Tree Physiology 20, 849–857

Carbon stocks and soil respiration rates during deforestation, grassland use and subsequent Norway spruce afforestation in the Southern Alps, Italy

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Received April 14, 1999

Summary Changes in carbon stocks during deforestation, reforestation and afforestation play an important role in the global carbon cycle. Cultivation of forest lands leads to substantial losses in both biomass and soil carbon, whereas forest regrowth is considered to be a significant carbon sink. We examined below- and aboveground carbon stocks along a chronosequence of Norway spruce (*Picea abies* (L.) Karst.) stands (0–62 years old) regenerating on abandoned meadows in the Southern Alps. A 130-year-old mixed coniferous Norway spruce–white fir (*Abies alba* Mill.) forest, managed by selection cutting, was used as an undisturbed control. Deforestation about 260 years ago led to carbon losses of 53 Mg C ha^{-1} from the organic layer and 12 Mg C ha^{-1} from the upper mineral horizons (A_h, E). During the next 200 years of grassland use, the new A_h horizon sequestered 29 Mg C ha^{-1}. After the abandonment of these meadows, carbon stocks in tree stems increased exponentially during natural forest succession, levelling off at about 190 Mg C ha^{-1} in the 62-year-old Norway spruce and the 130-year-old Norway spruce–white fir stands. In contrast, carbon stocks in the organic soil layer increased linearly with stand age. During the first 62 years, carbon accumulated at a rate of 0.36 Mg C ha^{-1} year^{-1} in the organic soil layer. No clear trend with stand age was observed for the carbon stocks in the A_h horizon. Soil respiration rates were similar for all forest stands independently of organic layer thickness or carbon stocks, but the highest rates were observed in the cultivated meadow. Thus, increasing litter inputs by forest vegetation compared with the meadow, and constantly low decomposition rates of coniferous litter were probably responsible for continuous soil carbon sequestration during forest succession. Carbon accumulation in woody biomass seemed to slow down after 60 to 80 years, but continued in the organic soil layer. We conclude that, under present climatic conditions, forest soils act as more persistent carbon sinks than vegetation that will be harvested, releasing the carbon sequestered during tree growth.

Keywords: biomass, carbon sequestration, forest succession, land use change, organic layer, Picea abies, radiocarbon dating, soil carbon.

Introduction

The role of forests in the global carbon budget is of great importance (Walker and Steffen 1996). Forests contain approximately 80% of the global terrestrial aboveground and 40% of the world's belowground carbon stocks (Dixon et al. 1994). Any change in land use or climate affecting this carbon pool will have significant impacts on the total carbon budget. Deforestation generally leads to substantial losses of carbon from vegetation and soils (Mann 1986, Davidson and Ackerman 1993). In particular, soils that are initially rich in carbon, like cambisols, lose large amounts of their carbon stock following tree harvest (WBGU 1998).

In contrast, regenerating forests and plantations may represent important carbon sinks as a result of carbon storage in both plant biomass and soils (IPCC 1996). Many studies have examined whether afforestation of former agricultural land can counteract the observed increase in atmospheric CO_2 concentrations. Burschel et al. (1993*a*) reported that afforestation activities in Europe have a major carbon sequestration potential. Wofsy et al. (1993) stressed the impact of historical land use and forest age on current carbon stocks. Even with no further afforestation, Cannell and Dewar (1995) concluded that British forests will continue to be a carbon sink until the year 2025 because of the growth of many young plantation forests, potentially causing a delay in the increase in atmospheric CO_2 concentrations (Vitousek 1991, Trolier et al. 1996). In contrast, carbon budgets for Austria (Körner et al. 1993) and Switzerland (Paulsen 1995) showed that very large new afforestation areas would be necessary to balance anthropogenic CO_2 emissions. Moreover, many forests in the temperate region are currently recovering from previous disturbances such as logging (Houghton 1993). Thus, for a long-term carbon budget, the processes of loss during disturbance and subsequent accumulation need to be considered.

Carbon accumulation rates during afforestation are dependent on tree species and length of the rotation period. Pearson et al. (1987) reported biomass sequestration rates of 1.5 Mg C ha^{-1} year^{-1} over 200 years for *Pinus contorta* Dougl. *ex* Loud. successions on former meadows. Burschel et al. (1993*b*) calculated carbon accumulation rates between 0.5 Mg C ha^{-1}

$year^{-1}$ for 20-year-old *Quercus* spp. forests and 4.1 Mg C ha^{-1} $year^{-1}$ for 60-year-old *Pseudotsuga menziesii* Mirb. Franco (Douglas-fir) forests on former agricultural land. Similar results were presented by Cannell and Milne (1995) for British forest ecosystems, with carbon accumulation rates between 1.8 and 7.3 Mg C ha^{-1} $year^{-1}$ during the first rotation period. However, carbon accumulation in living biomass generally slows or ceases completely when forests grow old or are harvested (Cannell and Milne 1995, Ryan et al. 1997).

In contrast to the relatively short-lived sequestration of carbon in forest biomass, carbon pools in the organic layer and the soil might continue to increase, even when maximum tree biomass has been reached. However, there are few data sets on soil carbon sequestration. Switzer et al. (1979) found a steady-state soil organic carbon stock after about 70 years of old-field succession to oak–hickory–pine forests, whereas no steady-state in the organic layer carbon pools was observed after 73 years in Douglas-fir forests regenerated after fire (Turner and Long 1975). Similarly, Boone et al. (1988) calculated that it took more than 100 years until the organic layer in a *Tsuga mertensiana* (Bong.) Carrière forest had recovered to pre-disturbance values in thickness and carbon storage.

Little is known about the magnitude of the soil carbon stock that can accumulate during forest regeneration on former agricultural land, or how it compares with the soil carbon stock of old-growth forests. Furthermore, there are few data on the temporal development of soil carbon pools after disturbance. In this study, we quantified carbon pools in tree biomass, soil organic layer and upper mineral soil, as well as soil respiration rates for natural Norway spruce (*Picea abies* (L.) Karst.) regeneration on abandoned meadows in the montane region of the Southern Alps, Italy. The study site provided ideal conditions for this purpose, because Norway spruce stands of different ages were growing relatively close to each other under similar environmental conditions.

Materials and methods

Study site

The study site is located in the Parco Naturale Paneveggio Pale di San Martino, on the northern ridge of the Valsorda valley, Northern Italy (Trentino). The vegetation above 1000 m elevation is dominated by Norway spruce. However, in older parts of the forest, white fir (*Abies alba* Mill.) is gaining dominance. Mosses (*Rhytiadelphus triquetrus* (Hedw.) Warnst., *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B.S.G.) and dwarf shrubs (*Vaccinium myrtillus* L., *V. vitis-idaea* L.) are the prevailing understory species, accompanied by the grasses *Deschampsia flexuosa* (L.) Trin. and *Calamagrostis arundinacea* (L.) Roth. During the 1950s and 1960s, many of the previously regularly mown meadows were abandoned because of a decreasing human population in this area (Bortolotti 1996). Consequently, there was a rapid natural regeneration of Norway spruce, leading to an almost complete forest cover.

Selection of forest stands

Old maps, aerial photographs and local experts were used to identify locations that had been meadows in former times. Ten stands were chosen along an age chronosequence, from cultivated and abandoned meadows (referred to as 0- and 3-year-old forest, respectively) to regenerating successional Norway spruce stands of different ages (15-, 25-, 33-, 47-, 54- and 62-year-old) as well as a windthrow area (Table 1). The age of the forest stands was determined by wood coring. A 130-year-old permanent Norway spruce–white fir forest stand was used as a control. In contrast to the successional stands, this forest has never been cleared for cultivation. As a result of selection cutting (Plenterwald), this forest is characterized by a broad mixture of different age classes originating from natural regeneration.

The region belongs to the metamorphic complex of the Southern Alps, and consists mainly of gneiss and quartz phyllite (Brugnara and Zannoner 1997). Cambisols are the typical soil types for all stands. The organic soil layer consists of L, O_f and O_h layers, except for the two youngest stands where the O_h layer is missing. The mineral soil is generally characterized by a dark brown A_h horizon of varying depths, followed by a yellow-brown B horizon. For the 130-year-old forest soil, an eluvial layer as well as a B_s horizon indicated podzolization, thus characterizing the soil as spododystric cambisol.

Carbon stocks in tree stems

Stem biomass and carbon stocks in this dominant biomass compartment were determined on a 100-m^2 plot in each forest stand. The diameter at breast height (dbh) of all trees present (n = 15 to 40) as well as the absolute height of five representative trees were measured. Stem volume (V) was calculated as:

$$V = (0.5\,\mathrm{dbh})^2 h \pi f, \quad (1)$$

where h = height of tree and f = form factor. The form factor was determined according to Assmann and Franz (1963) and ranged between 0.469 and 0.587. Carbon stocks in tree stems were quantified based on a wood density of 379 kg m^{-3} (Müller 1959) and a carbon concentration of 50% dry weight.

Carbon stocks in the soil organic layer and mineral horizon

The litter layer (L), the soil organic layers (O_f and O_h layer) and the A horizon were sampled within a square (30 × 30 cm) with known depth at the upper side of a 2-m-long ditch. Coarse and fine roots were separated from the soil material. The soil material was dried, passed through a 2-mm sieve, ground and analyzed for carbon with a C/N analyzer (Carlo Erba Instruments, Milano, Italy). Bulk density was calculated as dry weight of the sieved soil material divided by the excavated volume. Mean thickness of the organic layer and the mineral A horizon were measured at 5-m intervals along 50-m transects in each stand. Mean carbon stocks of the organic layer and the mineral A horizon were calculated based on carbon concentrations, bulk densities and mean horizon thickness.

Table 1. Stand characteristics. All trees > 5 m tall were measured, except for the 15-year-old stand, where all trees > 2 m tall were measured. Abbreviations: dbh = diameter at breast height; *L. decidua* = *Larix decidua* Mill.; *A. incana* = *Alnus incana* (L.) Moench.

Stand age (years)	Elevation (m)	Mean height (m)	Mean dbh (cm)	Stem density (no. ha^{-1})	Vegetation
0	1350	–	–	–	Cultivated meadow
3	1130	0.1	–	–	Abandoned meadow
15	1280	3.5	4.5	2500	*Picea abies*
25	1390	7	8.3	1750	*Picea abies*, some *L. decidua*
33	1230	7.5	9.0	1600	*Picea abies*, some *A. incana*
47	1200	26	28.5	400	*Picea abies*, some deciduous trees
54	1250	28	43	500	*Picea abies*
62	1210	26	24.6	1300	*Picea abies*, some *Abies alba*
130	1370	28	30.5	1250	*Picea abies*, *Abies alba*
Windthrow	1230	–	–	–	*Deschampsia*, *Calamagrostis*, *Rubus*

Measurement of soil CO_2 efflux and soil water content

Soil respiration rates were measured in September 1998 in eight stands (0-, 15-, 25-, 33-, 47-, 54- and 130-year-old stands and the windthrow stand) with a soil respiration chamber (LI-6400-09; Li-Cor, Lincoln, NE) connected to a portable photosynthesis system (LI-6400). Five PVC tubes (10 cm long, 10-cm inner diameter) were inserted in the soil of each stand, 24 hours before measurement. The soil respiration chamber was set on top of these tubes, allowing an undisturbed measurement of soil CO_2 efflux rates. The protocol recommended by Li-Cor was followed, except that we made five observations of a 10 μmol mol^{-1} change per measurement. Litter and organic layer thickness (O_f and O_h layer) as well as soil temperatures (at 5-, 10- and 15-cm soil depths) were measured adjacent to each PVC tube. Gravimetric soil water content was determined, based on three replicates per measurement. The wet soil samples were weighed, then dried to constant weight. Soil water content was expressed as percent dry weight.

Radiocarbon dating

Charcoal samples were collected at the lower end of the A_h horizon in the meadow and all successional stands. A pooled sample from several stands (0-, 3-, 33- and 47-year-old stands) and one sample from the 47-year-old stand were analyzed in the Leibniz-Labor für Altersbestimmung und Isotopenforschung at the Christian-Albrechts-Universität, Kiel, Germany (for calibration see Stuiver and Becker 1993, Stuiver and Reimer 1993).

Results

Effects of land use change on the soil profile

Effects of deforestation and subsequent grassland use were evident in a comparison of the soil profiles of the undisturbed control forest and the successional plots. The organic layers in the undisturbed Norway spruce–white fir forest were followed by an eluvial horizon (E horizon), whereas this layer was missing under the meadow and the successional stands. Moreover, in all successional stands and in the cultivated meadow, a charcoal layer at the lower end of the A_h horizon indicated burning of biomass and organic layers when the original Norway spruce–white fir forest was cleared for cultivation. This clearance took place 260 ± 40 years ago, based on the age of the charcoal as determined by radiocarbon dating. Thus, human impacts as well as erosion after deforestation resulted in the loss of the old A horizon that had developed during forest growth. This suggests that the present A_h horizon in the meadow and the successional stands was built up when the region was used as grassland.

Stem carbon stocks

Carbon stocks in stem biomass increased exponentially with stand age, reaching 169 Mg C ha^{-1} in the 62-year-old Norway spruce stand ($r^2 = 0.99$; Figure 1). This carbon pool was similar to the value of 207 Mg C ha^{-1} obtained for the 130-year-old Norway spruce–white fir stand. Thus, carbon accumulation slowed down after about 60 to 80 years. Carbon accumulation rates were low during the early stages of forest succession:

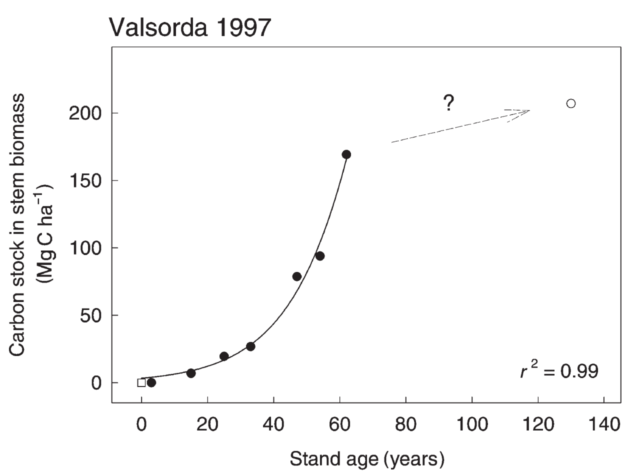

Figure 1. Development of carbon pools in stem biomass during forest succession (□ = cultivated meadow; ● = successional forest stands; ○ = undisturbed control stand). The relationship between carbon pools and stand age was significant at $P = 0.05$ and was described as: $y = 264.78/(1 + \exp(-(x - 90.99)/15.33))$.

0.46 Mg C ha^{-1} $year^{-1}$ between age 0 and 15, 1.3 Mg C ha^{-1} $year^{-1}$ between 15 and 25 years, and 0.9 Mg C ha^{-1} $year^{-1}$ between 25 and 33 years. Thereafter, rates increased to 3.7 Mg C ha^{-1} $year^{-1}$ between 33 and 47 years, and 6.0 Mg C ha^{-1} $year^{-1}$ between 47 and 62 years.

Soil carbon stocks

Soils showed a very different pattern of carbon sequestration with stand age compared with the vegetation. The thickness of the soil organic layer increased linearly with stand age (Figure 2), probably because of the increasing input of needle litter during stand development ($r^2 = 0.78$, $P < 0.05$). After 62 years of forest succession, the soil organic layer was 8 cm thick, compared with 17 cm thick in the 130-year-old Norway spruce–white fir forest. The depth of the mineral A_h horizon, probably originating from the former grassland, tended to decrease during forest succession ($r^2 = 0.54$, $P < 0.05$; Figure 2). The large standard deviations associated with the thickness of the A_h horizon were caused by the distinct surface structure of the former meadows, which is characterized by hummocks and hollows. Generally, the A_h horizon in the hollows was thicker than on top of the hummocks. Bulk density varied from 0.29 to 0.70 Mg m^{-3} in the mineral soil and from 0.21 to 2.44 Mg m^{-3} in the organic soil layer. The soil organic layer had higher values in older stands (data not shown). Soil carbon concentrations in the upper layers of the mineral horizon were 7–8% in the meadow and 13–19% in the forest stands.

Carbon accumulation in the organic layer increased linearly at a rate of 0.36 Mg C ha^{-1} $year^{-1}$ ($r^2 = 0.69$, $P < 0.05$; Figure 3) along the chronosequence. In the 62-year-old Norway spruce stand, it reached 28 Mg C ha^{-1} compared with 53 Mg C ha^{-1} in the undisturbed 130-year-old Norway spruce–white fir stand. Carbon concentrations of the soil organic matter remained constant at 46 to 48% (data not shown). Carbon storage in the A_h horizon showed a very different pattern (Figure 3). Carbon stocks of the A horizon increased steadily from 29 Mg C ha^{-1} in the cultivated meadow to 48 Mg C ha^{-1} in the 25-year-old Norway spruce stand, before they decreased sharply, reaching a minimum of 10 Mg C ha^{-1} in the 62-year-old stand. Part of these fluctuations reflected the different depths of the mineral horizon (see Figure 2). Standardized to the same thickness, soils of the 0- and 3-year-old forests showed lower carbon stocks in the upper layers of the meadow-derived A_h horizon than the older forest stands (data not shown). Carbon storage of both the organic layer and the mineral horizon resulted in maximum values of 65 Mg C ha^{-1} in the 130-year-old undisturbed forest stand compared with 29 Mg C ha^{-1} in the cultivated meadow.

Soil CO_2 efflux

Soil CO_2 efflux showed only a weak trend with increasing stand age (Figure 4A; Table 2). Soil respiration rates from the cultivated meadow soil averaged 5 μmol CO_2 m^{-2} s^{-1}, whereas soil respiration of the forest soils fluctuated between 2 and 4 μmol CO_2 m^{-2} s^{-1}. Lower soil CO_2 efflux rates were observed in stands where light attenuation was higher. Soil respiration rates of the windthrow stand, which was about 26 years old and densely covered with grasses and shrubs, did not exceed those measured in the forest stands.

Soil respiration rates were higher at higher soil temperatures (Figure 4B and Table 2). None of the other factors (soil water content, thickness of the litter or organic layer, or the carbon pool in the organic layer) explained a significant fraction of the variance in soil respiration rates ($P > 0.1$).

Discussion

Soil profile and carbon stocks during grassland use after deforestation

A striking characteristic of the mineral soil profiles in the stands investigated was the absence of both an eluvial E horizon and a humus- and sesquioxide-enriched B_s horizon in the cultivated meadow and the successional forest stands. These horizons were present in the undisturbed Norway spruce–white fir stand. Historic land use practices could explain this observation. During the first logging period in this area, about 260 ± 40 years ago, settlers burned the topsoil before growing cereals and vegetables (Cacciaguerra 1991). This was confirmed by the existence of a charcoal layer at the lower end of

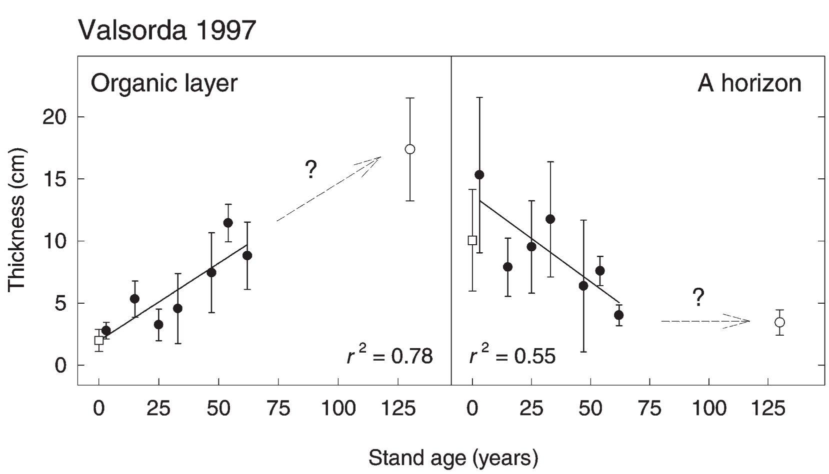

Figure 2. Thickness of the organic layer (left panel) and the mineral A horizon (right panel) during forest succession (□ = cultivated meadow; ● = successional forest stands; ○ = undisturbed control stand). Means and standard deviations are given ($n = 10$). Left panel: $y = 1.97 + 0.13x$, $P = 0.004$. Right panel: $y = 13.01 - 0.13x$, $P = 0.038$.

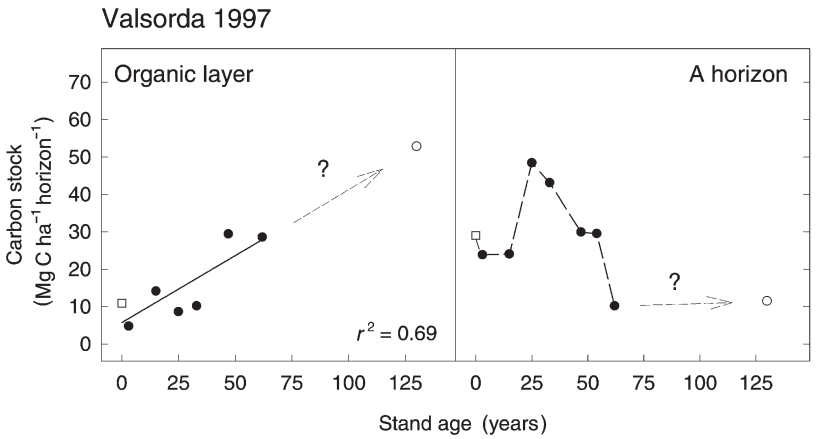

Figure 3. Carbon stocks in the organic layer (left panel) and the mineral A horizon (right panel) during forest succession (□ = cultivated meadow; ● = successional forest stands; ○ = undisturbed control stand). Left panel: $y = 5.78 + 0.36x$, $P = 0.02$. Right panel: relationship was non-linear, $P = 0.68$. Data for carbon stock in the organic layer of the 54-year-old stand were not determined.

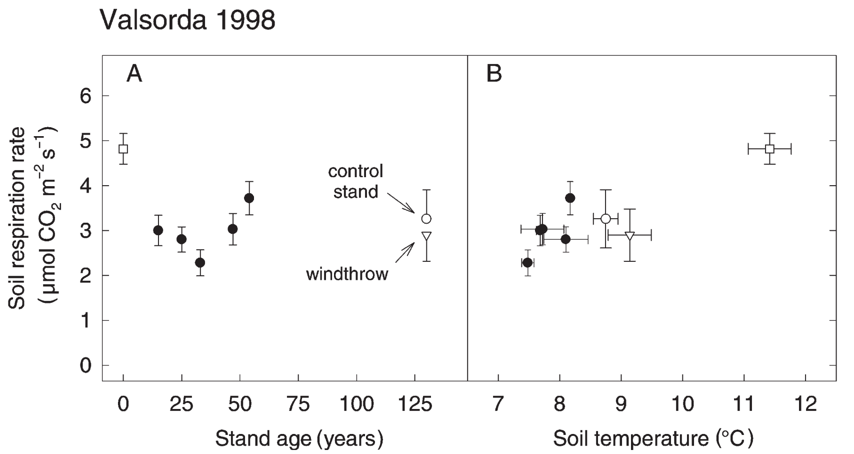

Figure 4. Relationships between soil respiration rates and stand age (A) and soil temperature in 5-cm depths (B). Means and standard deviation are given ($n = 5$). (□ = cultivated meadow; ● = successional forest stands; ○ = undisturbed control stand; ▽ = windthrow area).

the A_h horizon in all successional stands that was absent in the undisturbed control stand. Because of the high annual rainfall of 1350 mm (Zunica 1981) and the steep inclination of the slopes (25–30°), erosion of parts of the mineral soil including the E horizon probably occurred (Kalisz 1986).

The presence of a charcoal layer indicates that the entire A horizon must have been built up during approximately 200 years of grassland use, after deforestation of the Norway spruce–white fir (Figure 5). During this period, the new A_h horizon developed a thickness of 10 to 15 cm (0- and 3-year-old stands, respectively), sequestering about 29 Mg C ha^{-1}. Between 1740 and 1935, the carbon accumulation rate was 0.15 Mg C ha^{-1} $year^{-1}$. Based on the soil carbon stocks of the undisturbed Norway spruce–white fir forest (organic layers and mineral A horizon), soil carbon loss as a result of logging and burning was 65 Mg C ha^{-1} (53 Mg C ha^{-1} from the organic layer plus 12 Mg C ha^{-1} from the A_h and E horizons; cf. Figure 3 and Table 3). An additional 207 Mg C ha^{-1} was lost from stem biomass. Thus, the total carbon loss attributable to deforestation was 272 Mg C ha^{-1}.

Carbon stocks during afforestation

As early as 1959, Ovington recognized that planting coniferous forests on former agricultural land enhanced soil carbon sequestration (in Harrison et al. 1995). Ovington reported that, under these plantations, the organic layer grew more than 10 cm thick and stored substantial amounts of carbon. More recently, Dewar and Cannell (1992) pointed out that plantation ecosystems may act as major carbon sinks because of buildup of soil organic matter, mainly during the first rotation period.

Organic layer

We found a linear increase in soil carbon stocks in the organic layer over the first 62 years of forest regeneration at a rate of 0.36 Mg C ha^{-1} $year^{-1}$ (Table 4, see Type 2). In the few studies that focused on forests established on former agricultural land, accumulation rates varied between 0.04 and 0.57 Mg C ha^{-1} $year^{-1}$. Typically, regenerating forests produce litter that is more resistant to decomposition than that of the previous agricultural crop. Moreover, the annual aboveground litter input to the soil is higher in forests than in grasslands where aboveground biomass is frequently harvested or grazed. Because plant litter production exceeds decomposition rates in the establishing tree stand (Zak et al. 1990), there is an accumulation of material in the soil organic layer.

Soil respiration rates measured in the Valsorda valley also indicated carbon accumulation with stand age. Soil CO_2 efflux was not related to forest age or to the amount of carbon stored.

Table 2. Correlation analysis of potential factors influencing soil respiration rates. Abbreviations: SR = soil respiration rate (μmol CO_2 m^{-2} s^{-1}); Age = stand age (years); L = thickness of the litter layer (cm); O = thickness of the organic layer (cm); C_{org} = carbon stored in the organic layer (Mg ha^{-1}); T_5, T_{10}, and T_{15} = temperature (°C) at 5, 10, and 15 cm below the mineral soil surface, respectively; and θ = soil water content of the organic layer (% dry weight). The P values are below the correlation coefficients (α = 0.05).

	SR	Age	L	O	C_{org}	T_5	T_{10}	T_{15}	θ
SR		–0.717	0.679	–0.484	–0.039	0.947	0.934	0.858	–0.468
		0.086	0.104	0.205	0.476	0.007	0.010	0.031	0.213
Age			–0.384	0.827	0.642	–0.764	–0.494	–0.319	0.370
			0.261	0.042	0.122	0.066	0.199	0.300	0.270
L				–0.090	–0.018	0.784	0.852	0.825	–0.350
				0.443	0.489	0.058	0.033	0.043	0.282
O					0.815	–0.600	–0.233	–0.002	0.694
					0.046	0.143	0.353	0.498	0.097
C_{org}						–0.268	0.142	0.363	0.456
						0.332	0.410	0.274	0.220
T_5							0.911	0.788	–0.637
							0.016	0.057	0.124
T_{10}								0.971	–0.444
								0.003	0.227
T_{15}									–2.70
									0.330

Efflux rates were only slightly higher for the cultivated meadow (because of higher soil temperatures) than for the successional forest stands, indicating that litter production and litter decomposition were decoupled during forest development, resulting in thick soil organic layers in old stands. It is not known whether these carbon stocks can be maintained in a warmer climate when increased soil temperatures will accelerate decomposition processes (Moore et al. 1999).

Mineral soil

During forest regeneration on abandoned land, carbon stocks in the mineral A_h horizon showed no clear trend with stand age, although the layer declined continuously in thickness. The data suggest that carbon stocks increased for the first 25 years of tree growth, before declining rapidly. However, carbon stocks in the 25- and 33-year-old stands seem unusually high for this region (cf. Table 4), possibly because of additional carbon inputs: the 25-year-old stand was probably extensively grazed, causing inputs from animal faeces. In the 33-year-old stand, a density-dependent mortality wave occurred about 10 years ago, resulting in a substantial carbon input of decaying wood. If these two stands are regarded as outliers, the data suggest continuously declining carbon stocks in the meadow-derived A_h horizon during forest succession. This trend might be explained by three different processes. First, the thickness of the meadow-derived A_h horizon declined significantly as a result of organic matter mineralization within the soil profile during forest succession (cf. Figure 2). Second, there might be a decrease in organic matter input to the mineral soil. Accumulating Norway spruce litter is relatively resistant to decomposition (Mellilo et al. 1982), thus inhibiting substantial mixing or infiltration of dissolved organic carbon in the mineral soil as well as the development of a new, forest-derived A_h horizon. Third, carbon concentrations in the upper centimeters of the A_h horizon were higher in the forest soils than in the meadow soil, thus compensating for decreasing thickness with age.

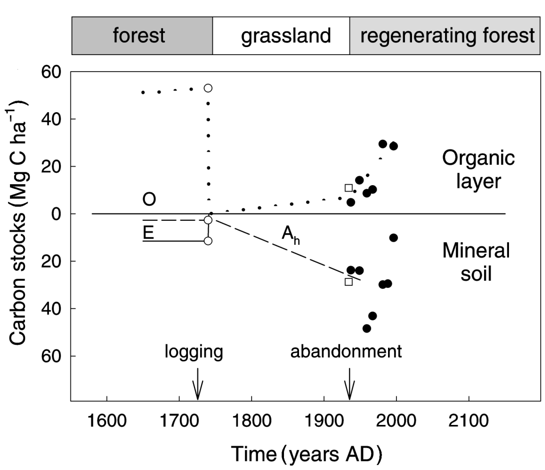

Figure 5. Changes in soil carbon stocks during deforestation, grassland use and afforestation (□ = cultivated meadow; ● = successional forest stands; ○ = undisturbed control stand). See text for explanation. Abbreviations: A_h = mineral layer; E = eluvial horizon layer; and O = organic layer.

Carbon accumulation rates

Although carbon storage in stem biomass in these successional forest stands exceeded the carbon stored in the soil profiles within the first 62 years, carbon sequestration in tree biomass is only short-term. Often, only 40% of the timber enters long-term carbon storage, defined as all products with a life span of more than 5 years (Harmon et al. 1990). In contrast, carbon storage in the soil compartment is generally

Table 3. Carbon stocks in the mineral soil under various forest types.

Vegetation	Country	Age (years)	Depth (cm)	C stocks (Mg C ha $^{-1}$)	Source
Picea abies	Italy	0	10	28.7	This study
		3	15	23.8	
		15	8	24.0	
		25	10	48.4	
		33	12	43.1	
		47	6	29.9	
		54	8	nd	
		62	4	10.2	
Picea abies/*Abies alba*		130	3	11.5	This study
Picea abies	Germany	56	25	166	Burschel et al. (1993*b*)
		99	25	245–268	
		150	25	183	
Picea abies	Germany	–[1]	90	118	Ulrich and Puhe (1994)
Abies amabilis	USA	175	60	243.96	Turner and Singer (1976)
Tsuga mertensiana	USA	25	30	37.4	Boone et al. (1988)
Pinus spp.	USA	50–100	Surface	12–13	Switzer et al. (1979)
Mixed coniferous	USA	12	Upper	83	Black and Harden (1995)
		79	A_h	100	
Boreal coniferous	Finland		50[2]	36–53	Liski and Westman (1995)
			50[2]	5–21	
Mixed stands	USA	0–28 / 99	0–15	56	Compton (1998)
Liriodendron tulipifera	USA	0–60	10[2]	15	Kalisz (1986)
			50[2]	34	

[1] Averaged over forests of various ages.
[2] Sampling of subsequent soil horizons.

long-term. Mean residence times of carbon storage in soil are much higher than those in biomass, exceeding several hundred years (Trumbore et al. 1990). Thus, forest soils as well as vegetation should be taken into account as important carbon stocks (IPCC 1996). Moreover, the carbon accumulation rate of 0.36 Mg C ha^{-1} year^{-1} in the soil organic layer of our Norway spruce stands implied that 132 years were required to regain the amount of carbon stored in the undisturbed organic layer (53 Mg C ha^{-1}; Figure 3). Based on a comparison of impoverished old-field forest soils with unploughed areas in central Massachusetts, Hamburg (1984, cited in Compton 1998) estimated that 200 years was necessary for the accumulation of the original soil organic matter. Soil carbon accumulation in Alaskan forest stands that regenerated naturally after wind-

Table 4. Carbon accumulation in the organic and mineral layers under different forest types. Type 1, old-field succession; Type 2, succession after disturbance (fire, harvest, etc.); Type 3, primary succession. Accumulation period is 28 years. Abbreviation: na = not available.

Vegetation	Country	Type	Age (years)	C Accumulation in organic layer (Mg C ha $^{-1}$ year $^{-1}$)	C Accumulation in mineral soil (Mg C ha $^{-1}$ year $^{-1}$)	Source
Picea abies	Italy	1	0–62	0–36	–0.30	This study
Coniferous forest	U.K.	1	15–45	0.57	–	Billett et al. (1990)
Coniferous forest	U.K.	1	60–100	0.21	–	Billett et al. (1990)
Pinus taeda	USA	1	12–16	2	–	Kinerson et al. (1977)
Pinus spp.	USA	1	25–65	0.04	0.1[1]	Switzer et al. (1979)
Mixed deciduous	U.K.	1	0–92	–	0.51[2]	Jenkinson (1990)
Herbaceous vegetation	USA	1	0–60		0.16[3]	Zak et al. (1990)
Pseudotsuga menziesii	USA	2	22–73	0.38	–	Turner and Long (1975)
Tsuga mertensiana	USA	2	25–225	0.027	–	Boone et al. (1988)
Pinus elliottii	USA	2	2–34	1.22	–	Gholz and Fisher (1982)
Northern hardwood	USA	2	15–64	0.29	–	Covington (1981)
			64–200	0.02	–	
Mixed forest	USA	3	na	–	0.34[4]	Sollins et al. (1983)

[1] Soil surface sampled; [2] sampling depth: 0–23 cm; [3] sampling depth: 10 cm; [4] sampling depth: 0–70 cm.

throw showed no trend toward a new equilibrium, even after 350 years of succession (Bormann et al. 1995). In contrast, soil carbon stocks in plantation systems mainly increase during the first rotation period (40–60 years; Cannell and Dewar 1995). Thereafter, they might fluctuate in response to forest management, without increasing any further (Dewar and Cannell 1992). In our Norway spruce stands, which regenerated naturally on abandoned agricultural lands, the soil organic layers continued to accumulate carbon even after maximum Norway spruce biomass had been reached. It is not known how long this accumulation will continue, nor how future forest management practices will affect this growing carbon sink. We conclude that natural or selectively used forests like those in the Valsorda valley provide a greater potential for long-term carbon storage in the soil organic layer than intensively managed forest plantations with short rotation periods.

Acknowledgments

This study was supported by the Parco Naturale Paneveggio Pale di San Martino. We are grateful to Dr. E. Sartori for permission to conduct this study in the area of the natural park. Special thanks to R. and G. Asche as well as to F. Thuille for field assistance.

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