

Effects of the extreme drought in 2003 on soil respiration in a mixed forest

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Abstract We present a field study on the drought effects on total soil respiration (SR_t) and its components, i.e., “autotrophic” (SR_a : by roots/mycorrhizosphere) and “heterotrophic” respiration (SR_h : by microorganisms and soil fauna in bulk soil), in a mature European beech/Norway spruce forest. SR_a and SR_h were distinguished underneath groups of beech and spruce trees using the root exclusion method. Seasonal courses of SR_a and SR_h were studied from 2002 to 2004, with the summer of 2003 being extraordinarily warm and dry in Central Europe. We (1) analyzed the soil temperature (T_s) and moisture sensitivity of SR_a and SR_h underneath both tree species, and (2) examined whether drought caused differential decline of SR_a between spruce

and beech. Throughout the study period, SR_a of beech accounted for 45–55% of SR_t , independent of the soil water regime; in contrast, SR_a was significantly reduced during drought in spruce, and amounted then to only 25% of SR_t . In parallel, fine-root production was decreased during 2003 by a factor of six in spruce (from 750 to 130 $mg\ l^{-1}\ a^{-1}$), but remained at levels similar to those in 2002 in beech (about 470 $mg\ l^{-1}\ a^{-1}$). This species-specific root response to drought was related to a stronger decline of SR_a in spruce (by about 70%) compared to beech (by about 50%). The sensitivity of SR_a and SR_h to changing T_s and available soil water was stronger in SR_a than SR_h in spruce, but not so in beech. It is concluded that SR_a determines the effect of prolonged drought on the C efflux from soil to a larger extent in spruce than beech, having potential implications for respective forest types.

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Introduction

Total soil respiration (SR_t), amounting to 77 Gt C year⁻¹ on a global scale (Raich and Potter 1995), represents the second largest flux in the global carbon (C) cycle (Schlesinger and Andrews 2000). Factors controlling the seasonal and interannual variability of the C efflux from soil currently represent a major research interest (Janssens et al. 2003), as they have been recognized as crucial determinants of carbon cycling and storage in ecosystems.

In European forests, 55% of the total amount of photosynthetically fixed C, on average, was released back into the atmosphere through belowground respiration (Janssens

et al. 2001). Total soil respiration (SR_t) is the sum of respiration of roots and rhizospheric microorganisms (here referred to as “autotrophic” soil respiration SR_a ; Andersen et al. 2005) and that of heterotrophic free-living soil bacteria, saprotrophic fungi, and soil fauna (defined as “heterotrophic” soil respiration SR_h ; Lavigne et al. 2004). In particular, estimates of SR_a and SR_h have been reported from temperate forest ecosystems (e.g., Buchmann 2000; Epron et al. 2001; Janssens et al. 2003); however, knowledge is scarce on factors that control both soil respiration components (Baggs 2006). SR_a and SR_h were shown to differently respond to increasing temperature, sometimes exhibiting different temperature sensitivity (Boone et al. 1998; Rey et al. 2002; Bååth and Wallander 2003). Effects of soil moisture limitation on SR_a and SR_h are commonly reported from controlled and field studies (Borken et al. 1999; Borken et al. 2003; Lavigne et al. 2004), in particular, on (semi-)arid ecosystems (Xu and Qi 2001; Reichstein et al. 2002). However, evidence from temperate forest ecosystems under naturally occurring summer drought is scarce (Davidson et al. 1998; Epron et al. 1999; Andersen et al. 2005).

C flux across forest ecosystem compartments may vary along the broad range of involved functional plant types (Raich and Tufekcioglu 2000; Subke et al. 2006). Deciduous broadleaved European beech (*Fagus sylvatica*) and evergreen coniferous Norway spruce (*Picea abies*) are two species representing contrasting extremes in growth habit and leaf physiology among the tree species of Central Europe. Beech and spruce cover a broad range of edaphic and climatic conditions (Ellenberg 1996), and their cultivation is of major interest in Central-European forestry (Rennenberg et al. 2004; Ammer et al. 2005; Geßler et al. 2007). The factor mainly limiting spruce in Central Europe at colline elevation on sites that are conducive to autochthonous beech forests is low water supply during summer (Schütt et al. 2002). Utschig et al. (2004) pointed out that during 1976—another year of extraordinary drought in Germany—radial stem growth in spruce growing outside the Alps stayed reduced throughout many subsequent years, whereas stem growth of beech recovered at comparable sites already during the following year. Soil water deficit during drought was found to result in contrasting belowground responses in both tree species, i.e., promotion versus inhibition of fine-root growth in beech (Leuschner et al. 2001) and spruce (Puhe 2003), respectively. Performance of stem and root growth in beech and spruce forests not only affect carbon stocks, but also carbon fluxes, in particular, under prolonged drought.

In the southern part of Central Europe, the summer of 2003 was characterized by above-average insolation, elevated daily mean temperatures, and below-average precipitation (Raspe et al. 2004; Ciais et al. 2005). These

conditions allowed the analysis of drought effects on the CO_2 efflux from soil in a mixed beech-spruce forest in southern Germany. In a previous paper (referring to an adjacent stand, Andersen et al. 2005), we reported on the seasonality of SR_a around individual adult beech and spruce trees, based on reductions in CO_2 efflux upon destructive girdling of tree trunks. The objective now was to investigate the seasonal and interannual stand-level variation of SR_t and its components SR_a and SR_h within groups of adult beech and spruce trees from 2002 to 2004 by means of the root exclusion method (Thierron and Laudelout 1996; Hanson et al. 2000). Given that most fine-root turnover at the study site occurred within the uppermost 10–15 cm of the soil profile (Mainiero, personal communication; Mainiero and Kazda 2006), the root exclusion method was employed on small trenched plots in the topsoil (Buchmann 2000). We investigated (1) the extent to which temperature and moisture conditions determine the temporal variation in both SR components under the severe environmental conditions of 2003, and (2) examined whether drought caused differential decline in SR_a between spruce and beech. The latter concern was based on observations of spruce tree decline under drought in southern Germany (Utschig et al. 2004). Empirical clarification is needed for reliable risk modeling of beech and spruce forests as affected by extreme seasonal weather conditions (Easterling et al. 2000, Kölling and Zimmermann 2007).

Materials and methods

Site and experimental design

Measurements were made in a mixed forest of adult European beech (*Fagus sylvatica* L.) and Norway spruce trees (*Picea abies* [L.] H. Karst) at “Kranzberger Forst” (48°25′08″N, 11°39′41″E, 490 m a.s.l.) near Freising/Germany (Pretzsch et al. 1998; Häberle et al. 2008). Spruce, planted in 1951, was the dominant species at the site, with beech established 7 years before as groups of 60–100 individuals, according to common silvicultural practices. An understory of *Rubus fruticosus* agg. L., *Oxalis acetosella* L., and the moss *Hylocomium splendens* (Hedw.) B.S.G. (ground coverage of 5–15%) was present only under spruce. Rooting depth of beech and spruce trees was about 1 m (Blaschke, unpublished data) in a luvisol (FAO classification), which had developed from loess over tertiary sediments. Thus, trees had no access to ground water. The depth of the litter layer was about 5 cm within groups of spruce and 3 cm within groups of beech trees. C/N within the uppermost 10 cm of the soil ranged between 14 and 17, with the highest ratios occurring

underneath beech (Schuhbäck 2004). The study site is classified as temperate based on a 30-year record (1970–2000) of mean daily air temperature and annual precipitation (7.8°C and 785 mm, respectively), and periods of snow cover between December and February.

In June 2002, ten sampling positions were selected within a group of beech and spruce trees each (distance between group centers about 25 m), five for employing the root exclusion method (Hanson et al. 2000) and another five as reference. Ground vegetation (i.e. mosses) was removed, when present, from all sampling positions, whereas litter was not. The reference positions were permanently marked by PVC-rings (length 3 cm and inner diameter 10 cm) clipped to the soil surface. At sampling positions for root exclusion, metal soil corers (length 10 cm, inner diameter 10 cm) were inserted into the forest floor to allow soil excavation and removal of roots from the defined soil volume (cf. Buchmann 2000). Root exclusion was applied within the shallow rooting zone, because approximately 70–80% of fine-root production and mortality occur within the top 10–15 cm of soil at this site (Mainiero, personal communication, Mainiero and Kazda (2006). Live roots of each soil sample were sorted, and the fine-root density (FRD, g m^{-2} ; root diameter < 2 mm) in each position of root extraction was determined as dry mass per unit of soil volume (Table 1). Soil including root necromass was refilled in the coring holes furnished with PVC tubes (length 10 cm, inner diameter 10 cm) according to the original position of the soil material along the corer length. The tube walls prevented lateral in-growth of roots. Ends of tubes were open to ensure aeration, wet and dry deposition, and drainage to be similar each to respective levels of the surrounding soil.

In July 2004, soil within tubes was checked for in-growth of fine-roots from below, and fine-root density was assessed at reference sampling positions by soil coring (Vogt et al. 1998). In comparison to initial root mass (June 2002), root in-growth within tubes from below in July of 2004 was 3% underneath spruce and 5% underneath beech. FRD determined in June 2002 and July 2004 did not differ between years underneath either tree species, although fine-root

biomass within the uppermost 10 cm of soil was two times greater in spruce than beech (Table 1).

To identify patterns in the interannual variability of the fine-root production and recovery rate underneath beech and spruce group, we established in-growth cores (Vogt et al. 1998; ten soil cores, length 20 cm, diameter 3.8 cm, extracted in March 2002 from the soil underneath each tree group). In the laboratory, living fine-roots were extracted by hand, rinsed with distilled water and dried at 65°C for 48 h. Each coring hole was refilled according to the natural profile with homogenized mineral soil and organic layer from the site. The annual fine-root production (FRP, in mg l^{-1}) was assessed in December 2002 by sampling the in-growth cores and extracting the newly formed fine-roots. The coring holes were refilled as described above and resampled in December 2003. Additionally, fine-root recovery rate (FRR, in percent of initial root density) was calculated. To this end, fine-root biomass in the in-growth cores at harvests (December 2002 and 2003) was related to the initial fine-root biomass in March 2002 (Hertel and Leuschner, 2002).

Measurements

CO₂ efflux assessment began at 3 weeks after soil refilling to ensure the observation of the system to return to respiratory equilibrium (Wiant 1967, after Hanson et al. 2000; differential infrared gas analysis, IRGA, in combination with a closed-chamber system, EGM-3 with SRC-1, PP-Systems, UK; chamber volume 1,170 cm³, enclosed soil surface area 78 cm²). Measurements were taken between 11 a.m. and 2 p.m. (time of average CO₂ efflux during the day, cf. Davidson et al. 1998). Soil respiration rate (SR_t) was calculated as the increase in CO₂ concentration (by a maximum of 80 $\mu\text{l l}^{-1}$) over time (maximum of 120 s) upon reaching steady-state efflux. Three readings were averaged at each sampling position. Soil temperature (T_s) was measured at 3 cm depth (probe STP-1, PP-Systems, UK) during efflux assessment (T_s variation typically $\pm 1.0^\circ\text{C}$ within tree groups).

CO₂ efflux was measured at reference sampling positions (SR_t) and positions of root exclusion (SR_h) at monthly intervals from July to November 2002, March to November 2003, and March to July 2004. SR_a was calculated as follows:

$$\text{SR}_a = \text{SR}_t - \text{SR}_h \quad (1)$$

The proportion of SR_a in SR_t was calculated at each sampling date as $(1 - \text{SR}_h/\text{SR}_t) \times 100$.

Modeling

Plant-available soil water (ASW, 0–40 cm soil depth) in beech and in spruce soils including the organic humus layer

Table 1 Density of live fine-roots (FRD) assessed within the uppermost 10 cm of the soil at positions of the root exclusion and at reference positions underneath beech and spruce

Date	FRD (g m^{-2}) ^a	
	Beech	Spruce
June 28, 2002, at positions of root exclusion	85.26 (8.30)	192.24 (19.35)
July 12, 2004, at reference positions	91.28 (10.50)	165.33 (21.29)

One-sided standard errors of means ($n = 5$) are shown in brackets

^a Calculated as the dry mass of living fine-roots per unit of soil surface area (g m^{-2})

(O-horizon) was modeled using LWF-BROOK90 (Hammel and Kennel 2001). The bulk of the roots are located in the upper 40 cm of the soil. The model was parameterized with meteorological data as obtained on a daily basis from an adjacent Level II monitoring site “Freising” (48°24′24″N, 11°39′22″E), standard vegetation parameters (Hammel and Kennel 2001), site and species-specific parameters (Tables 2, 3), and on-site measurements of soil temperature (T_s). The selected vegetation and soil parameters (Tables 2, 3) emphasized differences between beech and spruce in terms of seasonal foliage dynamics and rooting characteristics (Armbruster et al. 2004).

Model estimates of ASW were compared with volumetric soil water content (SWC) data collected from June 12 to July 3, 2003, using time-domain reflectometry (TDR, TRIME-MUX6, IMKO GmbH, Germany) at three positions underneath each tree species. Two-rod probes (P2Z, length 16 cm, measurement range 0–50%, accuracy $\pm 1\%$) were vertically placed into the humus layer and mineral soil.

Response of SR_a and SR_h to T_s and ASW was tested using two separate data sets based on different water limitation scenarios: data from 2002 and 2004 represented “nonlimited” and data from 2003 represented “limited” water supply. In each case, exponential functions were used to describe the respiratory T_s dependence underneath each tree species:

$$SR = a e^{b(T_s - 10)} \quad (2)$$

where SR is SR_a or SR_h , T_s is temperature at 3 cm soil depth, and a and b are coefficients derived through

nonlinear regression (Origin 6.0, Microcal Software Inc., USA). Because 10 is subtracted from T_s , the coefficient a is an estimate of SR_a or SR_h at 10°C. The coefficient b is a temperature coefficient relating to Q_{10} ($Q_{10} = e^{10b}$; Lavigne et al. 2004). Differences in a and b between soil water “nonlimited” and “limited” scenarios were analyzed for each tree species using a t test with Bonferroni correction (Bärlocher 1999).

To examine variations in SR caused by factors other than T_s , calculated SR_a and measured SR_h were normalized to $T_s = 10^\circ\text{C}$ (i.e. SR^{10}) by modifying Eq. 2:

$$SR^{10} = SR / e^{b(T_s - 10)} \quad (3)$$

where SR^{10} is SR_a^{10} or SR_h^{10} .

Thereafter, SR_a^{10} and SR_h^{10} were related to the mean daily ASW throughout the study period by using species-specific linear response function:

$$SR^{10} = c + d \text{ ASW} \quad (4)$$

Results

Climatic variation 2002–2004

Daily mean T_s was generally above 0°C throughout the three study years (Fig. 1). Growing season T_s was highest in 2003 and lowest in 2004 (Table 4, Fig. 1). Total annual precipitation (p_{an}) in 2002 and 2003 differed significantly from the long-term average (LTA, 1970–2000), whereas in 2004, p_{an} was similar to the LTA (Table 4). In 2002, p_{an} was greater by 30% relative to the LTA. Extreme

Table 2 Site-specific, vegetation-related input parameters of the model LWF-BROOK90 (Hammel and Kennel 2001) for 2002

Parameters	Beech	Spruce	Source
Stem diameter at breast height (cm)	23.06	28.65	Wipfler, personal communication
Stem height (m)	23.10	25.02	Wipfler, personal communication
Ground area-related number of trees (N ha ⁻¹)	1,123	1,066	Wipfler, personal communication
Leaf area index	5.8	9.5	Reiter (2004)
Thickness of organic layer (cm)	3	5	Schuhbäck (2004)
Total fine-root length ^a (cm l ⁻¹) (0–90 cm soil depth)	1,680	1,360	Blaschke, unpublished data

^a Presented as fine-root length density (e.g., fine-root length per soil volume, cm l⁻¹) across entire soil profile (i.e., rooting depth down to 90 cm)

Table 3 Site-specific, soil-related input parameters of the model LWF-BROOK90, according to Schuhbäck (2004)

Soil depth (cm)		Parameters				
Beech	Spruce	Soil density (kg m ⁻³)	Sand fraction (%)	Silt fraction (%)	Clay fraction (%)	C org (%)
3 to 0	5 to 0	40	0	0	0	100
0 to -5	0 to -5	200	8	88	4	4.6
-5 to -15	-5 to -35	1,500	8	88	4	2.3
-15 to -55	-35 to -85	1,700	10.5	75.7	14	1.1
-55 to -100	-85 to -100	1,900	30	40	30	1.1

Fig. 1 T_s , T_{air} , daily p , and SWC at “Kranzberger Forst” during 2002, 2003, and 2004. T_s was measured at the boundary between humus layer and mineral soil (at the study site), and SWC refers to 5 cm soil depth. Solid horizontal line of the upper graphs represents the zero-line of Celsius-temperature, dotted line of the lower graphs represent the threshold of SWC = 14%, below which soil water is not available to plants

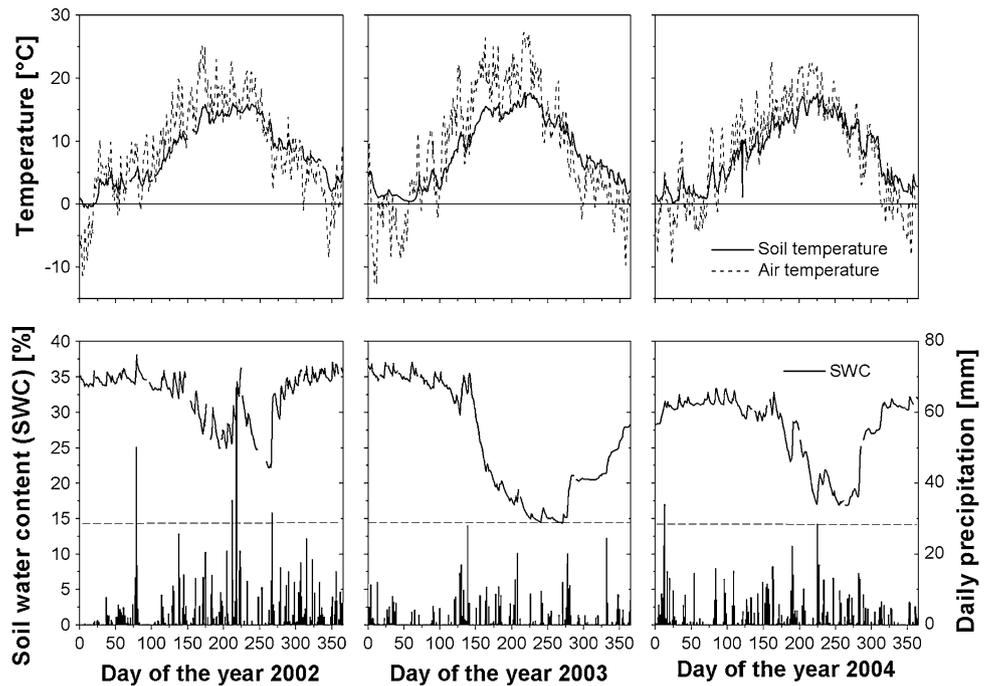


Table 4 Climatic data from 2002, 2003 and 2004

Year	Mean annual T_{air} (°C)	Mean T_{air} of growing season (°C)	Mean T_s (°C)	Mean T_s of growing season (°C)	Annual p (mm)	p during growing season (mm)
2002	8.88	15.74	8.13	13.44	1,015	539
2003	8.81	18.01	7.93	14.28	558	279
2004	8.07	15.13	8.09	13.04	779	373
1970–2000 ^a	7.82	14.81	ND	ND	786	442

Air temperature (T_{air}) and precipitation (p) are measured at the neighboring Level II monitoring site “Freising,” LWF. Soil temperature (T_s) was recorded at the study site “Kranzberger Forst,” and growing season was defined as May 1 to September 30 [according to Otto (1994), for forests] ND not determined

^a Data from Deutscher Wetterdienst (DWD) station “Weihenstephan,” <http://www.dwd.de>

summer drought prevailed in 2003 as the result of a 30% reduction in p_{an} and an increase in air temperature (T_{air}) relative to LTA. In 2003, SWC at 5 cm declined to 14%, which represents the limit of plant-available soil water (ASW) in this soil (Raspe et al. 2004). Recovery of SWC did not occur before December 2003. During 2004, SWC at 5 cm depth never reached the minimum level of 2003.

Modeling ASW

Annual variation in ASW differed among the three study years (Fig. 2). In 2002, both beech and spruce soils displayed similar seasonal variation in ASW. The greatest differences in ASW between spruce and beech soils occurred in 2003: ASW was completely depleted in 2003

under spruce by mid-July, under beech by mid-August, respectively. Precipitation in the autumn of 2003 increased ASW in both beech and spruce; however, the ASW level at the end of 2003 was still lower than that at the end of 2002. During the summer of 2004, ASW was 10–15 mm m⁻² lower in beech than spruce soils; however, underneath both tree species, ASW was higher than that during the summer of 2003.

From mid-June to mid-July 2003, mean daily SWC was highly correlated with modeled ASW in beech (linear relationship, $R^2 = 0.94$, data not shown) and spruce soils (linear relationship, $R^2 = 0.82$, data not shown). Higher SWC and ASW occurred in beech than spruce soils (SWC and ASW enhanced by up to 7% and 20 mm, respectively). During this period, depletion of ASW occurred only in spruce soils (Fig. 2).

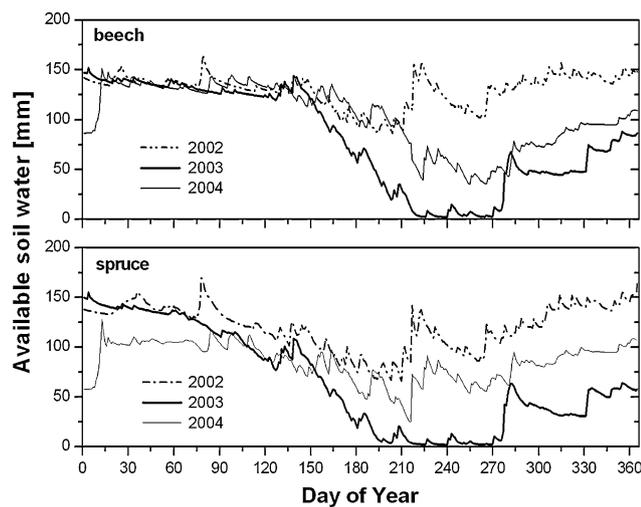


Fig. 2 Seasonal dynamics of ASW as modeled by “LWF-BROOK90” for soil underneath beech and spruce at “Kranzberger Forst.” Levels represent integrals across the uppermost 40 cm of the forest soil during 2002, 2003, and 2004

Soil respiration

Seasonal patterns of SR_t tended to follow that of T_s during the entire study period (Fig. 3). However, in November 2002 and 2003, SR_t increased nearly by 50% underneath beech relative to corresponding October levels. This effect coincided with autumnal leaf fall in deciduous beech. The SR_t increase was small and not statistically significant underneath evergreen spruce with minor needle shedding (cf. Pedersen and Bille-Hansen 1999).

Interannual respiratory differences were distinct at low soil water content during July and August 2003, when SR_t was reduced underneath beech to 30% and spruce to 50% relative to respective levels of the corresponding period in

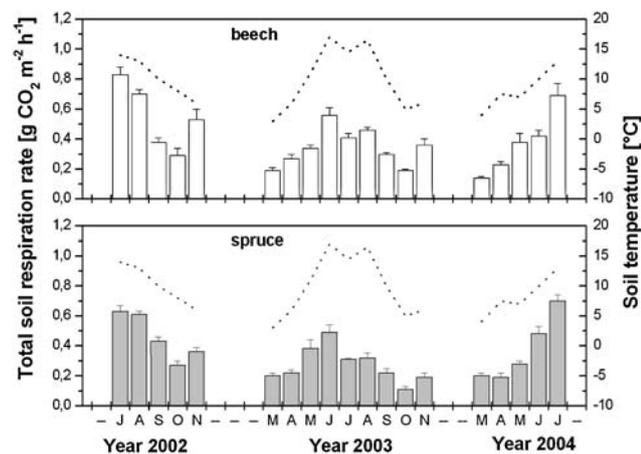


Fig. 3 Seasonal dynamics of SR_t in beech and spruce soil from July 2002 to July 2004 (no data from December 2002 to February 2003, and from December 2003 to February 2004); means ($n = 5$) \pm standard errors. Dotted line represents soil temperature at 3 cm depth

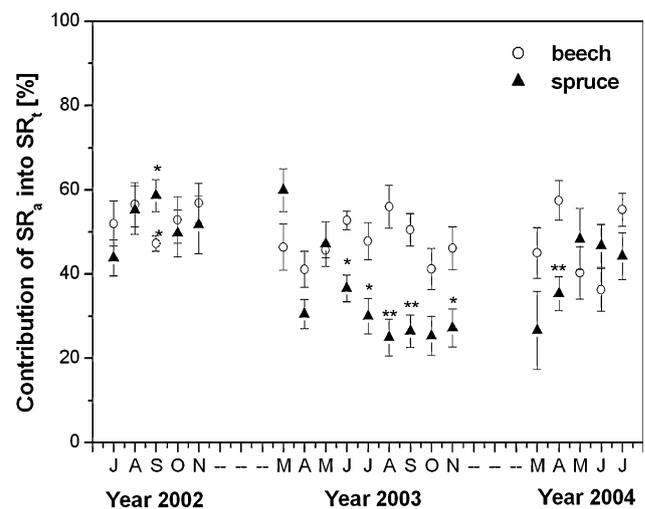


Fig. 4 Contribution of SR_a to SR_t (in percent) in beech and spruce soils from July 2002 to July 2004 (no data from December 2002 to February 2003, and from December 2003 to February 2004); means ($n = 5$) \pm standard errors. Asterisks show significant differences in the contribution of SR_a to SR_t between beech and spruce at $**P < 0.01$ and at $*P < 0.05$. The levels of significance were assessed by means of Wilcoxon-test

2002. During the entire study period, estimates of SR_a in beech soil were 45–55% of SR_t , independent of the soil water regime (Fig. 4). In contrast, SR_a was significantly reduced from July to December 2003 in spruce soil compared to the corresponding period of 2002, amounting on average to only 25% of SR_t (Fig. 4).

Responses of SR_a and SR_h to T_s and ASW

Because of the apparent stimulation of root and soil microbial activity due to litter fall (Hodge 2004; Hayes 1979), November rates of SR_a and SR_h underneath beech were excluded from T_s and ASW response analyses.

During 2002 and 2004, SR_a and SR_h were highly correlated with T_s in both beech and spruce (coefficient b , Table 5 and Fig. 5). During 2003, however, T_s response of SR_a changed in both tree species; although the relationship between SR_a and T_s was atypical under spruce. In spite of increasing T_s , SR_a remained constant in June 2003 and then dropped to rates, which are typical for the cold season. A different exponential fit was required from June to October 2003 to quantify the temperature dependence of SR_a underneath spruce. Under drought (second “autotrophic” function, June–November 2003, Table 5), SR_a was significantly lower in spruce soil than that during moist conditions (2002 and 2004) at a reference T_s of 10°C (coefficient a , $P = 0.05$, Table 5). In 2003, however, the T_s response of SR_h in spruce did not change significantly (coefficients a and b , Table 5 and Fig. 5). In comparison, the temperature response of beech was significantly lower

Table 5 Statistical results from exponential fit ($SR = a e^{b(t - 10)}$) of data shown in Fig. 5 showing the relationship between “autotrophic” soil respiration (SR_a), “heterotrophic” soil respiration (SR_h) and soil temperature (T_s) at 3 cm soil depth, with a and b being regression

coefficients, R^2 representing measure of determination, Q_{10} calculated from b ($Q_{10} = e^{10 \times b}$), and P giving levels of significance of the regression equations (ANOVA)

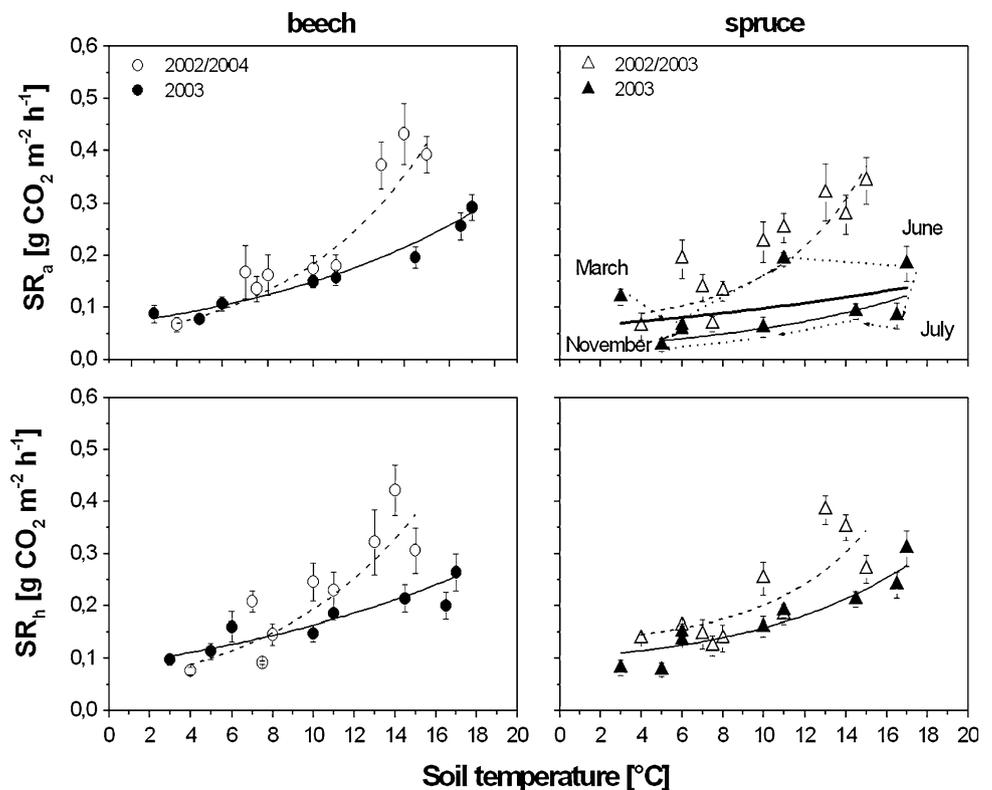
Year	Species	Component of soil respiration	a (g CO ₂ m ⁻² h ⁻¹)	b (°C)	n	R ²	Q ₁₀	P
2002/2004	Beech	“Autotrophic” (March–October)	0.184 (0.010)	0.161 (0.015)	9	0.92	5	<0.001
		“Heterotrophic” (March–October)	0.194 (0.009)	0.132 (0.014)	9	0.90	3.7	0.001
	Spruce	“Autotrophic” (March–November)	0.182 (0.011)	0.138 (0.013)	10	0.80	4	0.001
		“Heterotrophic” (March–November)	0.198 (0.008)	0.095 (0.010)	10	0.72	2.6	0.007
2003	Beech	“Autotrophic” (March–October)	0.149 (0.011)	0.090 (0.011)	8	0.97	2.4	<0.001
		“Heterotrophic” (March–October)	0.164 (0.009)	0.064 (0.010)	8	0.92	1.9	0.001
	Spruce	“Autotrophic (March–November)	0.100 (0.010)	0.056 (0.012)	9	0.23	1.8	0.362
		Second “autotrophic” (June–November)	0.053 (0.023)	0.080 (0.052)	6	0.73	2.2	0.027
		“Heterotrophic” (March–November)	0.154 (0.011)	0.082 (0.010)	9	0.86	2.3	0.001

Standard errors of a and b are shown in brackets

during drought in the cases of both SR_a and SR_h (coefficients b , $P = 0.05$, Table 5), although no differences in SR_a and SR_h were substantiated at a reference T_s of 10°C (coefficient a , $P = 0.05$, Table 5) under moist and drought conditions. In general, SR_a tended to be more sensitive to T_s relative to SR_h , independent of the soil moisture or tree species, as expressed by Q_{10} (Table 5, $Q_{10} = e^{10b}$). Drought in 2003 reduced the Q_{10} of SR_a in beech and spruce soil, whereas Q_{10} of SR_h was reduced only in the case of beech.

SR_a^{10} and SR_h^{10} were linearly related to ASW during the entire study period (Fig. 6, data shown only for SR_a^{10}). Spruce soil showed a stronger decrease in SR_a than beech soil at low levels of ASW, which is reflected by the different coefficients c and d in both species (Table 6). SR_h^{10} tended to increase in beech soil with increasing ASW up to 100 mm ($R^2 = 0.62$, $P = 0.034$) but decreased at higher ASW levels ($R^2 = 0.33$, $P = 0.83$). SR_h^{10} in spruce soil was not related significantly to ASW ($R^2 = 0.13$, $P = 0.136$).

Fig. 5 Relationship between soil respiration (SR_a , SR_h) underneath beech and spruce and soil temperature at 3 cm depth during the years 2002 and 2004 with nonlimited water supply (dotted line) and the year 2003 with limited water supply (solid line). Arrows denote a time course (i.e. hysteresis effect) in temperature response of SR_a underneath spruce. The function fitted to spruce data (dashed line) covers the period of June to November 2003; means ($n = 5$) ± standard errors. Regression results are provided in Table 4



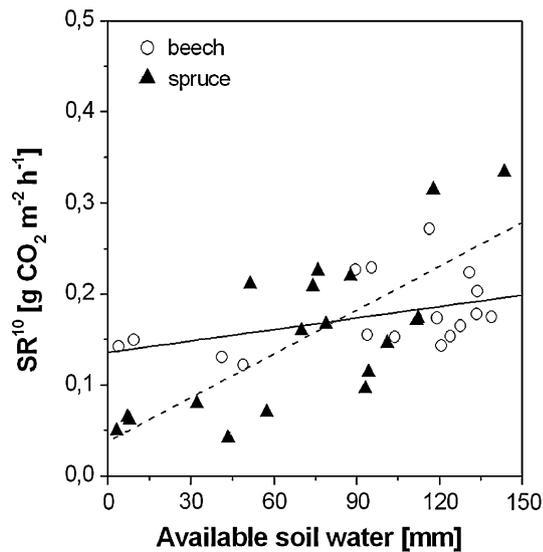


Fig. 6 Relationship between “autotrophic” soil respiration at 10°C (SR_a^{10}) and plant available soil water (ASW). Regression lines of beech are *solid* and *spruce dotted*. Regression results are provided in Table 6

Fine-root dynamics

In spruce, annual fine-root production (FRP) and fine-root recovery rate (FRR) in the topsoil were between three (FRP) and five times lower (FRR) in 2003 compared to 2002 (135.7 vs. 466.7 $\text{mg l}^{-1} \text{a}^{-1}$, respectively, for FRP, and 8.8 vs. 51.9%, respectively, for FRR; $P < 0.01$ each; Table 7). In contrast, FRP and FRR in beech remained, during 2003, on levels similar to each of those in 2002.

Discussion

Despite similar mean annual T_s , drought conditions of 2003 reduced SR_t in both tree species, although SR_t was reduced more strongly underneath spruce than beech. Similarly, Borken and Beese (2005) assessing SR of the organic soil horizons in pure and mixed stands of European beech and Norway spruce concluded a higher probability of drought stress underneath spruce than beech. Although water deficits persisted during 2003 underneath spruce and beech, periods of exhausted ASW were longer in spruce (i.e., 75 vs. 45 days in beech). Soil water regimes began to differ between the two tree species in spring of 2003 (Fig. 2), as the evergreen habit of spruce apparently led to appreciable water interception and transpiration during the dormant, i.e., leafless season of beech (Beier 1998). In addition, the growing season of 2003 was characterized by low precipitation. However, the funnel-like branching architecture of the crown and the smooth bark improved the rain water input in beech relative to spruce via substantial stem flow to the ground (Zirlewagen and von Wilpert 2001). This difference is ecologically significant, as trees had no access to groundwater. The morphological differences resulted in both tree species in different water relations followed by modified SR_t responses. In addition, the proportion of SR_a in SR_t also differed between beech and spruce during drought, which resulted from the different T_s response of SR_a and SR_h underneath beech and spruce under water limitation: the T_s response each of SR_a and SR_h was lowered to similar extent in beech, but to a larger extent in SR_a than SR_h in spruce.

Table 6 Regression results for the linear relationship between “autotrophic” soil respiration at 10°C (SR_a^{10}) and ASW (Fig. 6), where c and d are regression coefficients, R^2 is the coefficient of determination, and P gives the levels of significance of the regression equations (ANOVA)

Plots	Component of soil respiration	c ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$)	d ($\times 10^3 \text{ mm m}^{-2}$)	n	R^2	P
Beech	“Autotrophic”	0.136 (0.022)	0.420 (0.217)	17	0.20	0.071
Spruce	“Autotrophic”	0.038 (0.028)	1.600 (0.347)	19	0.56	0.003

Standard errors of c and d are shown in *brackets*

Table 7 Fine-root production (FRP) and fine-root recovery rate (FRR) in beech and spruce as assessed within the uppermost 20 cm of the soil during the study year

Parameter	2002		2003	
	Beech	Spruce	Beech	Spruce
FRP ($\text{mg l}^{-1} \text{a}^{-1}$)	473.5 (58.2)	755.7 (84.9)	466.7 (93.9)	135.7** (59.5)
FRR (%)	47.6 (4.6)	56.4 (4.8)	51.9 (7.6)	8.8** (1.8)

Standard errors of means ($n = 10$) are shown in *brackets* (no assessment in 2004)

Significance levels between years within beech and spruce groups were tested by means of Wilcoxon-test

** $P < 0.01$

Studies have shown current assimilates to largely drive SR_a (Högberg et al. 2001, 2002). Towards the end of August 2003, pre-dawn plant water potentials at our study site dropped to levels as low as -1.4 MPa in beech and -1.6 MPa in spruce (Löv, personal communication; Löv et al. 2006). However, the daily minimum water potential did not fall below -2.0 MPa in either tree species (consistent with general observations in temperate forests, Larcher 2001). The limit in minimum water potential suggests stomatal closure to prevent failure in whole-tree water transport (Tyree and Zimmermann 2002) and—as a consequence—limitation of photosynthesis (Löv et al. 2006).

Beech develops high uptake capacity for water due to a dense, deep-reaching, and homogeneous root system under the stem base where the water is led to preferentially by stem flow (Schmid and Kazda 2002). The root distribution of spruce, in contrast, is shifted towards upper soil horizons compared to beech forming a shallower root system (Schmid 2002), but with the same total rooting depth. Water exploitation of spruce depends mainly on the fine-roots in the top soil, where soil water was hardly available during the summer of 2003. In spruce soils, the absence of a T_s response of SR_a during May and June 2003 (Fig. 5) indicated a respiratory decline in fine-roots to the maintenance level. Progressive drought in July 2003 (Fig. 5) caused SR_a to decrease to levels typical for the cold season. Hence, fine-root biomass probably declined in spruce along with progressive drought, as fine-root production decreased by about a factor of six as compared to the humid growing season of 2002 (Table 7). Findings were consistent with those by Puhe (2003) and Kutschera and Lichtenegger (2002) and correspond to the long recovery period of stem increment in spruce after distinct summer droughts (Utschig et al. 2004; Rötzer et al. 2008).

The drought-induced decrease in T_s response of SR_a in beech was not statistically significant compared to the response during the “moist” period (Table 5), and was not associated with reduced fine-root production (Table 7). In a mixed *Fagus sylvatica*/*Quercus petraea* stand in Germany, Leuschner et al. (2001) found that finest root (<1 mm diameter) mortality of beech increased during a summer drought while compensatory FRP was stimulated. As a result, the living fine-root biomass remained unchanged. Sustaining fine-root biomass, although costly in terms of respiratory C use, may be advantageous for beech in capturing water upon rewetting of the soil (Nikolova et al. 2008). It is known that some tree species have the ability to use water resources from subsoil horizons, or to move water passively from moist to dry soil layers (Caldwell et al. 1998). Lifted water may facilitate favorable conditions for root metabolism in upper soil layers, perhaps maintaining SR_a as found in beech. The shallow rooting of

spruce relied, in contrast, during drought, on suberization of fine-roots (Nikolova 2007) to prevent water loss from the root surface to the soil. Consistently, SR_a^{10} was highly dependent on ASW only in spruce (Fig. 6 and Table 6), which clarified our research case in that drought differentially limited SR_a , namely to a higher extent under spruce than beech. The differential T_s – SR_a relationship and FRP response suggest contrasting strategies in beech and spruce of coping with drought: Use of internal C stores for new fine-root growth to ensure sustained resource uptake in beech, but reduced fine-root growth via entering dormancy in spruce to prevent resource loss.

Under nonlimiting water availability, both tree species displayed SR_h to be less sensitive to T_s than SR_a . Also, Epron et al. (1999) found higher Q_{10} for SR_a than SR_h , reflecting high seasonality in shoot and root metabolic activities (cf. Boone et al. 1998; Janssens and Pilegaard 2003; Davidson et al. 2006). The extraordinarily low pre-dawn water potential of beech and spruce at the end of August 2003 (Löv et al. 2006) indicate restricted water availability under both tree species. As for root respiration, Fierer et al. (2003) showed microbial respiration to strongly respond to changes in soil water potential, and as a consequence, C mineralization in surface rather than sub-surface soil was affected by drought. However, mixed microbial populations as in forest soils seem to decrease their activity at much lower water potentials than roots: respiration can be maintained by bacteria at a fairly high level even between -0.8 and -3 MPa before subsequently declining to negligible values below -5 MPa due to the high interspecific variability in drought sensitivity of soil microorganisms (Wilson and Griffin 1975; Parr et al. 1981). Especially, spruce roots reached the level of maintenance respiration in 2003 already above -2 MPa. Altogether, for the significantly different decomposition of SR_t into the two components SR_a and SR_h between beech and spruce, the higher drought sensitivity of the spruce roots is responsible. The drought sensitivity of the microbial communities underneath both species appeared to be comparable in spite of the much thicker humus layer of spruce soil leading to higher fluctuations in ASW of the needle litter even by the scarce rainfall events in 2003.

The established root exclusion technique (Hanson et al. 2000, Subke et al. 2006) was employed in this study to small-scale spots (10 cm diameter) in the topsoil including the organic humus layer, where, independent of the tree species, the majority of microbial biomass and fine-root turnover (Mainiero and Kazda 2006) was located. Given such an assessment, quantitative distinction between SR_a and SR_h is provided, as bias arising from application to larger ground area was not likely to occur (cf. Buchmann 2000). Such bias may be caused by raised soil moisture in zones of root exclusion and extensive disturbance of soil

structure, affecting decomposition and microbial C and N pools (Kuzyakov and Larionova 2005), and, hence, overestimating SR_h . Buchmann (2000) demonstrated in a *Picea abies* stand that soil moisture of trenched small-scale plots stayed similar to that of the control—being fundamental for unbiased assessment of CO_2 efflux rates—and that trenching of shallow fine-roots did not change the proportion between the so-called “root” and “soil microbial” respiration relative to effects occurring within larger trenching plots (e.g., $3 \times 3 \text{ m}^2$; Bowden et al. 1993). An alternative in situ method may be pulse-labeling with radioactive or stable carbon isotopes (Kuzyakov 2006; Baggs 2006; Subke et al. 2006; Hahn et al. 2006; Schuur and Trumbore 2006), which, however, increases experimental demand relative to small-scale root exclusion. The small-scale approach, when restricted to surface-near soil layers, prevents major bias upon trenching deep-reaching coarse roots, but may tend to overestimate SR_h (Subke et al. 2006), which appears tolerable in comparative studies.

In conclusion, reduced precipitation decreased SR_a and SR_h in spite of the high seasonal temperature regime of 2003, although SR_a —and as a consequence SR_t —decreased to higher extent in spruce than beech plots. Given this species-specificity and prognoses about water limitation in large areas of Central Europe carrying spruce forests (Kölling and Zimmermann 2007), SR_a apparently has the potential of a large-scale reduction of C flux from forest soils. Hence, conversion of lowland spruce monocultures into spruce/beech or beech forests may negatively influence the C budget of forest soils on the long-term (Borken and Beese 2005). Nevertheless, decline and potential break-down of drought-sensitive spruce monocultures under expected climate change conditions (Beierkuhnlein and Foken 2008) appear to become more adverse to soil C budgets of sites than the introduction of beech.

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