

# Effects of root trenching of overstorey Norway spruce (*Picea abies*) on growth and biomass of underplanted beech (*Fagus sylvatica*) and Douglas fir (*Pseudotsuga menziesii*) saplings

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Received: 22 March 2010/Revised: 16 October 2010/Accepted: 3 December 2010/Published online: 22 January 2011  
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**Abstract** In Central Europe, the conversion of pure Norway spruce stands (*Picea abies* [L.] Karst.) into mixed stands with beech (*Fagus sylvatica* L.) and other species like e.g. Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) is accomplished mainly by underplanting of seedlings beneath the canopy of overstorey spruce trees after partial cutting treatments what means exposure to shade and below-ground root competition by the overstorey to the seedlings. Particularly about the second factor, our knowledge is limited. Therefore, we carried out a below-ground competition exclusion experiment by root trenching and investigated the effects on soil resources, growth, and biomass partitioning of underplanted beech and Douglas fir saplings under target diameter and strip cutting treatments. The exclusion of overstorey root competition by trenching increased the soil water potential in the second year that had a fairly dry growing season and led to significantly higher foliar concentrations of most nutrients, particularly in Douglas fir, indicating an amended nutrient supply. Both

improvements were accompanied by an increase in length and diameter increment of the underplanted saplings, appearing in both species only after having surpassed a species-specific threshold light value (Douglas fir 16% of above canopy radiation, beech 22%). We also found significant interactions between trenching and light for specific fine root length and further biomass and morphological parameters. Judged by the much steeper increase in height and diameter growth with increasing light after release from below-ground competition, Douglas fir saplings appeared to be more sensitive to root competition than beech saplings what conforms to older findings for beech. According to our results, a strip cutting seems to be more appropriate than a target diameter cutting treatment to replace a pure spruce stand by a mixed stand with beech and Douglas fir.

**Keywords** Forest conversion · Cutting types · Root trenching · Juvenile growth · Shade tolerance · Below-ground competition · Light availability

Communicated by Rainer Matyssek.

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## Introduction

During the last two centuries, pure stands of Norway spruce (*Picea abies* L.) outside its natural range have often proven to be unstable and sensitive to abiotic and biotic stress factors (Spiecker et al. 2004). Because mixed stands are regarded as more stable, particularly against windstorm and drought, and economically profitable (Knoke et al. 2008), the conversion of pure spruce stands into mixed stands has become an important silvicultural aim in many Central European countries over the last decades, particularly in public forests (Otto 1995). In the face of expected climate change and higher probability of extreme events

such as storms or droughts, these efforts are gaining rising importance (Lüpke 2004).

The most frequently used species in conversion practice is European beech (*Fagus sylvatica* L.). In a literature review, Ammer et al. (2008) concluded that the enrichment of Norway spruce stands with beech improves soil properties, biodiversity, and productivity of pure spruce forests in many cases. To increase the resilience potential of forests further, Lüpke (2004, 2009) recommended to use further native and also non-native species with high adaptive and productive capability such as Douglas fir (*Pseudotsuga menziesii* Mirb.). In Central Europe, a widespread method for converting pure Norway spruce stands is planting of beech and/or other species beneath the canopy of mature spruce trees (Lüpke et al. 2004; Ammer et al. 2008). Survival and growth of underplanted seedlings is directly linked with the species capacity to grow under shade conditions. Since beech is well known as a shade-tolerant species (Röhrig 1967; Emborg 1998; Stancioiu and O'Hara 2006; Petritan et al. 2007), even slightly thinned spruce stands generally provide enough light for beech seedlings (Ammer 2002). But with less shade-tolerant species such as Douglas fir, which is described as moderate shade tolerant (Mailly and Kimmins 1997; Petritan et al. 2010), light can become a limiting growth factor.

Of the environmental factors governing the growth conditions in the understorey, light is considered the most important factor (Kimmins 1997) and therefore has been widely investigated (inter alia Röhrig 1967; Kobe et al. 1995; Kunstler et al. 2005; Stancioiu and O'Hara 2006; Petritan et al. 2007, 2009). On the other hand, the influence of overstorey root competition on growth of underplanted seedlings remains poorly investigated and understood (Coomes and Grubb 2000), although some studies found a strong below-ground competition between overstorey and understorey vegetation for water and nutrients (Christy 1986; McCune 1986; Riegel et al. 1992; Walters and Reich 1997; Wagner 1999; Lindth et al. 2003; Machado et al. 2003). In two reviews on root-trenching experiments (Grubb 1994; Coomes and Grubb 2000), the authors summarize that competition for below-ground resources is more severe on less fertile and/or drier sites.

A positive response of underplanted seedlings to the exclusion of overstorey tree roots by trenching has often been interpreted as a consequence of the improved soil moisture supply (Gerhardt 1996; Hauskeller-Bullerjahn 1997; Ammer 2002) and, in few reports (Coomes and Grubb 1998), of increasing nutrient availability. However, Coomes and Grubb (2000) stated that the effects of water and nutrient shortage are hardly to separate because water shortage is likely to reduce the rate of microbial release of N and P and to inhibit the rate of nutrient uptake by the roots. Furthermore, the results of trenching experiments are

not consistent. Some experiments reported differences both in soil water and in nutrient supply (Riegel et al. 1992, 1995; Devine and Harrington 2008) or in soil moisture alone (Lindth et al. 2003). Other studies detected differences neither in soil moisture (Christy 1986) nor in nutrient supply (Hart and Sollins 1998) and nor in both resources (Simard et al. 1997; Ricard et al. 2003). Moreover, there is only little information about the effect of spruce overstorey root exclusion by trenching on water and nutrient supply and on underplanted seedlings growth, and if there are any, they deal with the reaction of beech seedlings like in the study of Ammer (2002), whereas studies with Douglas fir seedlings are totally lacking. In addition, no quantitative information about the intensity of overstorey root competition (fine root density or fine root distribution) accompanied the trenching experiments.

A large-scale and long-term experiment with various logging and regeneration treatments, established in the Solling mountains (Lower Saxony, Germany) in 2003, gave us the possibility to enlarge our knowledge about the impact of overstorey spruce roots on soil water and nutrient availability and on growth of underplanted beech and Douglas fir seedlings. For this purpose, we conducted a trenching experiment in subplots of the two variants differing in canopy cover density: (1) target diameter and (2) strip cutting. Due to the assumption that seedling growth response to water and/or nutrient supply depends on light intensity reaching the understorey crown level (Drever and Lertzman 2001; Coomes and Grubb 2000; Devine and Harrington 2008), we expected the response to trenching being more pronounced in cutting systems with higher light transmissibility like strip cutting compared to systems with lower transmissibility like target diameter cutting. Further, an interaction between light level and soil moisture appears to influence the minimum requirements for light energy of a species (Atzet and Waring 1970). Whereas Carter and Klinka (1992) reported that on drier soils a lower light level is needed to reach a given growth compared to moist soils, more studies (Atzet and Waring 1970; Marshall 1986; Lüpke and Hauskeller-Bullerjahn 2004) supported the opposite, namely a decreasing light requirement with increasing soil moisture availability.

The response of underplanted seedlings to overstorey root competition is species-specific (Coomes and Grubb 2000; Lüpke and Hauskeller-Bullerjahn 2004) and seems to be linked with species shade tolerance. The last authors found that the moderately shade-tolerant sessile oak increased growth after exclusion of beech overstorey roots by trenching much more and already at a lower light level than shade-tolerant beech. Concerning this aspect, we tested in this study whether the underplanted species differing in shade tolerance—shade-tolerant beech and moderately shade-tolerant Douglas fir—will react differently to the

exclusion of competing overstorey spruce roots. Additionally, this response will be investigated both in growth and in biomass distribution patterns. The latter point is thought to test the multiple resource limitation theory (Chapin et al. 1987; Tilman 1990), suggesting that plants adjust to situations of resource imbalance by allocating more biomass to tissues that acquire the most strongly limiting resources. Under shade conditions, species should invest more biomass in foliage and branches to maximize light capture, while under drier conditions biomass allocation in roots should be enhanced to raise water uptake and total leaf area should be diminished to reduce evaporation (Valladares and Niinemets 2008).

Due to the scarcity of information about growth and biomass allocation pattern responses to the exclusion of overstorey root competition for underplanted beech seedlings (Ammer 2002) and the total lack of respective information for Douglas fir seedlings, we carried out an investigation to test the following hypotheses:

- (1) Overstorey spruce roots have a sizeable effect on soil water and nutrient availability for the regeneration in the understorey. After root cutting by trenching, supply of soil resources for underplanted saplings will increase.
- (2) Trenching has a positive effect on whole-plant growth, increases the total plant biomass proportions of leaves, stem, and branches, and decreases the proportion of roots.
- (3) The effect of root trenching on growth of underplanted seedlings will be species specific: compared with beech, less shade-tolerant Douglas fir will increase growth more strongly over the whole light range beginning already at a lower light level.

## Materials and methods

### Study sites and treatments

The study was carried out on two sites in the Solling Mountains (Lower Saxony, Germany, 51°47'N and 9°37'E). Both sites are characterized by well-drained dystric cambisol (podzolic brown earth). The Solling climate is classified as humid and sub-continental. For the first site—Neuhaus at 500 m a.s.l.—the following long-term mean values are given: 6.5°C annual temperature, 1,050 mm annual precipitation, thereof 470 mm during the growing season; for the second site—Otterbach at 300 m a.s.l.—the respective values are as follows: 7.5°C annual temperature, 900 mm annual precipitation, thereof 420 mm during the growing season. During the observation period of this study (2007 and 2008), the actually

measured precipitation deviated from those long-term means and reached the following values (measured by the Northwest German forest experimental station): at Neuhaus in 2007: 131% (year) and 170% (growing season), in 2008: 72% (year) and 46% (growing season); at Otterbach in 2007: 155% (year) and 183% (growing season), in 2008: 100% (year) and 89% (growing season). Thus, particularly at the Neuhaus site, the year 2008 was exceptionally dry, while 2007 was a fairly wet year on both sites, especially during the growing season.

On both sites, a large-scale and long-term research experiment with various logging and regeneration treatments was established in pure Norway spruce stands (ca. 95 years old) in autumn 2003 by the Northwest German Forest Research Station in Göttingen. Two harvest types (clear cutting and target diameter cutting) were carried out on both sites, and in addition a strip cutting at Neuhaus. The latter can be described as a sparse shelterwood of 30 m width, bordering the northern edge of the clear cutting, thus receiving a substantial amount of side light. At both sites, two 1-ha plots for each harvest treatment were established and each divided into several subplots on which various regeneration treatments were installed.

For the present investigation, we used the two replicated plots of each of the following harvest treatments: target diameter cutting at Neuhaus (TCN), target diameter cutting at Otterbach (TCO), and strip cutting at Neuhaus (SCN). On each of these plots, we used the following regeneration variants: underplanted beech seedlings spaced 2 × 1 m, and underplanted Douglas fir seedlings spaced 3 × 2 m. Within each of these 12 plots (3 harvest treatments × 2 replicates × 2 underplanting variants), we chose 32 saplings for the trenching experiment. To keep cost and labor for root trenching within tolerable limits, we treated the saplings in groups of two sizes according to the different spacing: each beech group encompassed 8 and each Douglas fir group 4 saplings, which made in total 72 groups (24 in beech, 48 in Douglas fir), adding up in total to 192 saplings for each species. Each of the six harvest treatment plots (3 treatments × 2 replicates) contained four beech and eight Douglas fir groups. A randomly selected half of these groups were encircled by trenches 60 cm deep and 26 cm wide in April 2007, performed by a mini excavator. Roots too large to cut by the excavator were cut with a hand- or chainsaw. The trenches were refilled with the excavated soil immediately after opening.

Trenching depth was chosen following published experiences in previous trenching experiments (e.g. 0.5 m in McCune 1986, 0.4 m in Ammer 2002, 0.5–0.75 m in Christy 1986, 0.3 m in Machado et al. 2003, 0.3–0.4 m in Ricard et al. 2003, 0.5–0.55 m in Devine and Harrington 2008) and the fact that Norway spruce generally exhibits a particularly shallow root system. According to Schmid and

Kazda (2002), normally more than three-quarters of the fine roots of spruce are located in the upper 30-cm soil zone. Even if our trenches did not exclude all overstorey root competition, the treatment probably excluded most of it, and definitely the roots within the rooting zone of the saplings.

We assumed a trench width of 26 cm as sufficient to prevent substantial root ingrowth into the trenched plots within the planned 2-year observation period. This assumption only has a small scientific basis. All we found within published results is a notion of Schmaltz (1964) who observed very little ingrowth of beech roots into trenched plots several years after trenching. However, in excavating our sample saplings at the end of our experiment, we could not detect any ingrowth of new spruce roots.

All plots of the trenching experiment were free of other noteworthy competitors like naturally regenerated spruce saplings, bushes, or herbaceous vegetation.

## Measurements

### *Fine root sampling of overstorey spruce trees*

Before the installation of the trenching experiment, we surveyed the fine root biomass of the Norway spruce overstorey in the planned treatment units by sampling soil cores next to each Douglas fir and to every second beech sapling in spring 2007. Soil cores were taken with a cylinder tube sampler (diameter 8 cm) at 30 cm distance from each sample sapling toward the nearest overstorey spruce tree. Fine roots from the humus layer were also sampled as they represent an important part of the total fine root biomass.

### *Basal area of overstorey spruce stand*

To provide an easy-to-measure proxy for overstorey competition intensity, we used the basal area of the overstorey spruce trees within a circle of 10 m radius around every root sample point. A 10 m radius appeared to be appropriate according to the results of spruce fine root distribution studies of Ammer and Wagner (2005), Ammer (2000), and Bolte and Villanueva (2006) as they found a maximum root-spread distance of 10 m for a tree 60 cm in dbh.

### *Light availability*

To quantify light availability, we took a hemispherical photograph just above the uppermost leaves of every sampled sapling in mid-summer 2007 with a Nikon digital camera with fisheye lens and a self-leveling mount. Photographs were processed with the Winscanopy software (Regents Instruments Inc., Sainte-Foy, Quebec 2003). As a

measure of light intensity, we used the total site factor (TSF) in percent of above canopy light, which is based on 40% direct and 60% diffuse radiation, specific to the region of our sites (Wagner 1996).

### *Soil water potential*

Soil water potential was measured weekly during the second growing season after trenching (2008) from end of May till end of September, using 138 mechanical tensiometers at a depth of 30 cm mineral soil. On each of the six harvest treatment plots, 23 tensiometers were installed, 12 inside the trenched plots (=2 per very plot) and 11 in control plots (on five plots 2 and on one plot 1 tensiometer). Unfortunately, more tensiometers were not available, and we had to accept this slightly biased distribution. During the measurement period, only very few tensiometers temporarily dropped out when soil water potential fell below  $-800$  hPa.

### *Foliar nutrient content*

Between August 13–20, 2007 and 2008, we sampled 7–9 beech leaves and 100–150 Douglas fir needles of every sample sapling to determine foliar chemical content. The leaves/needles were randomly chosen from the last terminal shoot. Whenever the amount of leaves/needles did not suffice, we completed it with leaves/needles of current year branches at the top of the crown. The sampled foliage was of course also included in total leaf mass determination. Foliar and fine root nitrogen and carbon ( $\text{N mg g}^{-1}$ ,  $\text{C mg g}^{-1}$ ) concentrations were measured with an elemental analyzer (Model 1500, Carbo Erba, Italy), foliar K, Mg, and Ca concentrations ( $\text{mg g}^{-1}$ ) photometrically with a flame atomic absorption spectrometer (SpectrAA 300, Varian Inc., USA), and foliar P concentration colorimetrically with the continuous-flow method (Skalar Inc., The Netherlands).

### *Growth and biomass measurements*

All 384 sample saplings were manually excavated and collected from end of September until mid of October, half of them in 2007 and half in 2008, and divided into leaves/needles, branches, stems, fine and coarse roots. For every sapling, the following data were recorded: total stem length, length of the last annual terminal shoot, and diameter at 1 cm above ground, all to the nearest millimeter. A stem disk was taken from 1 cm above ground for measuring the width of the last annual rings in two perpendicular directions. For further analyses, arithmetic means of the two measurements were used.

Wood components (branches, stems, and roots) were dried at 65°C for 5 days and non-wood components (leaves/needles) for 3 days, and all weighed to the nearest 0.1 g.

#### *Fine root measurements and parameters*

Fine roots (diameter < 2 mm) of sampled saplings and of overstorey spruce trees (extracted with soil cores) were separated from coarse roots, washed, and sorted according to vitality (live, dead) using the criteria of Murach (1984). Only live fine roots were included in the following analyses. After scanning, they were processed with WinRHIZO (Regents Instruments Inc., Quebec, Canada) to obtain fine root length and fine root surface area. Finally, roots were dried and weighed. Based on these measures, specific root length (SRL, ratio of fine root length to dry weight,  $\text{m g}^{-1}$ ) and specific root area (SRA, ratio of fine root area to dry weight,  $\text{cm}^2 \text{g}^{-1}$ ) were determined.

#### Data analysis

Within each of the harvest treatment plots (TCN, TCO, and SCN), differences between trenched and control plots in sapling dimensions (length, diameter) and light availability at the start of the trenching experiment were tested using ANOVA. Also, differences between harvest treatment plots (TCN, SCN, TCO) in light availability and basal area of overstorey spruces, differences between trenched and control plots of foliar nutrient content, fine root nitrogen content, soil water potential with trenching as factor, per year (2007, 2008), and plot (TCN, TCO, and SCN) were tested using ANOVA. As prerequisites for ANOVA, normality of residuals was assessed with the Kolmogorov–Smirnov test and homoscedasticity with the Levene test. In case the ANOVA yielded a significant treatment effect, we examined the differences between mean values by Scheffé post hoc test. Differences of fine root biomass of overstorey spruce trees between harvest treatment plots were tested with the non-parametric Mann–Whitney  $U$  test as the data did not comply with the requirements of parametric test methods. Almost all collected parameters (length and diameter growth, biomass distribution in % of total plant biomass for all compartments (stem, branches, root, and leaves/needles), shoot-to-root ratio, specific fine root length, and specific fine root area) were fitted to a general linear model with light availability (TSF, %) and two dummy variables (site with  $S = -1$  for Otterbach and  $S = 1$  for Neuhaus; treatment with  $T = 1$  for trench and  $T = -1$  for control) as explanatory variables. Also, annual length increment 2008 was regressed by soil water potential and light availability or by foliar nitrogen and phosphorus content and light availability using a general linear model.

All model parameters were estimated using least squares methods.

All data analyses were performed using Statistica 9.1 (StatSoft 2005, Inc., USA).

## Results

### General information about light availability and intensity of overstorey Norway spruce competition

The sample saplings grew under different light regimes, varying significantly from relatively dark target diameter plots with mean TSF values of 19.4% at Neuhaus (TCN) and 24.8% at Otterbach (TCO) to the brighter strip cutting plots at Neuhaus (SCN) with 49.8% (Table 1). The TSF values were inversely linked with the mean basal area of overstorey spruce trees within a 10-m-radius circle around each sample sapling and with the mean fine root biomass of overstorey spruce trees in the top 30-cm mineral soil. The highest basal area ( $52.8 \text{ m}^2 \text{ ha}^{-1}$ ) and the highest fine root biomass ( $184 \text{ g m}^{-2}$ ) were met at the darkest target diameter cutting plots at Neuhaus, and the highest light level at Neuhaus strip cutting plot corresponded to lowest basal area ( $33.4 \text{ m}^2 \text{ ha}^{-1}$ ) and fine root biomass ( $136 \text{ g m}^{-2}$ ) (Table 1).

Before the start of the trenching experiment, no significant differences in diameter and length of the sample saplings could be detected between trenched and control plots within one harvest treatment plot (TCN, SCN, TCO). Furthermore, the sample saplings on trenched and control plots grew under well comparable light conditions without significant differences between mean values within the harvest treatment plots (Table 2).

### Effect of trenching on soil moisture

As expected, we found in trenched plots significantly higher mean water potentials (from  $-92 \text{ hPa}$  on TCN to  $-125 \text{ hPa}$  on SCN, with an intermediate value of  $-102$  on TCO) than on control plots that exhibited on average about 300 (TCO) and 500 hPa (TCN and SCN) lower values. This pattern was independent of the underplanted tree species. Control plots on target diameter plots at Otterbach exceeded the respective plots at Neuhaus on average significantly by about 200 hPa what corresponded to the above-mentioned higher precipitation at Otterbach during the growing season 2008. There was no significant difference on trenched plots, neither between harvest plots nor between sites or tree species. The oscillation range during the measurement period was more expanded in control plots (Fig. 1).

**Table 1** Light availability in the understorey, basal area, and live fine root biomass of Norway spruce overstorey, as mean/median values for harvest treatment plots

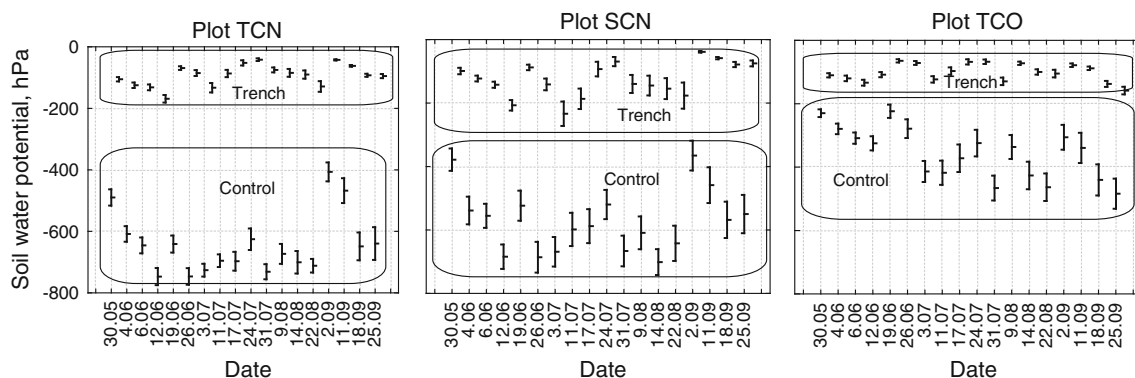
Attribute	Target diameter cutting at Neuhaus (TCN)	Strip cutting at Neuhaus (SCN)	Target diameter cutting at Otterbach (TCO)
Mean light availability (TSF %) (with min–max in brackets)	19.4 (14–29)a	49.8 (29–69)b	24.8 (15–37)ab
Overstorey mean basal area ( $\text{m}^2 \text{ha}^{-1}$ ) (with min–max in brackets)	52.8 (27–76)a	33.4 (5–61)b	43.9 (22–72)ab
Live fine root biomass of overstorey Norway spruces ( $\text{g m}^{-2}$ ) (median, with second and third quartile in brackets)	184 (116–260)a	136 (86–209)b	145 (86–224)ab

Values with the same letter denote non-significant differences between harvest treatment plots (ANOVA, Scheffé *post hoc* test and Mann-Whitney *U* test,  $P > 0.05$ )

**Table 2** Diameter and length of the saplings in autumn 2006 before the start of the trenching experiment in spring 2007, and light availability measured in summer 2007, per plot and treatment

Parameter	Species	TCN		SCN		TCO	
		Control	Trench	Control	Trench	Control	Trench
Diameter 2006, mm	Beech	8.7 (2.2)a	8.9 (1.6)a	12.4 (2.7)a	12.5 (2.6)a	8.0 (1.7)a	7.6 (1.7)a
	Douglas fir	9.0 (2.7)a	9.5 (2.9)a	16.2 (3.9)a	16.3 (4.1)a	11.3 (3.1)a	12.0 (3.0)a
Length 2006, cm	Beech	49.5 (13.7)a	50.9 (11.3)a	75.8 (20.4)a	71.4 (22.1)a	45.5 (10.7)a	52.1 (10.8)a
	Douglas fir	64.7 (15.9)a	65.9 (20.2)a	85.9 (19.3)a	93.7 (25.3)a	83.9 (20.2)a	92.5 (25.8)a
Light availability (TSF %)		19.8 (2.9)a	18.9 (1.8)a	49.3 (11.2)a	50.4 (11.5)a	25.4 (4.4)a	24.2 (4.8)a

Given are mean values with standard deviation in brackets. Values with the same letter denote non-significant differences between control and trenched plots (ANOVA, Tukey HSD *post hoc* test,  $P > 0.05$ )

**Fig. 1** Mean soil water potentials ( $\pm$ SE) for trenched and control plots within the three harvest treatment plots (TCN, TCO and SCN), measured with tensiometers from May 30, 2008 to September 25, 2008

### Effect of trenching on foliar nutrient content and on fine root nitrogen content

With very few exceptions—most notably the lower beech foliar Ca content—all our nutrient content values of control plots lay within the range of normal conditions (as given by Gussone and Reemtsma 1982 and van den Burg 1985) or exceeded them. Thus, the nutrient supply at our sites matched quite well the demands of beech and Douglas fir saplings. Regarding the effect of trenching, beech foliar nitrogen content showed little response, only on the strip

cutting variant (SCN) trenching led to a significantly higher nitrogen content in 2008 (Table 3). Douglas fir foliar nitrogen content was considerably more responsive. Saplings on trenched plots exhibited in all cases but one (TCO in 2007) higher nitrogen concentrations, most of them significant. Besides nitrogen, foliar content of other main nutritional elements was raised by trenching (Table 3), and significantly in following cases: (1) P on all three harvest plots in Douglas fir in 2008; (2) K on all three harvest plots in Douglas fir in 2008 and in beech on SCN and TCO in 2007, and on TCN and SCN in 2008; (3) Mg in beech on

**Table 3** Foliar and fine root nitrogen, foliar P, K, Mg, and Ca content response to trenching per species, year, plot, and treatment

	Species	Year	TCN		SCN		TCO		Normal value
			Control	Trench	Control	Trench	Control	Trench	
Foliar nitrogen content (mg g <sup>-1</sup> )	Beech	2007	24.0 (1.3)a	25.3 (0.6)a	21.2 (0.5)a	22.1 (0.5)a	22.9 (0.6)a	22.9 (0.5)a	20–22
		2008	24.4 (0.5)a	25.1 (0.2)a	22.4 (0.3)a	24.2 (0.3)b	23.1 (0.3)a	22.3 (0.5)a	
	Douglas fir	2007	15.8 (0.4)a	17.8 (0.4)b	18.8 (0.7)a	20.7 (0.7)a	20.3 (0.6)a	19.9 (0.3)a	14.1
		2008	16.5 (0.4)a	19.5 (0.4)b	16.3 (0.5)a	20.4 (0.3)b	18.1 (0.4)a	19.9 (0.5)b	
Fine root nitrogen content, (mg g <sup>-1</sup> )	Beech	2008	9.0 (0.3)a	11.1 (0.3)b	8.1 (0.1)a	9.0 (0.2)b	9.6 (0.2)a	10.3 (0.3)a	Not available
	Douglas fir	2008	8.1 (0.2)a	10.1 (0.2)b	7.2 (0.3)a	9.9 (0.2)b	8.0 (0.2)a	8.8 (0.2)b	
Foliar P content, mg g <sup>-1</sup>	Beech	2007	1.52 (0.11)a	1.28 (0.04)a	1.49 (0.04)a	1.52 (0.04)a	1.31 (0.03)a	1.26 (0.02)a	1.2–2.2
		2008	1.13 (0.08)a	1.18 (0.02)a	1.45 (0.07)a	1.54 (0.02)a	1.27 (0.03)a	1.27 (0.04)a	
	Douglas fir	2007	1.44 (0.11)a	1.43 (0.11)a	1.75 (0.29)a	1.64 (0.19)a	0.41 (0.11)a	0.58 (0.17)a	1.2–3.1
		2008	1.34 (0.06)a	1.60 (0.03)b	1.29 (0.05)a	1.90 (0.06)b	1.26 (0.08)a	1.58 (0.07)b	
Foliar K content, mg g <sup>-1</sup>	Beech	2007	5.38 (0.17)a	5.47 (0.15)a	5.09 (0.14)a	5.75 (0.19)b	4.58 (0.17)a	5.57 (0.16)b	4.4–7.4
		2008	4.87 (0.27)a	6.04 (0.28)b	4.65 (0.12)a	5.94 (0.29)b	5.31 (0.07)a	5.08 (0.18)a	
	Douglas fir	2007	9.22 (0.65)a	8.63 (0.64)a	7.06 (0.47)a	7.39 (0.25)a	8.48 (0.53)a	9.08 (0.49)a	5.9–12.5
		2008	8.87 (0.32)a	10.97 (0.34)b	6.75 (0.36)a	8.61 (0.19)b	7.95 (0.69)a	9.62 (0.39)b	
Foliar Mg content, mg g <sup>-1</sup>	Beech	2007	2.64 (0.17)a	2.67 (0.18)a	1.55 (0.10)a	1.72 (0.15)a	1.68 (0.08)a	1.41 (0.03)b	1.3–2
		2008	2.77 (0.29)a	2.56 (0.22)a	2.06 (0.11)a	1.81 (0.13)a	1.54 (0.04)a	1.50 (0.06)a	
	Douglas fir	2007	1.284 (0.05)a	1.647 (0.16)b	1.365 (0.07)a	1.429 (0.06)a	1.134 (0.06)a	1.185 (0.05)a	0.7–1.5
		2008	1.455 (0.06)a	1.944 (0.07)b	1.281 (0.08)a	1.332 (0.04)a	1.082 (0.07)a	1.292 (0.05)b	
Foliar Ca content, mg g <sup>-1</sup>	Beech	2007	7.37 (0.56)a	8.53 (0.41)a	6.25 (0.38)a	6.84 (0.34)a	9.04 (0.29)a	9.47 (0.27)a	11.2–16.3
		2008	7.84 (0.42)a	8.17 (0.48)a	8.39 (0.20)a	7.68 (0.39)a	8.33 (0.54)a	8.61 (0.28)a	
	Douglas fir	2007	2.25 (0.22)a	2.85 (0.22)b	2.80 (0.19)a	2.96 (0.13)a	3.01 (0.22)a	4.23 (0.24)b	2.6–4.4
		2008	2.78 (0.09)a	4.41 (0.22)b	2.54 (0.18)a	3.83 (0.11)b	2.84 (0.27)a	4.71 (0.29)b	

Significant differences between control and trenched plots are depicted by different letters (ANOVA, Scheffé *post hoc* test,  $P > 0.05$ ), standard error of mean in brackets. Normal values of foliar nutrient concentrations were taken for beech from van den Burg (1985) and for Douglas fir from Gussone and Reemtsma (1982)

TCO in 2007 and in Douglas fir on TCN in both years and on TCO in 2008; (4) Ca in Douglas fir on all three harvest plots in 2008 and on TCN and TCO in 2007. Fine root nitrogen content could only be determined in 2008 (Table 3). Douglas fir possessed on all three harvest plots significantly higher concentrations on trenched than on control plots, beech only at the Neuhaus site.

#### Diameter and length growth responses to trenching

As there were no significant differences between the two sites the following results are based on a merged data set. In the first year (2007), no significant influence of trenching on both growth parameters was detectable (Table 4). Light availability alone was the decisive factor, which explained 64% of the total variation in diameter growth and 33–35% in length growth. In the second year, length growth of both species and diameter growth of Douglas fir were significantly influenced by the interaction between trenching and light, explaining 61–64% of the total variation in length

growth in both species and 57% of the total variation in Douglas fir diameter growth (Table 4). Figure 2 illustrates the effects of light and trenching on length and diameter increment in 2008. The light level at which saplings on trenched plots started to significantly surpass those on control plots was determined as the lowest TSF value where the 95% confidence intervals of the trenched and control curves ceased to overlap. In length growth, Douglas fir reached this point at 16% TSF, beech not until 22% TSF. At the maximum light availability of approximately 70% TSF both species reached their maximum length increment on trenched plots (beech 57 cm, Douglas fir 81 cm). On control plots, length increment was considerably less, in beech by 36 cm and in Douglas fir by 47 cm. A significant higher diameter increment of Douglas fir saplings as a trenching effect started at ca. 26% TSF.

In three further regression analyses, we omitted the variable trenching and replaced it by soil water potential, foliar nitrogen, and phosphor content, each with light as a second explanatory variable (Table 5). An improvement in

**Table 4** Results of the regression analyses of diameter and length increment of Douglas fir and beech saplings as a function of light availability (L), treatment, and site (general linear model with treatment (T) and site (S) as dummy variables (T = 1 trench and T = -1 control; S = 1 Neuhaus and S = -1 Otterbach)

Variable	Species	Year	Model	Coefficients						
				Estimate	SE	df	t value	P value	R <sup>2</sup>	
Diameter increment	Beech	2007	(Intercept)	0.41	0.21	92	1.99	<0.05	0.64	
			L	0.08	0.01	92	13.23	<0.0001		
		2008	(Intercept)	0.51	0.28	92	1.75	0.056	0.65	
			L	0.10	0.01	92	12.58	<0.0001		
	Douglas fir	2007	(Intercept)	-2.27	0.65	93	-3.48	<0.0001	0.64	
			L	0.25	0.02	93	12.98	<0.0001		
		2008	(Intercept)	0.34	0.69	91	0.49	0.623	0.57	
			L	0.20	0.02	91	9.52	<0.0001		
Length increment	Beech	2007	(Intercept)	9.21	2.38	92	3.86	<0.0001	0.33	
			L	0.45	0.06	92	6.71	<0.001		
		2008	(Intercept)	8.55	1.77	92	4.81	<0.0001	0.64	
			L	0.51	0.05	92	9.81	<0.0001		
	Douglas fir	2007	(Intercept)	4.54	3.97	93	3.97	0.294	0.35	
			L	0.81	0.11	93	0.11	<0.0001		
		2008	(Intercept)	11.82	3.18	91	3.75	<0.0001	0.61	
			L	0.75	0.09	91	7.81	<0.0001		
				L × T	0.30	0.04	91	7.94	<0.0001	

The factor site was not significant and is not shown in the table

soil water or foliar nitrogen content or phosphor content led to significant increases in length growth in 2008 in both species, but more pronounced in Douglas fir. In every case, these effects significantly interacted with light. The combined effects explained at least 44% of the total variation in length growth (foliar nitrogen effect on beech) and at most 64% (foliar nitrogen effect on Douglas fir).

#### Effect of trenching on biomass distribution

As we also for the biomass distribution variables did not find significant differences between the two sites, we could again merge the data. Regression analyses with light and trenching as explanatory variables rendered in most cases significant results, but they could only explain a small fraction of the total variation of the response variables (Table 6). The shoot-to-root biomass ratio in 2007 increased significantly only with light, whereas in 2008 a significant effect of trenching alone or in interaction with light appeared (Fig. 3). An increasing shoot-to-root ratio means that relatively less biomass has been allocated to roots, what in our case could be explained by increasing light availability or the exclusion of overstorey root competition by trenching. Generally, beech invested relatively more biomass into roots than Douglas fir (s. intercept

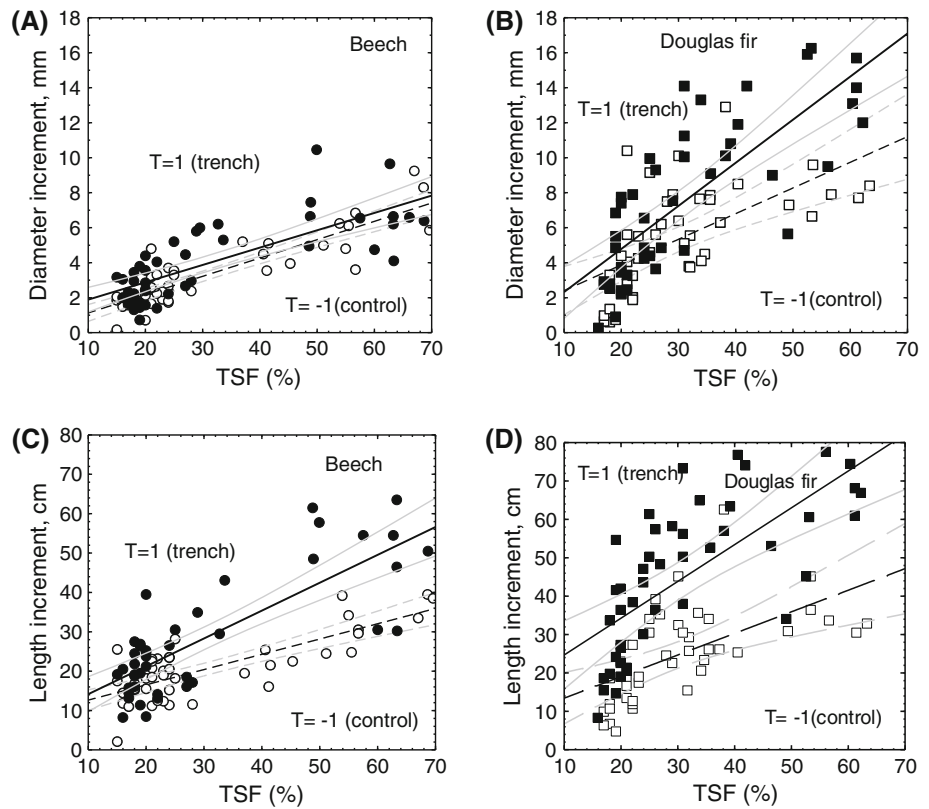
values in Table 6 for % roots in 2008: beech 32.8% vs. Douglas fir 20.08%). All other plant compartments (stem, branches, and leaves/needles) did not show any noteworthy change in biomass partitioning induced by trenching in both study years (Table 6).

#### Effect of trenching on fine root characteristics

In both species, the two investigated fine root parameters—specific fine root length (SRL) and specific fine root area (SRA)—declined with increasing light (Table 7; Fig. 4). Trenching interacted significantly with light in both species and in both years. It led to higher values in Douglas fir across the whole light gradient in both years, whereas in beech the superiority of the trenched variants was highest under low light and gradually decreased with increasing light until it became negative from more than 40–50% TSF. Douglas fir consistently had smaller specific fine root length values than beech what points to thicker Douglas fir roots and finer beech roots (s. intercept values for SRL in 2008 in Table 7 with 3.77 m g<sup>-1</sup> for Douglas fir vs. 4.97 m g<sup>-1</sup> for beech). In other words, beech can use an equal amount of root biomass for a greater total fine root length and more intensive soil exploitation than Douglas fir.



**Fig. 2** Annual diameter (a, b) and length increment (c, d) as a function of light availability (in % TSF) and treatment (T = 1 trench, full lines and filled symbols; T = -1 control, broken lines, and open symbols) for beech (a, c) and Douglas fir (b, d). The graphs show diameter and length increment in the second growth period after trenching (2008). 95% confidence intervals are shown



**Table 5** Results of the regression analyses of 2008 length increment of Douglas fir and beech seedlings as a function of light availability (L) and soil water potential (W) and as a function of light availability and foliar nitrogen (N) or foliar phosphor (P) concentration (general linear model)

Variable	Species	Model	Coefficients					
			Estimate	SE	df	t value	P value	R <sup>2</sup>
Light (L), Water potential (W)								
Length increment 2008	Beech	(Intercept)	8.48	2.08	68	4.06	<0.0001	0.62
		L	0.71	0.07	68	10.56	<0.0001	
		L × W	0.00064	0.00019	68	5.37	<0.0001	
	Douglas fir	(Intercept)	11.23	3.87	64	2.89	<0.01	
		L	1.17	0.13	64	8.68	<0.0001	
		L × W	0.00119	0.00017	64	6.63	<0.0001	
Light (L), Foliar nitrogen (N)								
Length increment 2008	Beech	(Intercept)	7.54	2.30	91	3.27	<0.0001	0.44
		L × N	0.023	0.003	91	7.96	<0.0001	
		Douglas fir	(Intercept)	-38.16	8.92	89	-4.28	
	N		2.56	0.50	89	5.08	<0.0001	
	L × N		0.04	0.01	89	8.97	<0.0001	
	Light (L), Foliar P (P)							
Length increment 2008	Beech	(Intercept)	-10.68	8.96	89	-1.19	0.236	0.54
		P	20.17	8.32	89	2.42	<0.05	
		L × P	0.21	0.06	89	3.51	<0.0001	
	Douglas fir	(Intercept)	-4.76	3.66	89	-0.71	0.473	
		P	13.81	5.26	89	2.62	<0.05	
		L × P	0.41	0.06	89	6.33	<0.0001	

**Table 6** Results of the regression analyses of shoot-to-root ratio and biomass distribution in % of total plant biomass, as a function of trenching, site and light availability, for the compartments: stem, branches, roots, and leaves/needles of Douglas fir and beech seedlings (general linear model with treatment (T) and site (S) as dummy variables)

Variable	Species	Year	Model	Coefficients							
				Estimate	SE	df	t value	P value	R <sup>2</sup>		
Shoot to root biomass ratio	Beech	2007	(Intercept)	1.37	0.11	93	13.48	<0.001	0.08		
			L	0.008	0.003	93	2.88	<0.001			
		2008	(Intercept)	2.14	0.14	89	14.67	<0.0001	0.15		
			L	0.01	0.04	89	2.56	<0.05			
	Douglas fir	2007	(Intercept)	2.9	0.22	93	12.57	<0.001	0.09		
			L	0.02	0.006	93	2.93	<0.01			
		2008	(Intercept)	4.08	0.09	89	46.78	<0.0001	0.08		
			T	0.24	0.09	89	2.78	<0.05			
% Stem	Beech	2007	NS						–		
		2008	(Intercept)	29.99	1.38	91	21.68	<0.0001	0.11		
			L	0.12	0.04	91	3.06	<0.001			
	Douglas fir	2007	(Intercept)	31.13	0.66	93	47.11	<0.0001	0.09		
			L	–0.04	0.02	93	2.03	<0.05			
		2008	NS						–		
% Branches	Beech	2007	NS						–		
		2008	NS						–		
		Douglas fir	2007	(Intercept)	17.11	1.25	93	13.58	<0.0001	0.15	
	L			0.14	0.04	93	3.89	<0.0001			
	2008		(Intercept)	19.52	1.32	88	14.69	<0.0001	0.09		
	L	0.11	0.04	88	2.44	<0.05					
% Roots	Beech	2007	(Intercept)	42.52	1.53	93	27.61	<0.0001	0.06		
			L	–0.11	0.04	93	–2.41	<0.05			
		2008	(Intercept)	32.83	1.27	89	25.72	<0.0001	0.14		
			L	–0.09	0.04	89	–2.55	<0.05			
	Douglas fir	2007	(Intercept)	27.38	1.30	93	21.00	<0.0001	0.10		
			L	–0.11	0.04	93	–3.07	<0.05			
		2008	(Intercept)	20.08	0.40	88	50.43	<0.0001	0.09		
			T	–0.98	0.39	88	–2.47	<0.05			
		% Leaves/needles	Beech	2007	(Intercept)	10.86	0.47	93	23.13	<0.0001	0.16
					L	0.05	0.01	93	4.11	<0.0001	
2008	NS								–		
Douglas fir	2007		NS						–		
	2008		NS						–		

The factor site was not significant and is not shown in the table

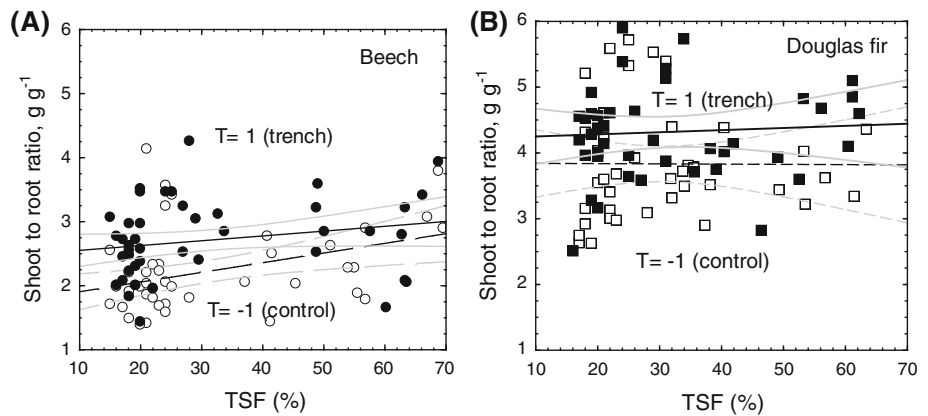
## Discussion

### Effect of trenching on soil water and nutrient content

The exclusion of overstorey spruce tree roots had a sizeable effect on soil moisture. Water potential 30 cm below the humus layer was 3.5- to 6.8-fold greater on trenched compared to control plots. The least increase was found on target diameter cutting plots at Otterbach,

the greatest on the same cutting treatment at Neuhaus (Fig. 1). Since the fine root biomass of Norway spruce overstorey was not significantly different between the two diameter target cutting plots (Table 1), we concluded that the smaller effect of the trenching treatment at Otterbach was caused by higher precipitation during the growing season 2008 with 375 mm of rain, whereas at Neuhaus only 216 mm fell. This complies with the statement of Grubb (1994) and Coomes and Grubb (2000) that root

**Fig. 3** Shoot-to-root biomass ratio of beech (a) and Douglas fir saplings (b) as a function of light availability (in % TSF) and treatment (T = 1 trench, full lines, and filled symbols; T = -1 control, broken lines, and open symbols) for the second growth period after trenching (2008). 95% confidence intervals are shown



**Table 7** Results of the regression analyses of specific fine root area (SRA) and specific fine root length (SRL) as a function of trenching, site, and light availability for Douglas fir and beech seedlings (general linear model with treatment (T) and site (S) as dummy variables)

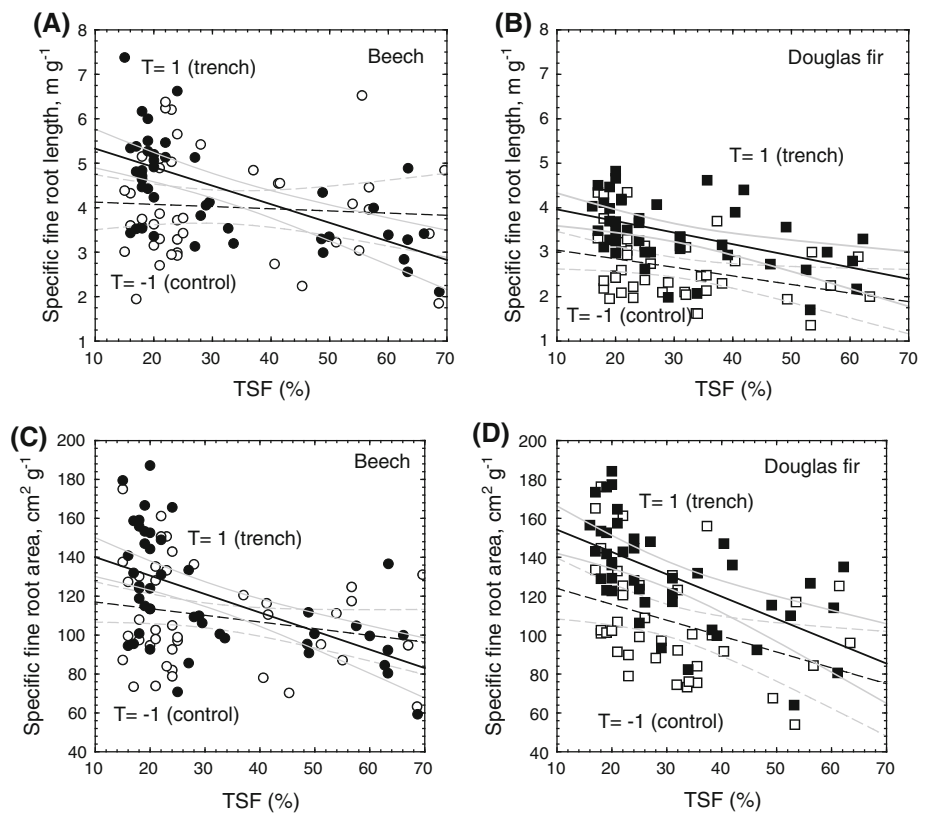
Variable	Species	Year	Model	Coefficients					
				Estimate	SE	df	t value	P value	R <sup>2</sup>
SRA, cm <sup>2</sup> g <sup>-1</sup>	Beech	2007	(Intercept)	196.57	10.56	90	18.60	<0.0001	0.15
			T	32.65	10.56	90	3.09	<0.0001	
			L	-0.69	0.31	90	-2.29	<0.01	
		L × T	-0.86	0.31	90	-2.86	<0.05		
		2008	(Intercept)	133.51	6.03	88	22.13	<0.0001	
			T	16.11	6.03	88	2.67	<0.0001	
	L		-0.57	0.17	88	-3.36	<0.01		
	Douglas fir	2007	(Intercept)	147.53	5.91	92	24.94	<0.0001	0.11
			L	-0.45	0.17	92	-2.66	<0.01	
			L × T	0.14	0.07	92	2.09	<0.05	
		2008	(Intercept)	150.38	6.83	89	22.01	<0.0001	
			L	-1.03	0.21	89	-5.01	<0.0001	
L × T			0.29	0.08	89	3.65	<0.0001		
SRL, m g <sup>-1</sup>	Beech	2007	(Intercept)	6.07	0.37	90	16.20	<0.0001	0.15
			T	1.11	0.37	90	2.96	<0.0001	
			L	-0.025	0.01	90	-2.38	<0.05	
		L × T	-0.026	0.01	90	-2.48	<0.05		
		2008	(Intercept)	4.97	0.27	88	18.45	<0.001	
			T	0.64	0.27	88	2.36	<0.05	
	L		-0.024	0.007	88	-3.16	<0.001		
	Douglas fir	2007	(Intercept)	3.69	0.17	92	21.14	<0.0001	0.13
			L	-0.014	0.005	92	-2.84	<0.01	
			L × T	0.004	0.002	92	2.29	<0.05	
		2008	(Intercept)	3.77	0.194	89	19.41	<0.0001	
			L	-0.024	0.006	89	-4.11	<0.0001	
L × T			0.010	0.002	89	4.41	<0.0001		

The factor site was not significant and is not shown in the table

competition for belowground resources is more considerable on drier sites. Also, the finding that roots of overstorey trees can substantially diminish soil moisture

corresponds to other investigations (Hauskeller-Bullerjahn 1997; Ammer 2002; Lindth et al. 2003; Devine and Harrington 2008).

**Fig. 4** Specific fine root length (SRL) (a, b) and specific fine root area (SRA) (c, d) of beech (a, c) and Douglas fir (b, d) saplings as a function of light availability (in % TSF) and treatment (T = 1 trench, full lines, and filled symbols; T = -1 control, broken lines, and open symbols) in the second growth period after trenching (2008). 95% confidence intervals are shown



Trenching of roots from overstorey trees did not only lead to higher soil water supply, but also in some investigations into higher nutrient availability (Riegel et al. 1992; Chapin et al. 1994; Hauskeller-Bullerjahn 1997). This could be explained partly as a consequence of the improved soil moisture supply alone (Coomes and Grubb 2000). But in addition or even paramount, the disruption of nutrient uptake by cutting the overstorey roots, and thereby excluding the main competitors, certainly had a direct effect on the improvement in nutrient supply for the underplanted saplings. On the other hand, an extra supply from the decomposition of cut fine roots can most probably be eliminated as an essential contribution according to other studies (Bauhus 1994; Coomes and Grubb 2000). Fine root decomposition obviously is too slow to play an important part in improving nutrient supply of the understorey within a couple of years.

In our study, foliar concentration of major nutritional elements served as an indicator for nutrient supply of the underplanted saplings. With only few exceptions, the foliar content of the major nutritional elements of both species on control plots lay within the normal range according to Gussone and Reemtsma (1982) and van den Burg (1985). On trenched plots, Douglas fir could take up considerably higher amounts nutrients what is indicated by significantly higher foliar contents of almost all major nutrients (N, P,

K, and Ca). Thus, trenching contributed to an amendment of soil nutrient supply (Table 3). It is remarkable that Douglas fir achieved these higher concentrations together with a superior growth compared to beech. Insofar, the increased nutrient uptake has overridden a possible dilution effect of enhanced growth.

The observed species-specific responsiveness probably is influenced by different characteristics of beech and Douglas fir. Coomes and Grubb (2000) predicted that generally the most nutrient responsive species are at the same time most responsive to increasing irradiance and possess higher potential growth rates. We demonstrated in a companion study (Petritan et al. 2010) as well as in the present study (Fig. 2) that Douglas fir accelerated growth under brighter light conditions definitely more than beech. Also, it is well known as a species of higher growth potential (Röhrig et al. 2006).

#### Growth and biomass partitioning response to trenching

The exclusion of overstorey root competition led to augmented annual diameter and length growth of underplanted saplings (Fig. 2). The enhancement was particularly noticeable in the second growing season (2008) after trenching, while in 2007 only a non-significant trend appeared. A possible explanation could be the considerably

lower amount of precipitation during this growing season, since root competition has a higher impact on understorey seedlings growth under drier conditions (Coomes and Grubb 2000). Also Devine and Harrington (2008) found a significantly increased height increment as a response to the exclusion of root competition only in a year with less growing season precipitation. In addition, the stronger response in the second year after trenching could be explained by a “carry-over effect” (Löf and Welander 2000) since growth conditions of the previous year can affect current year increment.

A greater growth response in diameter and length of both our species under higher light availability (Fig. 2) supports our expectation that the effect of trenching should be stronger under higher light conditions. Both species showed a greater length growth due to trenching with increasing light availability (Fig. 2) what matches results of Lüpke and Hauskeller-Bullerjahn (2004) with European beech and sessile oak saplings. Also, it corroborates the hypothesis that Douglas fir requires less light under good soil moisture supply to reach a given growth value (Atzet and Waring 1970; Marshall 1986) and contradicts the finding of Carter and Klinka (1992) stating the opposite. In addition, greenhouse studies have shown that the ability of tree seedlings to respond to increased soil resources diminish with decreasing light level (Canham et al. 1996; Walters and Reich 2000). Also, Petritan et al. (2007) found on a better water-supplied site a higher length growth only above a given light availability (>17% of above canopy light with beech, ash and maple saplings). Drever and Lertzman (2001) observed in Douglas fir saplings a significantly greater length growth on fresh and rich sites compared to dry rich and dry poor sites only above 43% light, and for diameter growth above 60%. They concluded that until a given light level, light is the main determinant of growth rate and moisture and nutrient regime play a secondary role. In their investigation with Douglas fir saplings, diameter increment was not as responsive to differences in site quality along a light gradient as height increment. In agreement with those observations, we found under limiting light conditions (at the target diameter cutting plots) only for length growth a significant response to trenching and not for diameter growth. This is in accordance with the general hierarchy of photosynthate allocation, which under increasing shortage of resources attributes the least priority to diameter growth (Oliver and Larson 1996).

A lower seedling growth on soils with poor nutrient and water supply is partly explained as a result of lower biomass allocation to leaves due to higher root allocation (Lambert and Poorter 1992; Valladares and Niinemets 2008). However, in our study no significant effect of trenching on foliar biomass allocation could be detected.

But root biomass allocation was lower in trenched variants than in controls what in our case is demonstrated by higher shoot-to-root ratios. In Douglas fir, this effect could significantly be explained by trenching alone, whereas in beech it was caused by an interaction of trenching with light availability (Fig. 3; Table 6). Similarly, Chan et al. (2003) found that under limited soil water supply Douglas fir allocated more mass to roots. Our results for further biomass distribution variables are partially in agreement with those of Machado et al. (2003) who showed that below-ground resources limited seedling growth in forest understoreys, but did not alter biomass distribution in any species.

Biomass investment in fine roots is usually large under infertile or dry conditions (Persson 1983; Vanninen and Mäkelä 1999). But fine root biomass alone may not accurately indicate the capacity of roots for water and nutrient uptake (Lehmann 2003). According to Ostonen et al. (2007), trees develop two fine root strategies to raise their nutrient uptake efficiency and adapt to different soil conditions: either by enhancing their carbon investment to increase both, fine root biomass and specific root length (SRL), or by building fine roots with higher specific root area (SRA). These two indicators of fine root morphological adaptations, SRA and SRL, have often been used to describe the variation in soil water and nutrient regimes and characterize soil resources exploitation efficiency (Bauhus and Messier 1999). Ostonen et al. (1999) found high SRA and SRL on high fertility sites and Löhmus et al. (1989) considered SRA as an ecomorphological index of optimal soil conditions. Further investigations showed these parameters being very responsive to water regime modifications: mainly specific fine root length (SRL) was reduced under drier conditions (Van Hees 1997; Ostonen et al. 2007; Meier and Leuschner 2008; Brunner et al. 2009). Similarly, SRA tends to decrease in response to drought (Aspelmeier and Leuschner 2006; Meier and Leuschner 2008). In our study, both fine root morphological parameters increased with improved soil water and nutrient supply caused by trenching in both species, yet significantly only under lower light conditions and concurrently higher root competition of overstorey trees. In almost all cases, SRA and SRL possessed higher values in 2007 compared to 2008 what reflects a better soil water supply due to higher precipitation in 2007 (Table 7).

#### Interspecific differences in growth response

The intensity of saplings' growth response to the improvement in water and nutrient supply after removal of overstorey root competition was species specific. Our prediction that less shade-tolerant Douglas fir will react to

trenching already at a lower light level and stronger in growth than beech could be confirmed. In 2008, Douglas fir saplings showed a greater annual length growth after root trenching (Fig. 2d; Table 4) along the entire light gradient, whereas beech saplings did this only in higher light conditions (Fig. 2c). A greater annual diameter increment was singly observed in Douglas fir under higher light availability (i.e. on strip cutting plot) (Fig. 2b). This is consistent with other studies on beech saplings that confirmed a lower sensitivity against root competition from overstorey beech trees than for less shade-tolerant species like sessile oak (Lüpke and Hauskeller-Bullerjahn 2004) or common ash (Wagner 1999). Under limiting light conditions, diameter increment of Douglas fir saplings in our study responded to trenching not as responsive as length increment. This agrees with a frequently observed characteristic of many less shade-tolerant species tending to invest preferentially into height growth rather than into lateral growth and by this increasing the chance to reach the forest canopy more quickly (Chen 1997; Chen and Klinka 1998; Petritan et al. 2009).

Our observation that beech needed a higher light level (22% TSF, in comparison with 16% for Douglas fir) to start with a positive length growth reaction to trenching (Fig. 2c, d) was in line with other results (Coomes and Grubb 2000; Lüpke and Hauskeller-Bullerjahn 2004). Accordingly, species differ in the minimum light level at which they react to soil resources enhancement, and a characteristic of shade-tolerant species seems to be a tendency to respond only above higher light levels than more light demanding species.

In our study, both species reduced their investment in root biomass (here expressed as an increased shoot-to-root ratio, Table 6) as a reaction to trenching in a similar way. The relative reduction of Douglas fir root biomass was accompanied by a slight increase in branch biomass, whereas the relative proportions of needle and stem biomass of both species were not significantly affected by trenching (Table 6). Specific fine root length (SRL) was substantially higher in beech saplings than in Douglas fir. Therefore, beech should be able to exploit larger soil volumes per unit fine root biomass. This morphological adaptation could be a possible explanation for the lower sensitivity of beech seedlings to overstorey root competition that was observed in our study and also in other investigations cited earlier.

Summarizing, our findings corroborate the assumption that growth of shade-intolerant species is more affected by limited resources than growth of shade-tolerant species what probably is a consequence of slower growth rates and/or high storage capacities of these latter species (Chapin 1980; Messier et al. 1999).

## Silvicultural conclusion

This study confirms the widespread notion of practical foresters that understorey light conditions are in most cases decisive for the success of regeneration measures beneath an overstorey canopy. But our study also shows that below-ground root competition of overstorey trees can additionally exert a sizeable influence on growth of the regeneration, particularly in dry growing seasons. This result might be valid for all less water-supplied sites, but a generalization of our results has to be verified by further studies. However, even with the actual knowledge, it seems reasonable to recommend a lower density of retained overstorey trees for regeneration measures under drier site conditions. Harvest systems like strip cutting, a sparse shelterwood or group selection with wider openings are more appropriate on these sites than a dense shelterwood or a weak target diameter cutting. In the face of climate change, this point certainly will get more importance.

We also showed that the response to the exclusion of overstorey root competition was species specific. Douglas fir as the less shade-tolerant species suffered more from below-ground competition than the shade-tolerant beech. Regeneration measures should pay attention to this different behavior. As an example, for establishing a mixed stand beneath a patchy overstorey the less sensitive species beech should be planted below the denser parts of the overstorey, while the more sensitive Douglas fir should be planted on the central parts of openings. This is not new in silvicultural practice, but the results of our trenching experiment put an additional weight on it.

In conclusion, we confirm the statement of Lüpke and Hauskeller-Bullerjahn (2004) that particularly for the development of mixed species stands the “understorey tolerance”—which includes also the below-ground competition of the old stand—would be more meaningful than the more widely used “shade tolerance” that includes light conditions only.

**Acknowledgments** We thank Ulrike Westphal, Martina Knaust, Michael Unger and Andreas Parth from the Department of Silviculture and Forest Ecology of the Temperate Zones of the University of Göttingen for their help with collecting the field data and performing the laboratory work, Uwe Klink and Hendrik Rumpf of the Northwest German Forest Research Station for helpful information about sites and for providing the precipitation data. We appreciate the permission given by the leader of Northwest German Forest Research Station, Prof. Dr. Hermann Spellmann, to conduct the study on the long-term logging system experiment. The funding of this study by Deutsche Forschungsgemeinschaft (DFG) under Lu 452/9-1 is gratefully acknowledged. Two anonymous reviewers gave valuable advice for improving the manuscript.

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