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Variation of soil and biomass carbon pools in beech forests across a precipitation gradient

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Abstract

Temperate forests have recently been identified as being continuing sinks for carbon even in their mature and senescent stages. However, modeling exercises indicate that a warmer and drier climate as predicted for parts of Central Europe may substantially alter the source/sink function of these economically important ecosystems. In a transect study with 14 mature European beech (*Fagus sylvatica* L.) forests growing on uniform geological substrate, we analyzed the influence of a large reduction of annual precipitation (970–520 mm yr^{-1}) on the carbon stocks in fast and slow pools, independent of the well-known aging effect. We investigated the C storage in the organic L, F, H layers, the mineral soil to 100 cm, and in the biomass (stem, leaves, fine roots), and analyzed the dependence of these pools on precipitation. Soil organic carbon decreased by about 25% from stands with >900 mm yr^{-1} to those with <600 mm yr^{-1}; while the carbon storage in beech stems slightly increased. Reduced precipitation affected the biomass C pool in particular in the fine root fraction but much less in the leaf biomass and stem fractions. Fine root turnover increased with a precipitation reduction, even though stand fine root biomass and SOC in the organic L, F, and H layers decreased. According to regression analyses, the C storage in the organic layers was mainly controlled by the size of the fine root C pool suggesting an important role of fine root turnover for the C transfer from tree biomass to the SOC pool. We conclude that the long-term consequence of a substantial precipitation decrease would be a reduction of the mineral soil and organic layer SOC pools, mainly due to higher decomposition rates. This could turn temperate beech forests into significant carbon sources instead of sinks under global warming.

Keywords: carbon sequestration, climate change, drought, *Fagus sylvatica*, fast carbon pools, fine roots

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Introduction

Approximately 60% of organic carbon contained in the terrestrial ecosystems of the world is stored in soils (Trumbore *et al.*, 1996), with the largest part of it found in forest soils (IPCC, 2007). Atmospheric CO_2 enters the forest soil through the decomposition of shoots and roots, root exudates, cell sloughing, and via C transfer to mycorrhizal fungi and their turnover (Kuzyakov & Domanski, 2000; Godbold *et al.*, 2006). Depending on the chemical composition and recalcitrance of the organic substances supplied with these fluxes, and on the physical and chemical environment, the carbon transferred to the soil will reside either in more labile or stable fractions of soil organic matter (SOC). Four organic matter pools are usually defined according to their stability (Walse *et al.*, 1998): easily decomposable carbohydrates (polysaccharides such as cellulose, hemicellulose, and chitin), more stable alkyl structures (lipids and waxes, i.e., cutin and suberin), even more stable lignin, and charcoal as the most recalcitrant structure for decomposition. Important site factors controlling the partitioning of carbon on pools with rapid or slow turnover are climate (temperature and precipitation), soil properties (in particular clay content), the type of forest vegetation (tree species and stand structure), and stand history (Paul, 1984; Sollins *et al.*, 1996; Gleixner *et al.*, 2001; Gonzalez & Laird, 2003; Huygens *et al.*, 2005; Van Miegroet *et al.*, 2005; Mueller & Koegel-Knabner, 2009). Conventionally, leaf and fine root biomass and the organic litter layers atop of the soil are considered as 'fast C pools', SOC in the mineral soil and carbon in wood biomass as 'slow pools' (Norby *et al.*, 2002).

Increasing temperatures and decreasing summer rainfall, as predicted for parts of Central Europe in the

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course of climate change in the coming decades, may influence C sequestration in soil and biomass of temperate forests through differential effects on plant productivity and associated debris supply to the soil, on decomposition, and on C loss with DOC output via seepage water. Higher summer temperatures will extend the vegetation period and increase the net carbon gain of temperate trees, while summer heat waves and more pronounced drought should decrease forest productivity. Decomposition is likely to increase with higher temperatures, while extended dry periods may retard it (Trumbore *et al*., 1996; Garten *et al*., 2000; Sanderman *et al*., 2003; Sotta *et al*., 2007). Thus, temperate forests could in theory respond to warmer and drier summers with a higher or lower tree biomass, and a higher or lower SOC pool, depending on the magnitude of climate change, tree species composition and environmental conditions. While modeling studies have made predictions about the response of forest carbon pools to a drier and warmer climate (e.g., Schimel *et al*., 1994; Nakane, 2001; Tremblay *et al*., 2002; Smith *et al*., 2006; Sitch *et al*., 2008), empirical data are virtually absent. Extrapolation from greenhouse or microcosm studies with tree seedlings or saplings and soil columns to mature forests simplifies the complexity of the natural ecosystem to only the restricted number of factors being relevant in pot experiments. A source of information can be comparative studies in forest stands along precipitation gradients, which may provide valuable information for understanding climate effects on C sequestration in forests if the sites are carefully selected and other environmental site factors are kept sufficiently constant.

In Central Europe, *Fagus sylvatica* L. (European beech) forms monospecific stands under a broad variety of site conditions ranging from humid to semiarid climates (>2000 to <500 mm of precipitation per year) and from basic to acid soils (Ellenberg & Leuschner, 2010). This allows the investigation of long-term adaptation processes of forest ecosystems to decreasing precipitation (and increasing temperatures) independently of tree species or soil influences, factors that can be held sufficiently constant.

In this study, we used a transect approach with 14 mature European beech forests on the same bedrock (Triassic sandstone) to analyze the size of carbon pools in soil and plant biomass (above- and belowground) across a steep precipitation gradient (970–520 mm yr^{-1}) with similar annual temperature range in a temperate broad-leaved forest ecosystem. Study aims were (i) to analyze the dependency of carbon pools in soil and biomass on precipitation, and (ii) to assess the relative importance of fast and slow carbon pools along the precipitation gradient. We tested the hypotheses that (1) both SOC and plant biomass decrease with a decrease in precipitation from 970 to 520 mm yr^{-1}, and (2) decreasing precipitation results in a relative shift of carbon from labile pools (leaf and fine root biomass, soil organic layer) to stable pools (SOC and wood biomass) which would reflect the growing importance of more durable, structural plant components over dynamic organs, and more recalcitrant organic compounds under conditions of increasing drought stress.

Materials and methods

Study sites and climate

We investigated the carbon pools in biomass and soil in a transect study with 14 mature beech stands across a 150 km-long precipitation gradient (970–520 mm yr^{-1}) between the Solling Mountains and the Thuringia Basin (Central Germany) in the center of the distribution range of *F. sylvatica* (Table 1). Among the five 'ecosystem state factors' influencing soil development as defined by Jenny (1941) – climate, relief, organisms, parent material and time – four could be held sufficiently constant in this study to investigate the influence of the role of the fifth factor, climate, on ecosystem carbon storage. Variation in parent material and relief could be reduced to a minimum by selecting suitable beech stands on the same geological substrate (Triassic sandstone of Middle Bunter, formation 'Hardegsen Folge') with absent or insignificant cover layers of quaternary loess and in similar topographic positions (230–440 m asl) within a limited area (approximately 450 km^2 in size). The soil texture was loamy-silty sand to clayey loam and the soil types were mainly Cambisols, or Umbrisols at the moister stands, with a variety of subtypes. The time factor had a similar influence at all studied forest sites, because all soils have developed since the end of the Weichselian glaciations for about 12 000 years, and all beech stands were monospecific and of similar stand age (100–140 years old; extremes: 90 and 157 years). Stands were sufficiently comparable with respect to canopy closure (closed canopy without major gaps and with additional tree layers and shrubs being mostly absent) and stand structure (stem densities 175–250 ha^{-1}; understory vegetation mostly absent). We compared single-species stands of the same tree species, which largely eliminates the influence of the organism factor on the properties of the forest floor and the mineral topsoil.

The 14 mono-specific beech stands were selected along a precipitation gradient from more suboceanic to more subcontinental climate in the rain shadow of the Solling and Harz mountains. Mean annual precipitation decreased from the west (970 mm yr^{-1}) to the east (520 mm yr^{-1}), while the corresponding summer rainfall

Table 1 Topographic, edaphic, and climatic characteristics and stem biomass of 14 beech stands on Triassic sandstone along a precipitation gradient in central Germany

Site #	Altitude (m asl)	Aspect	Inclination (°)	Humus form	Soil type	Precipitation (mm yr^{-1})	Temperature (°C)	Stem biomass (kg m^{-2})
1	400	NW	9.1	lm	pU	970	7.3	38.7
2	380	NW	4.0	lm	U-L (p)	950	7.4	34.2
3	340	NW	4.3	lm	U (p)	910	7.7	38.6
4	250	SW	7.4	lm	L-U (p)	860	8.2	30.4
5	410	NE	1.6	m	L-C	820	7.3	41.4
6	440	NW	6.7	vm	L	800	7.1	29.1
7	250	N	1.2	m	C	680	8.2	25.3
8	340	SW	9.5	m	C	670	7.7	31.4
9	320	S	4.3	vm	L-C	650	7.8	38.6
10	320	NW	4.8	vm	L-C	580	7.8	43.6
11	280	NW	2.3	m	C	580	8.0	34.6
12	230	SW	5.2	lm	C-eL	550	8.3	22.0
13	240	SE	3.0	m	C-L	550	8.3	37.5
14	280	NW	1.3	m	C	520	8.0	58.0

Mean annual precipitation and temperature were derived from weather station data that was corrected for altitude.
Humus form (cf. Green *et al*., 1993): lm,leptomoder; m,mullmoder; vm,vermimull.
Soil type (WRB): C, Cambisol; e, eutric; L, Leptosol; p, podzolic; U, Umbrisol.

(May–September) decreased from 420 to 270 mm yr^{-1}, west to east. Mean annual temperature was 7.8 °C with a tendency for slightly higher temperatures in the eastern, more continental section of the gradient.

Soil sampling and chemical analyses

The soil chemical sampling took place in one 30 m × 30 m plot in the center of each stand. A soil profile examination was carried out at every study site in a soil pit in the center of the plot following the criteria of 'Arbeitskreis Standortskartierung' (1996). Humus forms were classified according to Green *et al*. (1993), soil types after IUSS *et al*. (2006). Soil samples were taken with a soil corer of 5 cm diameter in April 2004 at five randomly chosen locations within the 30 m × 30 m study plot in both the organic layer and the mineral soil (0–10 and 10–20 cm depth). In a second campaign in May 2008, mineral soil samples were collected with a Pyrckhauer corer to 100 cm depth or to the depth of the bedrock. Samples were taken at 20–40, 40–60, 60–80, and 80–100 cm depth in direct proximity of the earlier campaign. Thus, the soil chemical data given in this paper are averages of five replicate samples each. To account for spatial variability, each of the five samples itself consisted of four subsamples that were taken at random locations within each a 50 cm radius around every respective sampling point. These subsamples were mixed and used for a single analysis. Sample preparation and chemical analyses mainly followed the protocol given by BMELF (1994).

In the organic layer, the pools of organic matter and carbon were determined by sampling the entire layer with its L, F, and H horizons to the surface of the mineral soil with a soil corer (diameter 5 cm, length 10 cm), drying the material (105 °C, 48 h) and weighing it. The pool was calculated by relating the organic mass of the entire layer to corer aperture. Total carbon and nitrogen in the humus material were determined in samples dried at 70 °C (48 h) using a C/N elemental analyzer (vario EL III, elementar, Hanau, Germany). The transition from the organic layer to the mineral soil was defined by morphological criteria and the organic matter/mineral content ratio according to BMELF (1994); 0 cm mineral soil depth stands for the level of this transition.

The bulk density of the mineral soil was measured by weighing dried soil samples (105 °C, 48 h) of 100 cm^3 volume and by accounting for the gravel and stone content (>2 mm size) of the soil. Total carbon and nitrogen in the mineral soil (0–100 cm) were determined in samples dried at 70 °C (48 h) using a C/N elemental analyzer. The carbonate content was measured by a Scheibler calcimeter. Fresh mineral soil samples (0–10 and 10–20 cm depth) were analyzed for the pH of the soil solution using a 1 : 2.5 soil: 1 M KCl-suspension. The concentrations of salt-extractable cations were determined by percolating 2.5 g of soil with 100 mL of 1 M NH_4Cl-solution for 4 h. The solution concentrations of Ca, K, Mg, Fe, Mn, and Al were analyzed by atomic absorption spectroscopy (Fe was assumed to be Fe^{2+}). The concentration of hydrogen ions at the cation

exchangers was calculated from the observed pH change during the percolation process. The base saturation gives the percentage portion of Ca, K, and Mg to the sum of all extractable cations in the NH_4Cl-extraction (Meiwes *et al.*, 1984). Sodium was neglected in the analyses because its portion in CEC was <1% throughout. Plant-available phosphorus (P_a) according to Bowman & Cole (1978) was extracted by resin bags (anion exchange gel; Dowex 1 × 8–50; Dow Water & Process Solutions, Edegem, Belgium) that were placed for 16 h in a solution of 1 g soil material suspended in 30 mL water (Sibbesen, 1977). P_a was re-exchanged by NaCl and NaOH solutions and analyzed by blue-dyeing (Murphy & Riley, 1962) and photometric measurement at 712 nm against water (spectrophotometer, Libra S 21, Biochrom, Cambridge, UK).

Measurement of climate parameters

Mean annual precipitation and temperature were derived from weather station data of the closest weather stations corrected for altitude. For the moistest and the driest stand, the amount of precipitation estimated from the weather station data was validated by rain gauge measurements in the stand in the 2004 growing season. We were not able to monitor soil moisture continuously at the 14 sites; however, soil moisture measurements with a mobile TDR probe were conducted every second month in 0–20 cm soil depth in all stands. According to these occasional soil moisture measurements, the lower rainfall at the dry end is corresponding to lower absolute soil moisture minima and a longer duration of low soil water contents in summer in comparison with the sites at the moist end of the gradient as expected from the rainfall data (cf. Meier & Leuschner, 2008a). Air temperature in 1.3 m height and soil temperature in 10 cm depth were continuously measured with i-button sensors (Thermochron, Maxim, Dallas, TX, USA) from July 2004 to June 2005.

Leaf and fine root analyses and estimation of stem wood mass

Leaf litter was collected by litter trapping in ten litter buckets (aperture: 0.28 m^2) per plot that were installed in spring 2003 and were sampled once immediately after the autumnal litter fall in all 14 stands (for measuring details, see Meier & Leuschner, 2008a). Fine roots were collected with a 4 cm-soil corer in the organic layer and the mineral soil to 20 cm soil depth in summer 2003 and sorted into live and dead fine root mass under a stereomicroscope (for measuring details, see Meier & Leuschner, 2008b). The ingrowth core method was used for assessing the growth potential of the fine roots in the 14 stands. By relating root increment per year to the standing stock of fine root biomass in the direct proximity of the cores, we calculated relative fine root ingrowth rate as a rough estimate of root turnover (in $year^{-1}$). Leaf and fine root samples were dried (70 °C, 48 h) and ground. Total carbon and nitrogen of the samples were determined by elemental analysis. The carbon isotope composition of fine root biomass (as an indicator of carbohydrate availability for root growth) was analyzed by mass spectroscopy (Delta plus, ThermoFinnigan, Bremen, Germany). Stem volume was calculated based on the tables of Dagnelie *et al.* (1999) with stem circumference and tree height of eight randomly chosen beech individuals per stand as inputs. The stand carbon pool in aboveground stem wood was calculated as C (stems) = cumulative stem volume $\times 560\,kg\,dm\,m^{-3} \times 0.49\,kg\,C\,kg^{-1}$ (according to Vande Walle *et al.*, 2005).

Statistical analyses

Means and standard errors of the soil chemical data were calculated from each five samples per horizon and study site. Statistical analyses were conducted with the package SAS, version 9.1 (Statistical Analyses System, SAS Institute Inc., Cary, NC, USA). Probability of fit to normal distribution was tested by a Shapiro–Wilk test. Since the data had a Gaussian distribution, study site means were compared by a Scheffé test. We employed linear regression analyses to quantify the influence of edaphic, stand structural and climatic parameters on soil organic carbon (SOC) pools. Significance was determined at $P \leq 0.05$ in all tests.

Results

Carbon pools in forest soils

SOC in the 14 stands varied between 893 and 1793 mol $C_{org}\,m^{-2}$ (or 11–22 kg C m^{-2}) in the soil profile to 20 cm depth and between 1046 and 2494 mol m^{-2} (or 13–30 kg m^{-2}) in the profile to 100 cm depth (Fig. 1). The organic carbon pool in the mineral soil significantly increased from 1054 mol $C_{org}\,m^{-2}$ 20 cm^{-1} in stands with <600 mm yr^{-1} to 1447 mol m^{-2} in stands with more than 900 mm yr^{-1} (Fig. 2b). A similar trend was found in the profile to 100 cm depth, where the organic carbon pool increased from 1303 in the drier to 1698 mol $C_{org}\,m^{-2}$ 100 cm^{-1} in the moister stands ($r = 0.44$, $P = 0.06$). The slopes of the regression lines for the 20 and 100 cm-profiles indicate a decrease of the storage of SOC by about 96 mol C m^{-2} with a precipitation reduction of 100 mm yr^{-1}. Thus, beech stands growing with <600 mm yr^{-1} of precipitation had, on

average, a by 23% smaller C-sequestration in the mineral soil than stands receiving >900 mm yr^{-1}. The C pool in the organic L, F, and H layers was more or less similar for stands with 500–800 mm yr^{-1} (48–75 mol m^{-2}), while in stands with more than 850 mm yr^{-1}, the mean carbon pool in the organic layer increased exponentially to 137 mol m^{-2} (Fig. 2a). On average, only 6% of the total C_{org}-pool in the soil profile to 100 cm depth was stored in the organic layer on top of the soil, while 94% was located in the mineral soil.

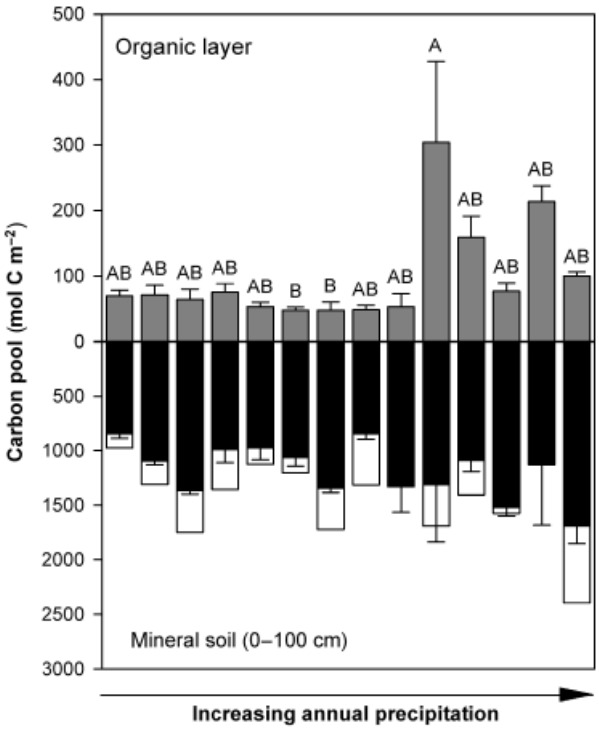

Fig. 1 Organic carbon in the soil organic layer and the mineral soil (0–100 cm) of 14 beech stands on Triassic sandstone along a precipitation gradient in central Germany (mean and standard error of five sampling locations per study site). Organic layer (L, F, H layers): gray bars, mineral soil: filled bars: 0–20 cm, open bars: 20–100 cm. Different letters indicate significant differences in the organic carbon content among the study sites ($P \leq 0.05$).

Carbon in the biomass and the relative importance of slow and fast pools

The storage of carbon in slow pools [C in stem biomass and in the mineral soil (0–100 cm) according to the definition of Norby *et al.*, 2002] was on average of similar size for these two fractions (1450 and 1470 mol C m^{-2}, respectively). However, the relative importance of the mineral soil for long-term carbon storage in the ecosystem tended to decrease from sites with >900 mm yr^{-1} (mean proportion: 52%) to sites with <600 mm yr^{-1} (46%), while concurrently the C-storage in beech stems increased from 48 in the moist to 54% in the dry sites (Table 2).

The most important of the 'fast' C pools (defined as the C pools in leaves, in live and dead fine root mass, and in the organic L, F, and H layers) was the carbon stored in the organic layer, which had a five times larger size than the pool in fine root mass (biomass and necromass) and was seven times larger than the C stored in leaf biomass (Table 2). C-pool in fine root mass varied between 8.3 and 30.3 mol C m^{-2} in the 14 stands (mean 19.0). Carbon stored in fine root necromass slightly exceeded the amount stored in fine root biomass (means of 10.2 and 8.8 mol C m^{-2}). The carbon pool in total fine root mass (biomass and necromass) significantly increased with increasing annual precipitation (Fig. 3a). Forest stands with >900 mm of annual precipitation stored 21 mol C m^{-2}, while those with

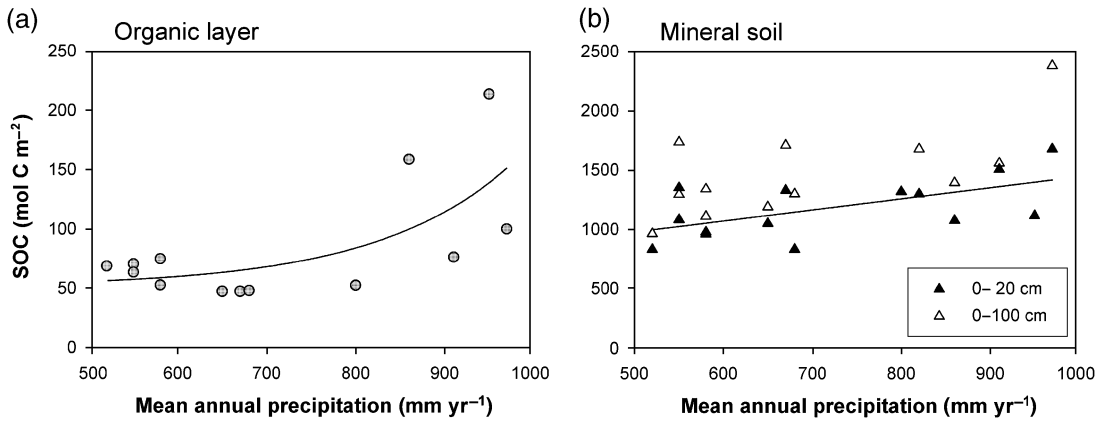

Fig. 2 (a–b) Relationship between mean annual precipitation and soil organic carbon (SOC) in the organic layer (a, L, F, H layers) or in the mineral soil (b) along a precipitation gradient in central Germany (mean of five sampling locations per study site; organic layer: y = 51 + exp(0.01(× −267)), $r = 0.68$, $P = 0.02$; mineral soil, 0–20 cm: y = 511 + 0.9 × , $r = 0.60$, $P = 0.01$; mineral soil, 0–100 cm: $r = 0.44$, $P = 0.06$). Regression line for 0–100 cm not drawn. Note different scaling of Y-axes.

Table 2 Carbon storage in fast and slow pools and leaf mass/root mass ratio of 14 beech stands on Triassic sandstone along a precipitation gradient in central Germany

		Carbon in fast pools (mol C m^{-2})					Carbon in slow pools (%)	
Site #	Precipitation (mm yr^{-1})	Leaf mass	Fine root biomass	Fine root necromass	Organic layer	Leaf mass/fine root mass ratio	Living stems	Mineral soil
1	970	11.6^{CDE}	8.6^{e}	15.1^{BC}	100^{ab}	1.3	39.8	60.2
2	950	15.3^{A}	14.8^{b}	6.8^{G}	214^{ab}	1.0	55.3	44.7
3	910	15.7^{A}	8.9^{e}	8.1^{F}	77^{ab}	1.8	50.0	50.0
4	860	13.7^{B}	10.2^{d}	20.1^{A}	159^{ab}	1.4	46.9	53.1
5	820	13.0^{BC}	18.2^{a}	10.0^{E}	304^{a}	0.7	50.0	50.0
6	800	12.8^{BC}	3.9^{i}	12.1^{D}	53^{ab}	3.1	47.1	52.9
7	680	12.8^{BC}	5.3^{h}	14.9^{BC}	48^{ab}	2.5	44.0	56.0
8	670	11.6^{DE}	11.6^{c}	7.5^{FG}	48^{b}	1.0	42.6	57.4
9	650	11.2^{E}	12.0^{c}	15.7^{B}	48^{b}	0.9	56.7	43.3
10	580	12.6^{CD}	5.7^{g}	5.0^{HI}	53^{ab}	2.1	61.3	38.7
11	580	13.7^{B}	4.1^{i}	4.1^{I}	75^{ab}	3.2	51.0	49.0
12	550	15.0^{A}	4.8^{h}	5.6^{H}	64^{ab}	3.1	33.9	66.1
13	550	12.1^{CDE}	7.2^{f}	2.8^{J}	71^{ab}	1.8	53.9	46.1
14	520	15.2^{A}	7.6^{f}	14.8^{C}	69^{ab}	2.0	70.8	29.2

Fast pools are defined as leaves, fine root biomass and necromass (organic layer and 0–20 cm of mineral soil) and organic L, F, and H layers of the soil. Slow pools are defined as SOC in 0–100 cm of mineral soil and C in woody biomass of the beech trees. Different letters indicate significant differences among study sites ($P \leq 0.05$).

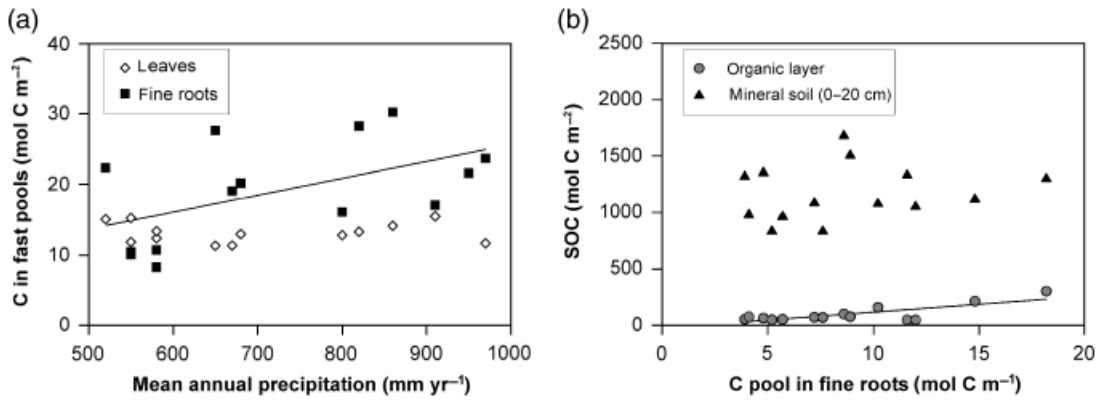

Fig. 3 (a) Relationship between mean annual precipitation and carbon storage in fast pools (leaf and fine root mass) of 14 beech stands on Triassic sandstone along a precipitation gradient in central Germany (mean and standard error of six and 12 samples per study site, respectively; leaves: ns; fine roots: y = 1.7 + 0.02 ×, $r = 0.53$, $P = 0.02$). (b) Relationship between the carbon pool in the fine root biomass in the upper soil layers and SOC in the organic layer (L, F, H layers) or in 0–20 cm of mineral soil along a precipitation gradient in central Germany (organic layer: y = −24 + 14 ×, $r = 0.78$, $P = 0.002$; mineral soil: ns). Lines were drawn only for significant relationships.

<600 mm yr^{-1} contained only 12 mol C m^{-2} in fine root mass. Between 11.2 and 15.7 mol C m^{-2} was stored in leaf biomass (mean 13.3) with no correlation to mean annual precipitation (Table 2).

SOC pools as influenced by climate, soil chemistry and leaf and fine root biomass

In single factor linear regression analyses, the organic carbon pool in the upper mineral soil (0–20 cm) showed a close correlation with annual and growing season precipitation and temperature, and soil nitrogen content (Table 3). Higher precipitation and soil nitrogen content and lower temperatures were related to a significantly larger organic carbon pool in the mineral soil. By contrast, carbon storage in the organic layer was found to be unaffected by temperature and soil nitrogen, but was strongly influenced by the size of the C pool in fine root biomass in the upper soil layers, with the organic layer C pool significantly increasing with the size

Table 3 Results of correlation analyses between the organic carbon pool in the soil organic (L, F, H) layer, in 0–20 cm of mineral soil or in the entire soil profile (organic layer and 0–100 cm of mineral soil), and several climatic, biometric or edaphic parameters of 14 mature beech forests on Triassic sandstone along a precipitation gradient in central Germany

	Organic carbon pool					
	Organic layer		Mineral soil		Profile	
	r	*P*	*r*	*P*	*r*	*P*
Precipitation*	0.52	0.06	**0.60**	**0.02**	**0.52**	**0.05**
Precipitation†	**0.58**	**0.03**	**0.54**	**0.04**	0.47	0.09
Soil moisture‡	0.07	0.80	−0.04	0.88	0.13	0.67
Air temperature*	−0.38	0.19	**−0.53**	**0.05**	−0.35	0.23
Air temperature†	−0.37	0.19	**−0.55**	**0.04**	−0.35	0.22
Soil temperature‡	−0.38	0.20	−0.39	0.19	−0.22	0.46
Site inclination	−0.18	0.53	**0.63**	**0.02**	0.51	0.06
Leaf litter mass	0.19	0.50	−0.12	0.67	−0.25	0.39
C return with leaf fall	0.15	0.63	−0.03	0.91	−0.11	0.71
Fine root biomass	**0.76**	**0.002**	0.18	0.53	0.25	0.38
C pool in fine roots	**0.78**	**0.002**	0.19	0.54	0.25	0.40
Total litter mass	0.17	0.56	−0.26	0.36	−0.36	0.21
Stand age	0.47	0.09	0.48	0.08	0.30	0.30
Clay content	−0.16	0.29	0.27	0.17	0.13	0.33
pH(KCl)	**−0.63**	**0.02**	−0.20	0.50	−0.27	0.36
N_t	−0.29	0.32	**0.79**	**0.001**	**0.54**	**0.05**
P_a	−0.28	0.33	0.27	0.35	0.06	0.83
N/P_a	−0.04	0.89	−0.10	0.75	0.08	0.79
CEC	−0.24	0.41	0.44	0.12	0.25	0.39
Base saturation	**−0.54**	**0.05**	0.09	0.77	−0.10	0.73
Ca_{ex}	−0.45	0.11	0.20	0.49	0.06	0.84

*Long-term mean ($n = 30$ years).
†Long-term mean from May to September.
‡May 2004.
a, plant-available content, ex, NH_4Cl-exchangeable content; t, total content.
Values given are the Pearson correlation coefficient *r* and the probability of error *P*.
All significant correlations ($P \leq 0.05$) are in bold.

of the fine root biomass C pool (Fig. 3b). Growing season precipitation had a positive, and pH and base saturation in the mineral soil a negative, influence on the carbon pool in the organic L, F, H layers.

Discussion

Pools of SOC in European beech forests

This study revealed a substantial reduction in the SOC pool in mature European beech forests with a decrease in precipitation: stands with less than 600 mm yr^{-1} sequestered only 77% of the SOC of stands receiving more than 900 mm yr^{-1}. On average, 1448 mol C_{org} m^{-2} (17.4 kg C m^{-2}) were stored in the 0–100 cm profile of the 14 stands. This compares well with a global mean given by Jobbágy & Jackson (2000) for temperate deciduous forests, but our mean is higher than the estimated pre-anthropogenic SOC pool of cool temperate forests (14.5 kg SOC m^{-2}; Adams, 2004). Indeed, Central European forests have increased their carbon storage in the mineral soil by approximately 20% from pre-anthropogenic times until present (Liski *et al.*, 2002). Our mean also exceeds the SOC pool reported by Mund (2004) for beech forests in Central Germany (9.2 kg SOC m^{-2}), who stressed the importance of silvicultural practice for the carbon budget of temperate forests. Clear-cutting or other disturbances can result in large amounts of soil carbon released to the atmosphere (Heinsdorf *et al.*, 1986; Schlesinger, 1997). Even decades after logging, regenerating boreal forests can remain net sources of carbon dioxide (Schulze *et al.*, 1999). On the other hand, unmanaged old-growth temperate forests have been identified to be continuous C sinks in recent time, which contrasts with the long-standing view that they should be carbon neutral (Luyssaert *et al.*, 2008).

In this study, the organic carbon pool in the mineral soil represented about half of the C-pool of the entire

beech forest ecosystems (soil and phytomass); another 48% was located in tree biomass and 4% in fast pools. Investigations in other temperate broadleaf deciduous forests, in which decaying logs were quantitatively important, estimated that about 40% of the ecosystem carbon pool was located in the mineral soil and another 15% in the organic layers and the dead wood (Vogt *et al.*, 1995; Fahey *et al.*, 2005). Global meta-analyses of carbon storage in forest ecosystems assumed the mineral soil C pool to be more important (60–70% of the ecosystem C pool; Zinke & Millemann, 1986; Harrison *et al.*, 1995). In this study, the percentage of carbon storage in living stems tended to increase with decreasing mean annual precipitation, but this relationship was not significant ($r = -0.37$, $P = 0.10$). Under a drier climate, the carbon storage in the mineral soil tended to decrease in favor of C-storage in stem biomass; yet the absolute amount of carbon stored in beech stems remained similar across the precipitation gradient.

Climatic influences on the long-term C-storage in the mineral soil

The amount and vertical distribution of organic carbon in the soil is to a large extent dependent on climate, in particular on temperature and precipitation. In general, the SOC pool is smallest in tropical forests; intermediate in temperate forests, and largest in boreal forests, reflecting the influence of both climate and differences in tree functional types (Jobbágy & Jackson, 2000). Climate was found to be more important than soil texture in explaining the variability of SOC in the upper soil layers (Jobbágy & Jackson, 2000; Homann *et al.*, 2007). In a number of studies, the SOC pool in the upper mineral soil has been found to be positively related to mean annual precipitation, evapotranspiration, and clay content, while negative exponential relationships to temperature were detected (Post *et al.*, 1982; Zinke & Millemann, 1986; Schimel *et al.*, 1994; Jobbágy & Jackson, 2000; Amundson, 2001; Thuille & Schulze, 2006; Homann *et al.*, 2007). In a zonal sequence of soils in a N–S transect in western Eurasia, the stability of SOC increased from the tundra biome to podzolic soils in the boreal forest ecosystems, and further to leached chernozems under steppe vegetation in the arid South, which had the highest C storage capacity (Semenov *et al.*, 2008), indicating a stabilizing role of both low temperatures and drought. However, the temperature dependency of SOC stocks varies among the biomes and may be lacking in certain environments. Across a moisture and temperature gradient in the Tropics, SOC was significantly related to soil moisture, but not to temperature (McGroddy & Silver, 2000). In forests of western Oregon (Homann *et al.*, 1995) and Finland (Liski & Westman, 1997), SOC decreased, rather than increased, with decreasing temperature. In a compilation of C-decomposition data from five continents, Giardina & Ryan (2000) found that decomposition rates from forest mineral soils were remarkably constant across the biomes. Ågren & Bosatta (2002) and Krull *et al.* (2003) argue that SOC decomposition is less temperature-sensitive than often considered from short-term laboratory incubations, which examine only the decomposition of the easily degradable carbon pool. Our study revealed a strong positive (and not negative) relationship of SOC to precipitation and additionally a negative correlation with temperature in the upper mineral soil: SOC decreased by a third with a temperature increase of 2 K, while a precipitation reduction of $100\,\mathrm{mm\,yr^{-1}}$ caused a SOC reduction by 9%.

Higher precipitation amounts towards the moister end of our rainfall gradient could also have a profound effect on soil chemical properties and the nutrient status of forest soils by accelerating rock weathering and the leaching of basic cations and nitrate in a temperate suboceanic climate, and by higher atmospheric deposition of acids at the precipitation-rich sites (Quilchano *et al.*, 1995; Walse *et al.*, 1998; Raich *et al.*, 2000). In fact, beech forests at the moist end of the transect grow on more acid soils and possess a larger fine root biomass and also necromass than drier stands (Meier & Leuschner, 2008b). Thus, root litter input may well be larger under higher precipitation, while leaf litter fall was found to be unaffected by the amount of annual precipitation. Higher precipitation will affect soil carbon sequestration mainly through a higher soil acidity and lower base saturation at the exchange sites, thereby reducing litter decomposition rate. Similarly, altitudinal changes in SOC pools have mostly been attributed to differences in decomposition rates (Garten & Hanson, 2006). In acid forest soils, conditions for litter decaying earthworms and other deep-dwelling invertebrates are unfavorable (Judas *et al.*, 1997), which in turn leads to reduced mixing of the organic layer with the mineral soil (Jug *et al.*, 1999; Jongmans *et al.*, 2003) and accumulation of ectorganic matter at the surface. Other soil fauna groups (collembolans, larvae of dipterans and coleopterans) occur at lower densities in acid forest soils as well, and microbial activity of saprophytic fungi remains rather low, which corresponds with a generally lower soil respiration rate (Wolters & Schaefer, 1994; Saetre *et al.*, 1999).

The stability of SOC is not only influenced by the physical and chemical environment (primarily soil moisture, temperature, pH, and aeration), but also by the chemical composition of the organic matter itself and its susceptibility to decay, and the physical accessibility of the organic matter to microbial attack and

exo-enzymes (Sollins *et al*., 1996; Gleixner *et al*., 2001). Rasse *et al*. (2005) found that carbon derived from roots generally has a longer residence time than shoot-derived organic matter due to a higher chemical recalcitrance of root tissue and physical protection through the formation of stable aggregates. The transformation of plant residues into clay–humic complexes is a stabilizing process. Therefore, SOC has been found to increase with increasing clay content (Paul, 1984; Gonzalez & Laird, 2003). Clay mineralogy influences the residence time of carbon, which is longer in soils dominated by smectite than by low-activity minerals, due to the formation or accumulation of humic complexes (Wattel-Koekkoek *et al*., 2003; Paul *et al*., 2008). However, in our study, the estimated clay content of the upper mineral soil layers was found to have no significant influence on the SOC pool in the organic layer or mineral soil, despite some variation in soil clay content (Table 3).

Importance of fine roots as a source of soil carbon

Allocation of C to the fine root system is one of the most important, but least well quantified, carbon fluxes in terrestrial ecosystems (Hendrick & Pregitzer, 1992; Matamala *et al*., 2003). By regression analysis, we detected that the strongest influence on the organic layer C pool was exerted by the carbon pool in fine root biomass, while carbon return with leaf litter fall had no significant effect. The effect of fine root C on carbon storage in the organic L, F, H layers was even stronger than climatic or edaphic factors, including mean annual precipitation and soil acidity. This result underlines the importance of fine root mass as a source of carbon for the SOC pool in temperate forests. In the 14 beech forests, fine root biomass stored on average 8.8 mol C m^{-2}, which was about 67% of the C-storage in leaves. According to an ingrowth core-experiment, 3.2 mol C m^{-2} was turned over annually with fine root growth and death (Meier & Leuschner, 2008b), which represents 24% of the carbon input with leaf litter fall. However, the magnitude of the C-flux with fine root turnover is most likely underestimated, due to a number of artifacts associated with the ingrowth core method (Steele *et al*., 1997; Hertel & Leuschner, 2002). Other authors estimated that the carbon accumulating in the upper mineral soil, which originated from root-related sources (fine root turnover, root exudates, cell sloughing, and turnover of mycorrhizal fungi), accounted for about 30–40% of the C input with aboveground litter (Vogt *et al*., 1986; Godbold *et al*., 2003). In a poplar plantation in Italy, the mycorrhizal extraradical mycelium was found to be the dominant pathway through which carbon entered the SOC pool, even exceeding the input via leaf litter and fine root turnover (Godbold *et al*., 2006). In contrast, in an experiment with Douglas-fir, the majority of carbon transferred to the litter layer was from inputs via roots and not from mycorrhizal fungi or leaf litter fall (Hobbie *et al*., 2004).

In a related investigation in the transect of this study, both the δ^{13}C-signature of fine root mass and the ingrowth core data pointed at a higher fine root turnover in the drier stands, caused by a higher fine root mortality under drought and subsequent compensatory fine root production (cf. Meier & Leuschner, 2008b). However, the standing stock of fine root biomass decreased toward the drier stands, as did the SOC pool. It appears that reduced precipitation does not increase the carbon allocation to roots relative to shoots in mature beech trees (Meier & Leuschner, 2008b), and thus does not increase the C transfer to the soil with root mortality. We hypothesize that a summer-drier climate enhances carbon losses from beech forest soils mainly through a temperature-induced stimulation of soil microbial and root respiration and thus acceleration of decomposition. Our results lead to the conclusion that climate warming together with a higher frequency and severity of summer droughts, as is predicted for parts of Central Europe, will reduce the carbon stored in temperate broad-leaved forests dominated by beech. According to our results, largest carbon losses are to be expected in the upper horizons of the mineral soil and in the organic L, F, H layers, with a larger effect exerted by temperature increase than by precipitation reduction. The expected larger C source strength of warmer and drier forest soils could more than balance the C sink function due to an increase in forest productivity, which has been postulated to result from extended growing season length and elevated CO_2 (Grace, 2004). Thus, climate warming might turn these ecosystems into C sources.

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