & Johnson (1989)
USA, Southeast	Arable land	Pine	40	Overall (vegetation and soil) increase but less than 1% in soil, decrease in subsoil	Richter <i>et al.</i> (1999)
Australia	Arable land	Pine; eucalypt	0–10	Decrease at 1.7% yr ⁻¹	Paul <i>et al.</i> (2003)
			10–40	Increase at 0.82% yr ⁻¹	
Subtropical region	Arable land	Deciduous	40	Increase	Paul <i>et al.</i> (2002)

Time gives the period elapsed since onset of forest development. #, meta analysis; ~, review; ns, annual precipitation. The upper half of the table represents studies dealing with afforestations of former grasslands (pastures, hayfields etc.) while the lower part lists studies examining forest development on former arable land (ploughed to grow cereals, vegetables etc.).

tion of organic matter accumulation in the older successional forest stands on calcareous soil in this study.

Mineral soil

The choice of chronosequences on different types of bedrock and in various climatic regions allows an

analysis of the influence of climate and soil properties on the mineral soil carbon stocks and their changes during forest development. Despite an altitudinal gradient of more than 1000 m and the related differences in mean annual temperature and precipitation as well as altitude, mean soil carbon stocks of the entire chronosequences did only show a significantly positive

relationship with annual rainfall, leading to higher stock levels in the Vilstal, Val Canali, and Valsorda chronosequences as compared with the low mean mineral soil carbon stocks at Kienberg and especially in the Eichsfeld. Studies on a global scale also showed increasing mineral soil carbon stocks at higher precipitation (Post *et al.*, 1982; Jobbágy & Jackson, 2000) as well as a variety of studies in different ecosystem types and climatic regions (Jagnow, 1969; Ulrich & Puhe, 1994; Hontoria *et al.*, 1999; Rodríguez-Murillo, 2001; Callesen *et al.*, 2003). As shown for American grassland ecosystems (Burke *et al.*, 1989; Ihori *et al.*, 1995), the cause for this relationship in forests, too, could be the higher net primary production and thus a higher carbon input to the soil by litter fall and fine root turnover at higher precipitation.

In contrast to the increasing amounts of carbon stored in the organic layers, there was a decline in mineral soil carbon stocks of 20–40% during forest development. Even after 100 years of forest development, none of the successional forest except the oldest stand in Valsorda had reached more than 90% of the initial mineral soil carbon stock. In recent years, several investigations concerning the development of carbon stocks after the afforestation of arable land or grassland have been conducted (Table 7). The results of these studies range from 40% loss from the upper mineral soil of pine plantations established on former meadows in New Zealand (Scott *et al.*, 1999) to gains up to 103% of the initial mineral soil carbon stocks during reforestation of former agricultural land in the US (Huntington, 1995). Despite eventual gains in later stages of forest establishment, as indicated in this study for the upper mineral soil, many investigations revealed carbon losses in the initial 10–15 years. Thereafter gains were reported for former arable land, while on converted grassland carbon stocks did not always increase after initial losses. In Great Britain for example, carbon stocks declined within the first 15 years planting of sitka spruce on former grassland, thereafter, they remained constant (Harkness & Harrison, 1989). Likewise, pine plantations on former pastures in New Zealand did not show any net carbon accumulation in soil after 20 years (Ross *et al.*, 1999). One might argue that arable land has lost a great amount of carbon during cultivation, thus allowing carbon stocks to rise after forest establishment, whereas on former grassland, losses upon afforestation prevail. In this study, mineral soil carbon stocks of the succession forests decreased relative to the initial grasslands, but did not differ significantly from those in the continuously forested stands. These findings are supported by a study in the US which yielded higher stocks in the upper 40 cm of mineral soil under meadows as compared with forests (Garten & Ashwood, 2002). Forest

succession on former grassland thus lead to an increase of carbon stored in vegetation and organic surface layers, but diminished carbon stocks in the mineral soil.

Model results

As a next step to understand the processes leading to increasing organic layer carbon stocks but decreased the amount of carbon stored in the mineral soil, a model was developed from the chronosequence data and additional sources from the literature. Different changes in soil carbon stocks during forest development over a period of 100 years could be explained by varying input parameters like bioturbation, fine root turnover, and soil respiration. The sensitivity analysis showed the pronounced effect of sustained meadow fine root input in early stages of forest development. Immediate cessation of this carbon input which could be the result of soil preparation before spruce establishment caused strongly declining carbon stocks. Fine root turnover is slower in forests than in grassland ecosystems, while in the meantime the dense fine root system of the former meadow is decomposed (Parfitt *et al.*, 1997). Changes in mycorrhiza can cause carbon oxidation, as the VAM mycorrhizae of grasslands, which mainly use soil minerals are replaced by ectomycorrhizae and ericoid mycorrhiza. Especially the latter are known for their ability to consume soil organic carbon (Read, 1994), causing declining mineral soil carbon stocks after the establishment of plantations on former grassland especially in deeper soil layers (Chapela *et al.*, 2001).

As stated earlier, soil fauna is less active in the acid soils developing under spruce forests, thus reducing the mixing of organic material into the soil and eventually causing a reduction in a horizon extension (Muys *et al.*, 1992). The development of a surface organic layer during forest succession shown in this study supports this hypothesis. Despite the low earthworm activity in coniferous forest soils, their total absences as tested by the sensitivity analysis, would lead to a further decline in mineral soil carbon stocks upon afforestation.

Hence, while less organic carbon enters the soil via litter and fine roots, an oxidation of organic material accumulated during grassland use begins, leading to declining mineral soil carbon stocks (Richter *et al.*, 1999). In several cases, no changes in overall carbon stocks could be detected upon afforestation, if organic layer and mineral soil were considered as a whole: losses in the mineral soil were compensated by gains in organic layers and coarse roots (Paul *et al.*, 2002; Mendham *et al.*, 2003). The situation might be different if agricultural land is afforested with deciduous trees, the litter of which can readily be integrated into the mineral soil by an active edaphon, thus causing carbon stocks in the

upper mineral soil to increase. This was shown for willow and poplar plantations in Germany, where the number of deep-burrowing earthworms increased after plantation establishment (Jug *et al.*, 1999).

Conclusions

Afforestation of former arable land or grassland provides the possibility to sequester atmospheric carbon at least for a certain time – as shown by carbon stocks rising from 75 tC ha⁻¹ in the studied grasslands to 350 tC ha⁻¹ (2.75 tC ha⁻¹ yr⁻¹) in the oldest successional forest stands. Suitable management options and adequate rotation length can help to reduce or compensate losses of mineral soil carbon and should therefore be considered in the management of afforestation projects, aimed to be carbon sinks according to the Kyoto protocol.

Sustained fine root input from grassland vegetation is necessary to offset losses of organic matter from the mineral soil: in order to maintain this vegetation as long as possible, soil preparation destroying it should be avoided.

If carbon losses in the upper mineral soil take place in the first years after forest establishment, carbon stocks will need at least 80 years to regain initial stock levels. Forests with shorter rotations should therefore be regarded cautiously with respect to climate change mitigation.

In deeper soil layers of older afforestations, soil respiration rates play an important role for the development of carbon stocks. Forest management with little or no soil disturbing may minimize such losses.

The current study deals with spruce afforestations, which are not favourable for soil fauna because of their acidifying litter. Deciduous trees promoting activity of earthworms and other deep-dwelling invertebrates will probably support continuous mixing of organic material with mineral particles, thus increasing mineral soil carbon stocks (Jug *et al.*, 1999; Jongmans *et al.*, 2003). Mineral soil carbon stocks are assumed to be more stable especially under changing climate and therefore sequester carbon over longer periods than the trees itself or the organic surface layers. Hence, a careful choice of tree species used for afforestations under the Kyoto protocol is needed to promote long-term climate change mitigation.

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Appendix: Description of model parameters

0–10 cm, increasing stock (subtype 1):

- meadow fine root input starting at $3 \text{ tC ha}^{-1} \text{ yr}^{-1}$, declining in steps of $0.1 \text{ tC ha}^{-1} \text{ yr}^{-1}$,
- forest fine root input starting at age 16 according to the formula given above,
- net DOC input 0.19,
- bioturbation in stands younger than 20 years at $0.1 \text{ tC ha}^{-1} \text{ yr}^{-1}$,

- soil respiration starting at $2.7 \text{ tC ha}^{-1} \text{ yr}^{-1}$, declining in steps of $0.1 \text{ tC ha}^{-1} \text{ yr}^{-1}$ until an age of 15 years, under forest rates declining from $0.95 \text{ tC ha}^{-1} \text{ yr}^{-1}$ at 16 years to $0.65 \text{ tC ha}^{-1} \text{ yr}^{-1}$ at age 30 years in steps of $0.02 \text{ tC ha}^{-1} \text{ yr}^{-1}$, thereafter in steps of $0.01 \text{ tC ha}^{-1} \text{ yr}^{-1}$ until $0.35 \text{ tC ha}^{-1} \text{ yr}^{-1}$ at age 60 years. In older stands, successive increase because of better light intrusion to $0.65 \text{ tC ha}^{-1} \text{ yr}^{-1}$ at age 70 years and $0.95 \text{ tC ha}^{-1} \text{ yr}^{-1}$ at age 80 years was assumed.

0–10 cm, slightly decreasing stock (subtype 2):

- meadow fine root input starting at $3 \text{ tC ha}^{-1} \text{ yr}^{-1}$, declining in steps of $0.2 \text{ tC ha}^{-1} \text{ yr}^{-1}$,
- forest fine root input starting at age 16 according to the formula given above,
- net DOC input $0.19 \text{ tC ha}^{-1} \text{ yr}^{-1}$,
- bioturbation in stands younger than 20 years at $0.2 \text{ tC ha}^{-1} \text{ yr}^{-1}$,
- soil respiration starting at $2.7 \text{ tC ha}^{-1} \text{ yr}^{-1}$, declining in steps of $0.1 \text{ tC ha}^{-1} \text{ yr}^{-1}$ every 2 years until an age of 10 years, then in steps of $0.1 \text{ tC ha}^{-1} \text{ yr}^{-1}$ every year until 15 years, thereafter like above.

10–20 cm, acid soils:

- meadow fine root input starting at $0.9 \text{ tC ha}^{-1} \text{ yr}^{-1}$, declining in steps of $0.05 \text{ tC ha}^{-1} \text{ yr}^{-1}$ until age 12 years,
- forest fine root input starting at age 12 according to the formula given above,
- net DOC input $0.1 \text{ tC ha}^{-1} \text{ yr}^{-1}$,
- no bioturbation,
- soil respiration starting at $1.3 \text{ tC ha}^{-1} \text{ yr}^{-1}$, declining in steps of $0.1 \text{ tC ha}^{-1} \text{ yr}^{-1}$ until yearn age of 11 years, thereafter $0.35 \text{ tC ha}^{-1} \text{ yr}^{-1}$, from 41 to 60 years declining to $0.15 \text{ tC ha}^{-1} \text{ yr}^{-1}$ until end.

10–20 cm, calcareous soils:

- meadow fine root input starting at $0.9 \text{ tC ha}^{-1} \text{ yr}^{-1}$, declining in steps of $0.05 \text{ tC ha}^{-1} \text{ yr}^{-1}$ until age 12 years,
- forest fine root input starting at age 12 according to the formula given above,
- net DOC input $0.02 \text{ tC ha}^{-1} \text{ yr}^{-1}$,
- no bioturbation,
- soil respiration starting at $1.3 \text{ tC ha}^{-1} \text{ yr}^{-1}$, declining in steps of 0.1 to $0.3 \text{ tC ha}^{-1} \text{ yr}^{-1}$, from 40 to 80 years 0.25 , thereafter $0.3 \text{ tC ha}^{-1} \text{ yr}^{-1}$ until end.