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Norway Spruce Shows Contrasting Changes in Below- Versus Above-Ground Carbon Partitioning towards the Alpine Treeline: Evidence from a Central European Case Study

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Abstract

The marked change in above-ground forest stand structure with elevation towards the alpine treeline has been widely recognized, while studies on altitudinal effects on the root system are still scarce. We studied Norway spruce stands along a 700-m-long elevational transect at Mount Brocken (Harz Mountains, central Germany) to test the hypothesis that fine root dry mass partitioning shows an inverse response to elevation towards the treeline compared to above-ground biomass. Microclimate measurements revealed that thermal conditions at the treeline of Mount Brocken are closely comparable to other treeline sites around the world. Above-ground structure did not differ significantly among stands at lower and mid elevations, but tree height and stem biomass decreased strongly with elevation upslope. Fine root biomass increased with elevation by a factor of nearly two. Annual fine root production was found to be highest at mid elevation but was only 40% lower than this maximum at the treeline. Consequently, the ratio of fine root production to above-ground stem biomass increased by a factor of 2–3 with elevation, indicating a strong shift of below- versus above-ground carbon allocation towards the treeline. We hypothesize that the enlargement of the fine root system at cold sites represents an adaptation to the unfavorable soil conditions, such as impaired nutrient supply.

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Introduction

Alpine treelines are considered to be among the most remarkable vegetation boundaries worldwide. For decades, many studies have focused on the ecology of treelines in many parts of the world (cf. reviews by Hermes, 1955; Troll, 1973; Tranquillini, 1979; Körner, 1998, 2003; Grace et al., 2002; Wieser and Tausz, 2007; Holtmeier, 2009). Despite the significant number of studies, there is still debate about the actual ecological reasons for the formation of alpine treelines. The decrease of tree height and above-ground biomass with elevation has often been attributed to reduced carbon gain under the cold conditions at higher altitudes (data reviewed by Stevens and Fox, 1991; Körner, 1998, 2003; Grace et al., 2002). Other stress factors such as strong winds, high snow charge, etc., might be of importance on a regional scale, but they are not likely to explain the phenomenon on a global scale (Körner, 1998; 2003). More recent results by Körner et al. have suggested that tree growth at the alpine treeline might be mainly limited by reduced metabolic allocation activity (Hoch et al., 2002; Hoch and Körner, 2003, 2005; Shi et al., 2006).

While altitudinal changes in above-ground stand structure and tree biomass are well documented in the literature (e.g. Wilson et al., 1987; Sveinbjörnsson et al., 1995; Barrera et al., 2000), responses of the tree root system to altered growth conditions with increasing altitude have rarely been studied. Recent investigations at different treeline sites worldwide have provided evidence that high-elevation forest stands—at boreal, temperate, or tropical treelines—are characterized by a disproportionally high fine root biomass that is in contrast to the decrease in above-ground biomass with elevation (Kitayama and Aiba, 2002; Leuschner et al., 2007; Hertel and Wesche, 2008; Hertel et al., 2008; Hertel and Leuschner, 2010). Investigations by Oleksyn et al. (1998) showed that Norway spruce saplings from high-elevation provenances have a systematically higher carbon investment to roots than those of lower elevation progenies. This corresponds with similar findings for herbaceous plants (Bloom et al., 1985; Körner and Renhardt, 1987). The actual reasons for this shift of carbon partitioning towards the fine root system at alpine treelines are not yet fully understood. This might be due in part to the presence of conflicting results from studies on the effects of low temperature on the fine root dynamics of trees. While some authors found the fine root growth of tree saplings to be clearly reduced under low soil temperatures (e.g. Turner and Streule, 1983; Häsler et al., 1999; Alvarez-Uria and Körner, 2007), results from other authors suggest rather high fine root dynamics of trees adapted to markedly low soil temperatures (Tryon and Chapin, 1983; Ruess et al., 2003; Gaul et al., 2008). Still, studies on tree root production and turnover from treeline sites are quite rare (e.g. Ruess et al. 2003; Graefe et al., 2008; Handa et al., 2008), which makes it difficult to assess the importance of changing climatic variables with increasing elevation towards the treeline for above- and below-ground carbon allocation in trees.

We investigated four mature stands of Norway spruce (*Picea abies*) along an elevation transect at the northern hillside of Mount Brocken in the Harz Mountains (Germany). The stands were located at altitudes ranging from 390 to 1100 m a.s.l. with the highest stand representing the upper treeline at Mount Brocken. The study was conducted to test the hypotheses that: (1) the decrease in tree height and above-ground biomass with elevation is paralleled by an inverse increase in fine root biomass, and (2) the

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TABLE 1

Morphological and chemical soil properties of four spruce stands along the elevational transect at Mount Brocken. Thickness of the organic layer and the mineral soil was recorded at 20 sampling locations per plot. The pH values, cation exchange capacity (CEC), base saturation, and C:N ratio were measured from five mineral soil samples per plot and refer to A horizons.

	Stand A (390 m)	Stand B (790 m)	Stand C (990 m)	Stand D (1100 m)
Thickness of organic layer (cm)	7.8	8.8	8.8	6.2
Thickness of mineral soil (cm)	6.8	21.4	18.5	15.3
pH(H_2O)/pH(KCl) mineral soil	3.9/2.9	3.5/2.7	3.8/3.0	3.8/3.0
CEC mineral soil ($\mu mol_c\ g^{-1}$)	419	378	225	204
Base cation saturation mineral soil (%)	47	14	16	24
C:N ratio mineral soil (mol mol^{-1})	30.1	30.1	20.4	19.5

ratio of below-ground to above-ground carbon allocation increases from the lower elevation sites towards the treeline. Furthermore, we intended to record the climatic variables along the transect in order to compare growth conditions at the treeline of Mount Brocken with those from other climatic treeline sites.

Study Sites and Methods

LOCATION OF THE STUDY SITES

The study was conducted on the northwestern slopes of the Harz mountain range in central Germany. In 2005, four mature stands of Norway spruce (*Picea abies* (L.) Karst.) were selected along a transect spanning from the mountain range base at Ilsenburg town (ca. 300 m a.s.l., 51°52′N, 10°41′E) to Mount Brocken, the highest peak of the Harz mountain range (1142 m a.s.l., 51°48′N, 10°37′E). The four stands (A–D) were located at (A) 390, (B) 790, (C) 990, and (D) 1100 m a.s.l. The highest forest stand (at 1100 m) represents the upper treeline at Mount Brocken and hence the upper distribution limit of connected forest patches in the area, following the definition given by Körner and Paulsen (2004) and Körner (2007). The stands had northerly aspects (stands A and D) or northeasterly (stands B and C), with moderate inclinations of 12–18°. Except for the lowermost stand, all sites were located within the protected area of the Harz National Park. The lowermost stand (A) was located below the natural distribution range for Norway spruce in this region and had a mean tree age of ca. 100 years. Stands B–D represent natural spruce forests ranging in age from ca. 100 years (stand B) to 260 years at treeline site D (information from the National Park administration, derived from local forest history archives; see also Firbas and Preuss, 1934, and Firbas et al., 1939). There was a thin layer of mosses and herbs (mainly *Avenella flexuosa*) of low cover in all four stands that did not vary among the sites; any shrub layer was absent.

SOIL PROPERTIES

The four spruce forest stands grew on acidic, nutrient-poor cambisols derived from the same facies of granite bedrock at all sites. The thickness of the mineral soil was ca. 15–21 cm in stands B–D, but it was only ca. 7 cm in the lowermost stand (Table 1). However, the development of mineral soils was restricted in all stands and the vast majority of the mineral soil material in the profile refers to A horizons. The thickness of the organic layer atop the mineral soil varied between ca. 6 and 9 cm. Soil acidity was high in all stands with pH(KCl) values of 2.7–3.0. The variability in cation exchange capacity was somewhat higher and base saturation tended to be especially low in the stands at higher elevations. The C:N ratios of the mineral soil were almost identical at the two lowermost sites while stands C and D had lower C:N ratios (Table 1).

CLIMATIC CONDITIONS

Microclimatic differences between the four stands were measured over the course of the year (July 2005 to June 2006) using mini-dataloggers (“iButtons” Maxim, Dallas, U.S.A.) for continuous records of air and soil temperature at +130 cm and −10 cm, respectively (one logger per site and location). Sensors in the air were screened against direct radiation with ventilated plastic caps. Single missing records—caused by the partial failure of data loggers (especially in the last months)—were compensated for by extrapolation from existing data, e.g. by the correlation of soil to air temperatures or the use of the strong dependence of air and soil temperature on elevation ($r^2 > 0.98$). The length of the growing season was estimated following the protocol given in Körner and Paulsen (2004) for their global survey on microclimatic treeline conditions. Accordingly, a soil temperature of 3.2 °C at 10 cm soil depth strongly coincides with an air temperature of 0 °C, which represents a threshold often used to indicate the beginning and end of the growing season for trees. Since soil temperature records are less susceptible to effects of direct or indirect insolation, we used this threshold to calculate the growing season length as the period during which daily soil temperature was continuously >3.2 °C.

Precipitation could not be measured separately for each of the four stands. However, data for the study year 2005 from the nearby weather stations at Wernigerode (250 m a.s.l., only a few kilometers from Ilsenburg town) and at the Mount Brocken summit (1142 m a.s.l.) indicate a clear increase in annual precipitation from 610 mm (Wernigerode) to 1570 mm (Mount Brocken summit) along the elevation transect. The mean annual precipitation (1961–1990) at Mount Brocken is even higher at 1808 mm (Deutscher Wetterdienst, 2005).

ABOVE-GROUND STRUCTURE OF THE STANDS

Mean tree height of the four spruce stands was measured using a Vertex III ultrasonic device (Hagloef, Sweden) from 10 randomly selected tree individuals per stand. Diameter at breast height (dbh) of all trees and stem density were measured in randomly selected plots in the stands. Plot size was 20 m × 20 m in the lower stands (A and B) and 15 m × 15 m and 8 m × 8 m for stands C and D, respectively. This allowed for the inclusion of a sufficient number of dominant tree individuals per plot. The data were used to calculate the stand basal area of the plots as well as stem biomass by applying allometric regression models and stem wood density values given in the literature (Müller and Zahn, 1958; Schmidt-Vogt, 1986). Tree slenderness in the stands was

TABLE 2

Micro-climatic conditions inside the four spruce stands along the elevational transect at Mount Brocken. For more detailed information on the methodology of climate measurements see methods description chapter section. Soil moisture contents are mean values ±1 SE; $n = 5$.

	Stand A (390 m)	Stand B (790 m)	Stand C (990 m)	Stand D (1100 m)
Mean annual air temperature (°C)	6.9	4.1	2.9	2.1
Mean annual soil temperature (°C)	6.9	5.2	4.3	3.8
Mean growing season soil temperature (°C)	9.2	8.2	7.2	6.7
Growing season length (days)	255	214	195	180

calculated as the ratio of tree height (m) to dbh (m) (Wang et al., 1998).

STRUCTURE OF THE FINE ROOT SYSTEM AND FINE ROOT MORPHOLOGY

In order to investigate living and dead fine root mass and its vertical distribution in the soil, root samples were taken with a soil corer (3.5 cm in diameter) from the organic layer and the mineral soil (0–20 cm) at 20 randomly selected locations per study plot at the beginning of July 2005. The soil samples were transferred to plastic bags and stored at 4 °C in the laboratory, where further processing was conducted within 30 days. The samples were cleaned of soil residues in water prior to the root extraction using a sieve with a mesh size of 0.25 mm. Only fine roots (roots <2 mm in diameter) of trees were considered for the analysis. However, sporadic analyses showed that herbaceous roots (easily distinguished from tree fine roots by their non-woody anatomy) were rare in the samples and did not account for a notable amount of root mass. Larger fine rootlets (>10 mm in length) were extracted by hand with tweezers. Living (biomass) and dead roots (necromass) were distinguished under the stereomicroscope by inspecting color, root elasticity, and cohesion of the cortex, periderm, and stele (e.g. Persson, 1978; Hertel and Leuschner, 2002). This fine root fraction represents the majority of living fine root mass, but a large proportion of the whole fine root necromass consists of smaller root fractions hardly recovered with this method (Bauhus and Bartsch, 1996; Hertel, 1999). Hence, one-third of the samples were subjected to a more detailed analysis of smaller root necromass particles (<10 mm in length) applying a method introduced by van Praag et al. (1988) and modified by Hertel (1999). After extraction of the large root fractions, the residue of the sample was evenly spread on a large sheet of filter paper (730 cm^2) with 36 squares marked on it. Six of the squares were randomly selected and analyzed under the stereomicroscope for even the smallest dead fine root fragments. Total mass of small dead rootlets was extrapolated by regression analysis of the ratio of small rootlets to large dead roots (>10 mm in length) recorded in the same subsample. Fine root biomass and necromass of each sample were dried at 70 °C for 48 h and weighed. The data were expressed as fine root dry mass at the respective soil depth, and as profile fine root mass total (in g m^{-2}).

One living rootlet per soil sample was randomly selected in order to analyze mean fine root diameter and specific root surface area (SRA, in cm^2 g^{-1}) using a WhinRhizo (Régent Instruments Inc., Quebec, Canada) visual analysis system with a scanner. Fine root area index (RAI, in m^2 root surface area per m^2 ground area) was calculated from the SRA values and fine root biomass values for each respective horizon. The abundance of fine root tips was determined by counting all living tips under the stereomicroscope in the same fine root sample used for analysis of SRA. Tip abundance was expressed on a dry mass basis (specific root tip abundance, n mg^{-1}) and on a stand ground area basis (root tip frequency, number of tips per m^2).

FINE ROOT PRODUCTION AND TURNOVER

The sequential coring approach was used to analyze annual fine root production and turnover along the elevation transect. Due to the high labor intensity associated with this procedure, the investigation was done only in the lowermost stand (A), the mid-elevation stand (B), and the uppermost stand (D). Soil samples from these stands were extracted in the same manner as described above at three additional sampling dates in August, September, and November 2005 (20 sampling locations per stand and date). The samples were separated according to the different soil depths and transferred to the laboratory, where fine root biomass and necromass were extracted as described above.

Annual fine root production, mortality, and turnover were estimated from seasonal changes in living and dead fine root mass with the minimum-maximum method using the decision matrix introduced by McClaugherty et al. (1982) (see also Fairley and Alexander, 1985). With this method, the annual fine root production is estimated as the difference between the maximum and minimum values of total fine root mass (fine root biomass plus necromass) in the sampling period (Vogt et al., 1998; Hertel and Leuschner, 2002). Only data with attached sampling dates where the minimum and maximum values for root mass were significantly different were used for this calculation. Fine root turnover was calculated as the ratio of annual fine root production to seasonal mean fine root biomass (Gill and Jackson, 2000).

STATISTICAL ANALYSIS

The data sets were analyzed for distribution of normality using a Shapiro and Wilk test. Normally distributed data were tested using an ANOVA procedure followed by pair-wise comparison after Scheffé ($P < 0.05$). Other data sets were tested with one-way Kruskal-Wallis single factor analyses of variance ($P < 0.05$). If H_o (no significant difference among the sites or horizons) was rejected, a non-parametric Mann-Whitney two-sample test (U-test) was applied to locate the differences ($P < 0.05$). All calculations were conducted with the package SAS, version 8.01 (SAS Institute, Cary, North Carolina, U.S.A.).

Results

MICROCLIMATE OF THE SPRUCE STANDS

Mean annual air temperature inside the forests decreased with elevation from 6.9 °C in the lowermost spruce stand to 2.1 °C in the treeline forest (Table 2). This corresponds to a mean lapse rate of 0.68 K 100 m^{-1} over the entire altitudinal distance, which varied between 0.60 and 0.73 for the four transect sections,

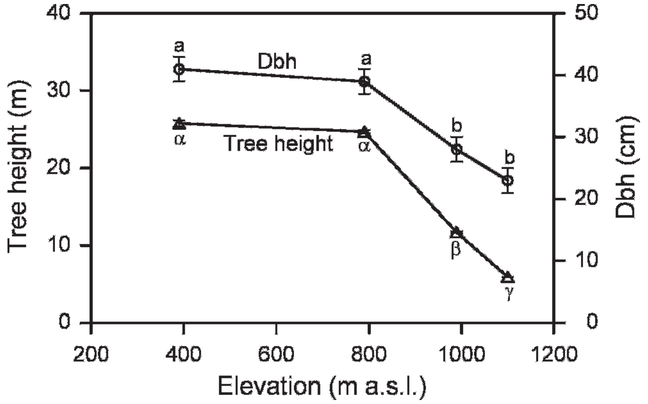

FIGURE 1. Tree height and stem diameter at breast height of four spruce stands along the elevational transect at Mount Brocken. Given are means ±1 SE. Different Latin or Greek letters indicate significant differences between the stands ($P < 0.05$).

indicating rather homogeneous air masses along the transect. Mean annual soil temperature at 10 cm soil depth also decreased linearly with elevation at 0.43 °C 100 m^{-1}. Calculation of mean soil temperature during the growing season according to the protocol given by Körner and Paulsen (2004) revealed a decrease from 9.2 °C from the lowermost to 6.7 °C in the uppermost stand. Growing season length also decreased from 255 to 180 days with elevation. Short-term measurements of the soil water content during the summer of 2005 showed highest soil moisture values at the treeline site (60% d.w.); however, no systematic dependence of soil moisture on elevation was found.

ABOVE-GROUND STRUCTURE OF THE SPRUCE STANDS

Above-ground structural parameters of the spruce stands showed clear dependence on the elevational position. Tree height was not significantly different between the two lowermost stands, but it decreased strongly from ca. 26 m at 390 m a.s.l. to less than 6 m at the treeline (Fig. 1). Diameter of the spruce stems showed a similar pattern with no difference in the lower part of the transect, but a strong decrease from mid-elevation stands towards the treeline. Stem density increased exponentially ($r^2_{\text{adj.}} = 0.92$) towards the treeline site (Table 3). Dead tree individuals were only present in the three natural spruce forests at upper elevations, and the percentage of dead trees in the total number of trees was especially high in the two uppermost stands. Tree slenderness was highest in the two lowermost stands and declined towards the treeline ($r^2_{\text{adj.}} = 0.99$), where very stunted tree individuals were present (slenderness < 25 m m^{-1}). Basal area of the stands did not show a clear elevational response. However, stem biomass was highest in the mid-elevation stand (B: 790 m a.s.l.) while it showed a lower record in the lowermost stand (A). Upslope, stem biomass of the stands decreased markedly, with the treeline stand showing only ca. 20% of the stem biomass present in stand B (790 m a.s.l.). Canopy cover varied somewhat among the stands but showed no elevational trend.

FINE ROOT MASS AND MORPHOLOGY

The investigation of the fine root system of the four stands also revealed marked differences dependent on the elevational site position. Fine root biomass significantly increased from the lowermost to the uppermost stand ($r^2_{\text{adj.}} = 0.91$) with the treeline stand having nearly twice the fine root biomass of the lowermost stand (Fig. 2). The mass of living fine roots was concentrated in the organic layer and the upper 10 cm of the mineral soil. However, on a soil volume basis, fine roots had much higher densities in the organic layer than in the upper mineral soil (Table 4). The ratio of living to dead fine root mass showed marked variation between stands and soil depths and was found to be especially low in both the organic layer and the mineral soil of the lowermost stand (A). In contrast, the fine root live:dead ratio was high in the uppermost stand while the two stands at mid elevation showed live:dead ratios of medium values.

Analysis of fine root morphological traits revealed only a few differences among the stands. Mean fine root diameter was almost identical at 0.5–0.6 mm in all stands and at both soil depths (Table 4). Specific fine root surface area showed lowest values in the lowermost stand and tended to increase with elevation. Specific root tip abundance varied from 4.5 to 10.7 tips mg^{-1} root dry mass, but no clear elevational effect could be observed. Occasional analysis revealed no differences in the percentage of root tips infected by ectomycorrhizal fungi among the stands.

On a ground area basis, elevation had a significant effect on the morphology of the fine root system. Root tip frequency (i.e. the number of root tips per square meter of ground area) increased from 1.4 million tips m^{-2} in the lowermost stand to 2.7 and 2.1 million tips m^{-2} in mid-elevation stands, and to 3.9 million tips m^{-2} at the treeline (Fig. 3A). Moreover, root area index RAI showed an exponential increase from 4.9 to 10.9 m^2 m^{-2} with elevation ($r^2_{\text{adj.}} = 0.91$) and, therefore, a doubling of the fine root system's surface area from the lowermost spruce stand to the treeline (Fig. 3B).

FINE ROOT PRODUCTION AND TURNOVER

Annual fine root production as estimated from the sequential soil coring did not reveal a clear elevational trend (rank correlation after Spearman at $P = 0.67$). The highest fine root production was found at the mid-elevation stand (B), followed by the lowermost stand (12% lower production), while the treeline stand revealed a 40% lower fine root production (Table 5). Annual fine root mortality showed similar differences among the stands. Compared to fine root production, annual fine root mortality was only somewhat lower in the lower and mid-elevation

TABLE 3

Above-ground structural characteristics of four spruce stands along the elevational transect at Mount Brocken.

	Stand A (390 m)	Stand B (790 m)	Stand C (990 m)	Stand D (1100 m)
Number of living trees per hectare	425	625	888	1406
Number of dead trees per hectare	0	175	1022	625
Slenderness of the trees (m m^{-1})	63.4	62.9	42.0	25.6
Basal area of the stands (m^2 ha^{-1})	55.2	75.9	54.5	57.7
Stem biomass of the stands (Mg ha^{-1})	88.8	114.7	43.5	24.5
Canopy cover (%)	60	60	65	75

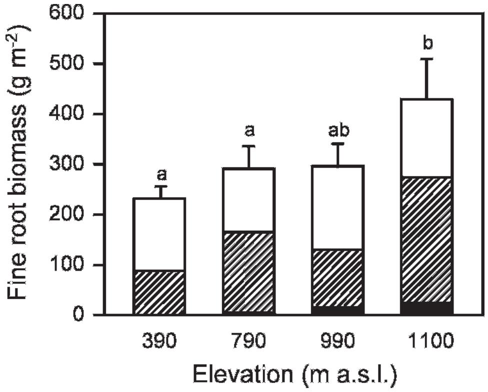

FIGURE 2. Fine root biomass of four spruce stands along the elevational transect at Mount Brocken. Given are means ±1 SE. Open bars: organic layer; hatched bars: 0–10 cm mineral soil; black bars: 10–20 cm mineral soil. Different letters indicate significant differences in the profile totals between the stands ($P < 0.05$).

forest, but clearly lower at the alpine treeline. Fine root turnover, on the other hand, showed a clear decrease with elevation (Spearman rank correlation coefficient $r_s = -1.0$, $P < 0.001$). However, relation of annual fine root production to stem biomass revealed a much higher below- to above-ground carbon allocation in the treeline stand compared to the lower and mid-elevation stands.

Discussion

CLIMATIC CONDITIONS OF THE NORWAY SPRUCE STANDS ALONG THE ELEVATIONAL TRANSECT

Despite the large number of investigations in past decades, there is still no consensus as to whether a single climatic factor is decisive in explaining the elevational changes of tree growth and the formation of the alpine treeline (see e.g. the conflicting views by Körner and Paulsen [2004] and Holtmeier and Broll [2005]). However, the clear decline in air temperature with increasing altitude has been widely recognized as the best candidate for the explanation of the elevational change in tree growth and its limit at the treeline (e.g. Hermes, 1955; Jobbagy and Jackson, 2002; Körner and Paulsen, 2004; Körner 2007). Mean annual air temperature of the spruce stands in our study decreased constantly at 0.68 K 100 m^{-1} along the 700-m-long elevational transect. This temperature lapse rate is well in accordance with the 0.58–0.72 K 100 m^{-1} range recorded for other spruce forests in eastern Europe and northeastern U.S.A. (Doležal and Šrutek, 2002; Richardson et al., 2004). Studies have shown that the treeline position is more closely associated with soil than with air temperatures (e.g. Sveinbjörnsson, 2000; Körner, 2003; Körner and Hoch, 2006). Körner and Paulsen (2004) found the treeline position around the world to coincide with a 6.7 °C growing season mean in the upper soil. Notably, the growing season mean soil temperature at the treeline site at Mount Brocken meets this global temperature threshold exactly, indicating that the thermal conditions correspond well with those at other alpine treelines. Some authors have emphasized the importance of locally specific climate conditions other than temperature for treeline formation (e.g. Troll, 1973; Gansert, 2002; Holtmeier and Broll, 2005). In fact, rainfall regime, cloudiness, and wind velocity were not constant along our elevational transect. Mean annual precipitation increases along the northern slope of Mount Brocken, from ca. 600 mm at the foothills to ca. 1800 mm at the summit (Deutscher Wetterdienst, 2005). The high rainfall amounts at higher elevations may produce unfavorable soil nutrient conditions through intense weathering and low nutrient mineralization rates (e.g. Meentemeyer, 1977). With a mean number of foggy days >300 $year^{-1}$, cloudiness is particularly high at the summit region of Mount Brocken (Deutscher Wetterdienst, 2005). This suggests strongly reduced plant-available solar radiation near the treeline. Wind velocity at the Mount Brocken summit can be very high, but strong winds are common, even on mountains that do not possess a natural alpine treeline. The climatic data from our transect clearly suggest that thermal conditions most likely constrict the growth of spruce trees at higher elevations. The high number of cloudy days may particularly contribute to the low temperatures at the treeline of Mount Brocken.

ABOVE-GROUND RESPONSES OF THE NORWAY SPRUCE TREES TO ALTERED GROWTH CONDITIONS TOWARDS THE ALPINE TREELINE

Above-ground structural parameters of the Norway spruce stands in our study were not very different in the two lowermost stands of the elevational transect (390 and 790 m a.s.l.). However, tree height and stem diameter both significantly decreased from mid elevation to the treeline while stem density increased. Moreover, stem biomass decreased by a factor of more than four

TABLE 4

Density of living fine root mass, live:dead ratio of fine root mass, and fine root morphological traits in the organic layer and the upper mineral soil in four spruce stands along the elevational transect. Given are means ±1 SE; $n = 20$. Different letters indicate significant differences between the forest stands ($P < 0.05$).

	Stand A (390 m)	Stand B (790 m)	Stand C (990 m)	Stand D (1100 m)
Organic layer				
Fine root biomass density (g L^{-1})	1.8 ± 0.2 a	1.6 ± 0.3 a	1.8 ± 0.2 a	2.7 ± 0.4 b
Live:dead mass ratio (g g^{-1})	0.3 ± 0.1 a	1.0 ± 0.3 bc	0.6 ± 0.1 b	1.3 ± 0.2 c
Mean fine root diameter (mm)	0.6 ± 0.03 a	0.6 ± 0.06 ab	0.6 ± 0.03 a	0.5 ± 0.07 b
Specific fine root area (cm^2 g^{-1})	217 ± 22 a	261 ± 32 ab	257 ± 21 b	288 ± 16 c
Specific root tip abundance (n mg^{-1})	7.0 ± 1.6 a	10.6 ± 1.9 b	5.6 ± 1.1 a	10.7 ± 0.1 b
Mineral soil (0–10 cm)				
Fine root biomass density (g L^{-1})	1.1 ± 0.2 a	1.3 ± 0.4 a	0.8 ± 0.2 a	1.9 ± 0.4 b
Live:dead mass ratio (g g^{-1})	0.25 ± 0.04 a	0.34 ± 0.08 ab	0.32 ± 0.06 a	1.3 ± 0.2 b
Mean fine root diameter (mm)	0.6 ± 0.03 a	0.5 ± 0.02 b	0.6 ± 0.04 ab	0.6 ± 0.03 ab
Specific fine root area (cm^2 g^{-1})	200 ± 13 a	235 ± 26 ab	288 ± 32 b	235 ± 19 ab
Specific root tip abundance (n mg^{-1})	4.5 ± 0.8 a	7.6 ± 1.0 a	8.4 ± 2.5 a	7.4 ± 0.9 a

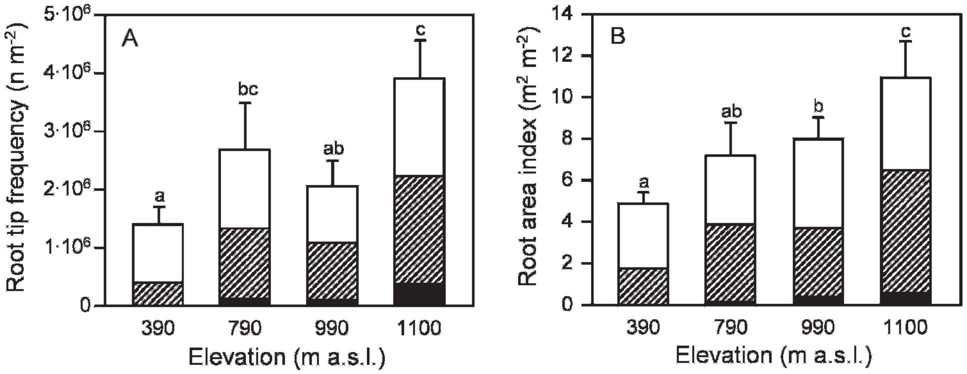

FIGURE 3. Root tip frequency (A) and root area index (B) of four spruce stands along the elevational transect at Mount Brocken. Given are means ±1 SE. Open bars: organic layer; hatched bars: 0–10 cm mineral soil; black bars: 10–20 cm mineral soil. Different letters indicate significant differences in the profile totals between the stands ($P < 0.05$).

towards the treeline, indicating a clear reduction in carbon allocation to the above-ground Norway spruce tree components. Similar changes in above-ground structure with elevation towards the treeline have been documented frequently in earlier studies (e.g. Ellenberg, 1966; Wilson et al., 1987; Li et al., 2003; Leuschner et al., 2007). Possible explanations for the elevational decrease in above-ground tree growth and treeline formation itself have been the subject of intense debate (see reviews e.g. by Stevens and Fox, 1991; Körner, 1998; Grace et al., 2002; Körner, 2003; Holtmeier, 2009). Some authors have attributed the phenomenon to reduced carbon gain ('source limitation') due to reduced photosynthetic activity and/or as a consequence of the short growing season near the treeline (e.g. Stevens and Fox, 1991; Cairns and Malanson 1998). The occurrence of strong winds, abrasion effects by blowing ice, large snow charge, and winter drought may additionally contribute to a constrained carbon balance near the treeline in temperate or boreal regions (Tranquillini, 1979; Wooldridge et al., 1996; Sveinbjörnsson, 2000; Gansert, 2004; Holtmeier, 2009). On the other hand, studies by Körner and co-workers have suggested that tree growth under cold climate conditions may be low due to reduced biosynthetic activity ('sink limitation') (Körner, 1998, 2003; Hoch et al., 2002; Hoch and Körner, 2003, 2005). The obvious reduction in tree size towards the treeline has also been explained as a result of evolutionary selection of tree growth pattern to cope with the unfavorable thermal conditions at higher altitudes. The tighter atmospheric coupling at sites with prevailing high wind velocities may have forced trees to adapt to the connective heat loss from the canopy surface by size reduction (Wilson et al., 1987; Wilkinson, 2009). In a common garden experiment, Oleksyn et al. (1998) showed that the growth pattern of Norway spruce saplings of different elevational provenances was indeed genetically determined. We have no data on genetic differences between spruce trees from different altitudes that would allow for an assessment of evolutionary selection of small trees near the treeline in our study. However, taller spruce trees near the treeline at Mount Brocken are characterized to a high extent by mechanical damage of the canopy and marked losses of branches by wind and snow break. This significant disturbance regime cannot be ignored for the interpretation of the elevational changes in above-ground tree stature of the spruce stands. This is illustrated by the fact that the proportion of standing dead trees was much lower (31%) at treeline site D, where the mean tree height was below 6 m, than in subjacent stand C (54%), where the trees were twice as high. Furthermore, dead trees are infrequent above the current treeline at Mount Brocken, where single spruce outposts reach a height of only ca. 2 m at a documented age of >200 years. We therefore conclude that the lower stature of the spruce trees near the treeline at least partly reflects an adaptation to the significant disturbance regime as well as to the cold and windy climate conditions. Our results on above-ground structural parameters do not allow for an assessment of whether above-ground growth at the treeline of Mount Brocken is constrained by sink rather than source limitation. However, by including data on below-ground dynamics of the spruce trees, we demonstrate in the following section another possible reason for the reduced above-ground carbon allocation near the treeline.

BELOW-GROUND BIOMASS PARTITIONING IN THE NORWAY SPRUCE STANDS ALONG THE ELEVATIONAL TRANSECT

Studies on the response of the root system of trees to altered growth conditions at different altitudes are still rare. Along the elevational transect of Norway spruce stands at Mount Brocken, fine root biomass increased by a factor of nearly two towards the treeline, though soil conditions (in terms of temperature and moisture) became increasingly less favorable. However, we found no significant effect of the changing growth conditions on the fine root morphology. On the contrary, root tip frequency (i.e. number of tips per m^2) and root area index (m^2 of fine root surface area per m^2) increased more markedly with altitude than fine root biomass. In a latitudinal transect study of 16 Norway spruce and Scots pine stands in Finland, Helmisaari et al. (2007) found that fine root biomass increased with decreasing temperature sum from lower to higher latitudes. For Norway spruce, Finér et al. (2007) showed that fine root biomass in boreal (and hence colder) forests was 17% higher than in temperate forests. A significant influence of the elevational position of the stands became apparent for the boreal

TABLE 5

Annual fine root production, mortality, turnover, and the ratio of fine root production to stem biomass in the lowermost, mid-elevation, and uppermost spruce stands of the elevational transect at Mount Brocken. Given are values of the total soil profile.

	Stand A (390 m)	Stand B (790 m)	Stand D (1100 m)
Annual fine root production (g m^{-2} yr^{-1})	1108	1258	752
Annual fine root mortality (g m^{-2} yr^{-1})	922	1192	413
Fine root turnover (yr^{-1})	4.2	3.3	2.0
Fine root production:above-ground stem biomass (yr^{-1})	0.13	0.11	0.31

spruce forests in this study. However, Leuschner and Hertel (2003) found a significant positive dependence of the fine root biomass of Norway spruce stands on elevation to be also true for temperate stands. The pattern of increasing fine root biomass with elevation in Norway spruce is consistent with recent findings by Hertel and Wesche (2008) and Hertel et al. (2008) from other tree species or biomes (i.e. high Andean *Polylepis* and southern Patagonian *Nothofagus*).

The analysis of fine root dynamics at three of the spruce stands in our study revealed relatively high annual fine root production estimates. The highest fine root production was found at mid elevation (ca. 1250 g m^{-2} yr^{-1}), but fine root production at the treeline stand was only 40% lower (ca. 750 g m^{-2} yr^{-1}). The measured values seem to be constrained by findings from soil respiration measurements (including both autotrophic and heterotrophic respiration) of $<$400 g C m^{-2} yr^{-1} under comparable climatic conditions (i.e. for boreal woodlands; Raich and Schlesinger, 1992). However, fine root production of Norway spruce stands given in the literature varies widely from $<$100 g m^{-2} yr^{-1} (e.g. Cole and Rapp, 1981; Godbold et al., 2003) to $>$400 g m^{-2} yr^{-1} (e.g. Kodrik, 1998; Cronan, 2003) and may even reach 670 g m^{-2} yr^{-1} (van Praag et al., 1988). A direct comparison to these data is hampered by differences in collection and calculation methods, the wide range of stand ages, and different elevational positions of sites in the studies. On the other hand, our fine root production estimates are well in concordance with results recorded by Grier et al. (1981). These authors found a fine root production of 1279 g m^{-2} yr^{-1} in a subalpine coniferous (*Abies amabilis*) forest in North America that accounted for 66% of the entire net primary production of the stand.

Along the elevational transect at Mount Brocken, annual fine root production decreased to some extent from the middle elevation to the treeline, whereas the ratio of fine root production to stem biomass (as the most important above-ground biomass component and a good predictor for above-ground net primary production) increased by a factor of three. This finding clearly indicates a strong increase of relative carbon allocation to the fine root system from lower and mid-elevation stands towards the treeline. In fact, the elevational change in the below- versus above-ground carbon allocation must be even stronger considering that the trees near the treeline were much older (ca. 250 yrs) than those at lower elevation (ca. 100 yrs), thus indicating a strongly decelerated annual stem growth at the treeline. Additionally, our results showed a decrease of specific fine root mortality with elevation from ca. 4 yr^{-1} at lower or mid elevations to 1 yr^{-1} at the treeline stand, indicating a high fine root vitality at the treeline. Several authors have stated that fine root growth might be reduced at alpine treeline sites due to low soil temperatures (Tranquillini, 1979; Körner, 1998, 2008; Wieser, 2007; Holtmeier, 2009). A review of the available literature data on the dependence of tree root growth activity on the temperature regime reveals a less clear picture. Experiments with planted or potted young trees indeed showed a stimulation of root growth by higher soil temperatures (Bilan, 1967; Turner and Streule, 1983; Lopushinsky and Max, 1990; Häsler et al., 1999; Lahti et al., 2005; Alvarez-Uria and Körner, 2007). In contrast, results from studies on adult trees in the field indicated much more dynamic fine root growth under cold growth conditions than might be expected from such sapling experiments. Such conflicting results were also reported by Tryon and Chapin (1983), who compared the root growth response of tree seedlings of various species from Alaska to different experimental soil temperatures with root growth observations of the same species under very cold field conditions. In their review on fine root dynamics in boreal forests, Ruess et al. (2006) stated that fine roots of trees in this cold ecotone were obviously adapted to function at low soil temperatures. Direct observations using the minirhizotrone technique revealed a high fine root turnover (lifespan: 108 days) of adult *Picea mariana* trees, though growing season soil temperature of the stands was only 3.0–5.6 °C (Ruess et al., 2003). Results of other studies showed that fine roots of temperate species seem to be similarly adapted to low soil temperatures. Benecke et al. (1978) demonstrated that fine roots of *Pinus contorta* and *Nothofagus solandri* at the treeline in New Zealand were physiologically active for at least 9 months of the year, despite the much shorter growing season. Sandhage-Hofmann and Zech (1993) observed large seasonal changes (factor 2.5 within 1–2 months) in fine root biomass and necromass of Norway spruce near the treeline in the European Alps. Gaul et al. (2008) directly observed significant fine root growth activity in adult Norway spruce even under soil temperatures below 0 °C. In a soil frost application experiment, these authors showed that over-winter mortality in the frost treatment led to a compensatory fine root growth at these low soil temperatures. Similar results indicating a stimulation of replacement root growth by increased fine root mortality in cold soil conditions were also documented by Ruess et al. (1998), Weih and Karlsson (2002), and Ruess et al. (2003).

In summary, studies on mature tree stands at the alpine treeline clearly indicate an enhanced carbon investment into the root system that is most likely genetically determined (Oleksyn et al., 1998; Sveinbjörnsson, 2000). This pronounced shift in biomass partitioning from above- to below-ground organs with increasing altitude towards the treeline has also been found in mature forests in New Zealand, Ecuador, Bolivia, and Argentina (Benecke and Nordmeyer, 1982; Leuschner et al., 2007, Hertel and Wesche, 2008; Hertel et al., 2008). These numerous findings do not support the hypothesis that closed tree canopies at the treeline impair root growth activity by preventing the warming of the soil, as was suggested by Körner (1998, 2003) and Wieser (2007).

More likely, the enhanced carbon investment into the root system represents a mechanism to compensate for reduced nutrient availability near the treeline. It is known that nutrient mineralization is often hampered under cold soil conditions (Meentemeyer, 1977; Sveinbjörnsson et al., 1995; Timoney, 1995; Sveinbjörnsson, 2000). Recent investigations along our study transect provide evidence that, in particular, net nitrogen mineralization is reduced towards the treeline (Plapp et al., unpublished data). Moreover, physical constraints of water and related nutrient uptake from soil to root and across root cells and vessels at low temperatures are likely to explain the marked increase of carbon investment into the root system at the treeline. According to Stevens and Fox (1991) and Sveinbjörnsson (2000), the long-distance transport of water and nutrients in trees requires a disproportionately larger carbon investment into the root system in cold, as compared to warmer, environments. This is confirmed from studies by Karlsson and Nordell (1996) and Weih and Karlsson (2001), who showed that the nitrogen supply of birch seedlings was reduced at cold soil temperatures due to the physiological inability of root nutrient uptake.

Conclusions

The results of our transect study at Mount Brocken reveal a clear increase of fine root biomass of Norway spruce stands with increasing elevation, and particularly towards the alpine treeline. This is in marked contrast to the simultaneous decrease of above-ground biomass. Moreover, fine root production was disproportionately high at the treeline site at Mount Brocken, despite the unfavorable thermal conditions that were similar to other treeline sites worldwide. We conclude from these findings that the enlargement of the fine root system of Norway spruce stands at cold sites represents a systematic adaptation to cope with unfavorable soil conditions. We speculate that the particularly high fine root biomass in these stands reflects constrained nutrient supply under cold climate conditions either by reduced nutrient mineralization and/or by physical constraints of nutrient uptake by the roots. The importance of maintaining such large fine root biomass would also explain the relatively high fine root production at the treeline that may compensate for losses of fine roots e.g. by over-winter mortality. The conspicuous carbon allocation into the fine root system at the treeline may also at least partly contribute to the strongly constricted above-ground biomass of the stands as compared to lower elevation sites.

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