

Fine roots of overstory Norway spruce (*Picea abies*): distribution and influence on growth of underplanted beech (*Fagus sylvatica*) and Douglas-fir (*Pseudotsuga menziesii*) saplings

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Abstract

The horizontal and vertical distribution of live fine roots (diameter < 2 mm) of overstory Norway spruce [*Picea abies* (L.) Karst.] and their influence on diameter and height growth of underplanted beech (*Fagus sylvatica* L.) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) saplings were studied on experimental plots in the Solling Mountains (Germany).

The aims of this study were to investigate how overstory fine root density varies with stand density, and how it influences growth of the underplanted saplings to changes in belowground resources availability in connection with simultaneously changing light availability.

Most fine roots were concentrated in the humus layer (more than 45%) and in the top mineral soil (0-5 cm, about 15%). Fine root biomass increases with overstory basal area and decreases with rising distance from the nearest overstory tree, reaching about zero within ca. 8 m distance.

Over the whole two-year study period, light availability alone was the decisive factor for growth of the beech saplings (5 resp. 6 years of age) while growth of the Douglas-fir saplings in the first study year (6 years of age) was additionally affected by a shortage of belowground resources due to root competition in a season with less than average rainfall.

This species-specific response of underplanted saplings to changes in above and belowground resources is of silvicultural importance for the establishment of a mixed stand beneath a mature canopy: the more sensitive Douglas-fir should be planted on the central parts of openings with little or none belowground competition while the less sensitive beech can be placed below the denser parts of the overstory.

Key words: forest conversion; fine roots; above- and belowground competition; juvenile growth; shade tolerance.

Resumen

Raíces pequeñas del dosel del pinabete (*Picea abies*): distribución e influencia en el crecimiento de hayas (*Fagus sylvatica*) plantadas y brinzales de abetos de Douglas (*Pseudotsuga menziesii*)

Se estudia la distribución horizontal y vertical de las raíces finas (diámetro < 2 mm) vivas del dosel de pinabete y su influencia en el diámetro y el crecimiento en altura de hayas plantadas y en brinzales de abeto Douglas en parcelas experimentales en las montes de Solling (Alemania). Los objetivos de este estudio es analizar cómo la densidad de raíces finas del dosel varía con la densidad del rodal, y cómo influye en el crecimiento de los árboles jóvenes del subpiso debido a los cambios en la disponibilidad de recursos en el suelo, en relación con el cambio al mismo tiempo en la disponibilidad de luz.

Las raíces más finas se concentra en la capa de humus (más del 45%) y en la parte mineral superior del suelo (0-5 cm, aproximadamente el 15%). La biomasa de raíces finas aumenta con el área bisimétrica del dosel y disminuye con la distancia creciente al árbol más cercano del dosel, hasta llegar a cero dentro de ca. 8 m de distancia.

Durante el periodo de estudio de dos años, la disponibilidad de luz era el único factor decisivo para el crecimiento de los plantones de haya (5 resp. 6 años de edad) mientras que el crecimiento de las plántulas de pino de Douglas en el primer año de estudio (6 años de edad) se vio afectado adicionalmente por la escasez de recursos en el suelo debido a la competencia de las raíces en una temporada con una precipitación menor del promedio.

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Esta respuesta especie-específica de los árboles del subpiso a los cambios en los recursos por encima y por debajo del suelo es de importancia silvícola para la creación de una masa mixta bajo un dosel maduro: la especie más sensible, pino de Douglas, se debe plantar en las partes centrales de las aberturas con poca o ninguna competencia bajo tierra, mientras que el haya, menos sensible, se puede colocar debajo de las partes más densas del estrato superior.

Palabras clave: conversión de bosques; raíces finas; competencia; crecimiento juvenil; tolerancia a la sombra.

Introduction

As a consequence of the high susceptibility of pure Norway spruce [*Picea abies* (L.) Karst.] stands to abiotic and biotic stress factors (Spiecker *et al.*, 2004), the conversion into mixed stands has gained an increasing importance in Central Europe over the last decades (Lüpke *et al.*, 2004). For this purpose, beech (*Fagus sylvatica* L.) and other native or non-native species with high adaptive and productive capability such as Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] are often planted under the canopy of Norway spruce stands (Weihs and Klaene, 2000; Lüpke, 2004, 2009). Many forest managers prefer underplanting because of several advantages like frost protection, reduced competition of ground vegetation, continuing wood production of the canopy trees, and its similarity with regeneration processes in natural forests. But survival and growth of underplanted seedlings depend on the capacity of the species to grow under shade conditions. Beech as a shade tolerant species (Röhrig, 1967; Stancioiu and O'Hara, 2006; Petritan *et al.*, 2007, 2009, 2010) is well adapted to these conditions, while less shade tolerant species such as Douglas-fir could be put at a competitive disadvantage (Mailly and Kimmins, 1997; Petritan *et al.*, 2010).

Overstorey trees affect seedling growth as they control aboveground resources (mainly light) and simultaneously belowground resources by root competition (Wagner, 1999; Ammer, 2002). Whereas the effect of light interception has been widely studied, the influence on belowground resources remains poorly investigated although several studies described a strong belowground competition between overstorey and understorey vegetation for water and nutrients (Riegel *et al.*, 1992; Walters and Reich, 1997; Lindh *et al.*, 2003; Machado *et al.*, 2003).

Leuschner *et al.* (1998) found that horizontal and vertical distribution of root biomass controls the assimilation capacity of trees for water and nutrients, and that a higher root biomass of an old stand limits the soil resources availability for young trees. This was confirmed by an exhaustive literature review on root

competition (Coomes and Grubb, 2000) showing that the amount of fine roots of overstorey trees strongly influences the availability of belowground resources. In some studies, soil moisture content and fine root biomass were negatively correlated (Coomes and Grubb, 2000; Ammer and Wagner, 2002) what was corroborated by root trenching experiments demonstrating an improvement in both soil water and nutrient supply as an effect of overstorey tree root elimination (Riegel *et al.*, 1995; Devine and Harrington, 2008). Thus, fine root biomass of overstorey trees is considered an important determinant for seedling growth (Wagner, 1999; Ammer and Wagner, 2005). Accordingly, in a study about the relative influence of light and belowground resources on beech seedling growth under a mature Norway spruce canopy, Ammer *et al.* (2008) used the fine root biomass of overstorey trees as a surrogate for belowground resource availability. However, it is difficult and expensive to obtain reliable information on fine roots due to their enormous spatial variation within short distances (Clemensson-Lindell and Persson, 1995; Borken *et al.*, 2007). Some studies tried to avoid these difficulties by using easily measurable variables of aboveground parts of trees as estimators for fine root biomass: Ammer and Wagner (2002, 2005) assumed that fine root biomass of Norway spruce trees increases with the diameter at breast height and decreases with increasing distance from the trunk. Other authors stated that basal area is a good predictor of fine root biomass (Vanninen and Mäkela, 1999, for Scots pine stands; Finer *et al.*, 2007, for beech, Norway spruce and Scots pine; Bolte and Villanueva, 2006, for Norway spruce). However, in a dataset compiled from literature, Chen *et al.* (2004) showed that without a data stratification (*e.g.*, according to site quality) only a weak though statistically significant ($r^2 = 0.21$) relationship between basal area and fine root biomass could be described.

In a companion study (Petritan *et al.*, 2011) on the same site as in the present study we showed that the removal of Norway spruce overstorey root competition by trenching led to an amended soil water and nutrient supply, particularly in a dry growing season, and a better growth of underplanted beech and Douglas-fir

saplings. The two species differed in their sensitivity to overstory root competition as Douglas-fir proved to be more sensitive than beech.

In the present study we investigated the vertical and horizontal variation of fine root parameters of Norway spruce in two cutting types—target diameter and strip cutting—with the following objectives:

(1) To describe the relationship between overstory fine root biomass and easily measurable aboveground characteristics (*i.e.*, basal area, tree size and distance to the nearest tree)

(2) To test whether fine root biomass is a good surrogate for belowground resources, and whether fine root biomass affects growth of Douglas-fir and beech saplings in a way similar to the results of the above mentioned root trenching experiment.

Material and methods

Study sites and treatments

A large-scale and long-term research experiment with various logging and regeneration treatments—established in autumn 2003 by the Northwest German Forest Research Station in Göttingen to test different methods in converting pure Norway spruce stands into mixed stands—offered the opportunity to carry out the planned investigation on the interaction between above—and belowground resources availability. The study was carried out in a pure, ca. 95 years old Norway spruce stand in the Solling Mountains (Lower Saxony, Germany, 51° 47' N and 9° 37' E) in the forest district Neuhaus (500 m a.s.l.). In order to cover a wide range of overstory basal area and fine root densities we used the two treatments «target diameter cutting» (TC) and «strip cutting» (SC), each on two 1 ha replicated plots. The strip cutting plot resembled a shelterwood of 30 m width, bordering the northern edge of a clear cutting, thus receiving a substantial amount of side light. The stand density increased evenly from an almost open canopy at the southern part of the strip to a closed canopy in ca. 30 m distance from the edge. Target diameter cutting is characterized by harvesting single trees with a dbh \geq 45 cm throughout the stand. This intervention reduced the basal area on average by 28 % in our stands (Heinrichs and Schmidt, 2009). The harvest will be repeated in 5-years cycles until the total stand is removed, and the regeneration of a new forest is established. In both treatments the first cutting took place in autumn

2003. At the beginning of our study in spring 2006 the two cutting treatments differed significantly in number of trees and basal areas per hectare. The higher basal area (53 m² ha⁻¹) and tree number (257 trees ha⁻¹) were met on the target diameter cutting plot (TC) whereas on the strip cutting plot (SC) a lower basal area (34 m² ha⁻¹) corresponded to a lower tree density (166 trees ha⁻¹).

The site is characterized by well drained dystric cambisol (podzolic brown earth). The climate is classified as humid and sub-continental with the following long-term mean values: 6.5°C annual temperature, 1,050 mm annual precipitation, thereof 470 mm in the growing season. During the observation period of this study (2006 and 2007) the Northwest German forest experimental station measured 821 mm annual precipitation, thereof 405 mm in the growing season in 2006, whereas in 2007, precipitation reached almost double values: 1,376 and 801 mm, respectively.

After cutting, bare-rooted two-year-old beech and three-year-old Douglas fir seedlings were planted without soil preparation in spring 2004 on each of the four harvest treatment plots. The plants were arranged on monospecific subplots in rows 2 m apart with beech seedlings spaced 1 m and Douglas-fir seedlings spaced 3 m within rows. Within each of these 8 experimental units (2 harvest treatments \times 2 replicates \times 2 underplanting variants) we chose randomly 30 saplings, free of other noteworthy competitors like naturally regenerated spruce saplings, bushes, or herbaceous vegetation. From initial total number amounted to 240 saplings, we used in this study 120 Douglas fir and only 60 beech saplings (see more details in the next paragraph). The research area was fenced against game browsing.

Measurements

Fine root sampling and assessment

In spring 2007 we surveyed the fine root biomass of the Norway spruce overstory by sampling soil cores in about 30 cm distance to each Douglas-fir and to every second beech sapling in a line toward the nearest overstory spruce tree. We chose this distance because it seemed near enough to characterize the belowground competitive situation of the sapling, and far enough to avoid any damage to its own roots. The reason for including only half of the initial selected beech saplings in soil coring is their narrower spacing. We assumed

that one soil core was sufficient to describe the below-ground competitive situation for two saplings being 1 m apart. Soil cores were taken with a cylinder tube sampler (diameter 8 cm, Murach, 1984) and encompassed in total 60 beech and 120 Douglas-fir saplings. Fine roots from the humus layer were also sampled as they represent an important part of the total fine root biomass. The extracted soil cores were divided into humus layer and the following four mineral soil layers: 0-5 cm, 5-10 cm, 10-20 cm and 20-30 cm. According to the method developed by Murach (1984), subsamples of 2 cm width were cut out centrally from the 5-cm layers and of 4 cm from the 10-cm layers of the mineral soil. According to the results of similar studies (Murach, 1984; Schmid and Kazda, 2002) and preliminary own tests we regarded a mineral soil depth of 30 cm as sufficient for sampling about 90 % of the total spruce fine roots. On similar sites like ours with a 30-40 cm top layer of mineral soil and solid bed rock below this depth Norway spruce is known as developing a shallow and widespread root system. Thus, we safely could assume that most of the Norway spruce fine root biomass belonged to the soil zone above 30 cm.

After washing, fine roots (diameter < 2 mm) were separated from coarse roots 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 various fine root attributes (length, surface area and diameter). Finally, roots were dried at 65°C for five days and weighed to the nearest 0.1 g. Based on these measures, the two morphological ratios «specific root length» (SRL, fine root length to dry weight, m g^{-1}) and «specific root area» (SRA, fine root area to dry weight, $\text{cm}^2 \text{g}^{-1}$) were calculated.

Basal area of overstory spruce stand

To provide an easily measurable proxy for the intensity of overstory competition we used the summed basal area of the overstory spruce trees within a circle of 10 m radius around every root sample point. We measured diameter at breast height and distance from each coring sampling point to the nearest stem in order to describe horizontal distribution of fine root biomass. 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 photo just above the uppermost leaves of every sampled sapling in mid-summer with a Nikon digital camera with fisheye lens and a self-leveling mount. Photos 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).

Diameter and length growth measurement

For every sapling length of the two last annual terminal shoots (2006, 2007) was recorded. In autumn 2007 a stem disc of the main shoot was taken from 1 cm height above ground for measuring the width of the last two annual rings (2006, 2007) in two perpendicular directions. For further analyses arithmetic means of the two measurements were used. Results about the diameter and height increment and saplings dimensions at the starting of study are given in Table 1.

Data analysis

To compare fine root attributes of the two logging system types we used a nonparametric test (Mann-Whitney U test, $p < 0.05$) as the data did not comply with the requirements of parametric test methods (normality was assessed with the Kolmogorov-Smirnov test).

Significant differences between logging system types within each of the five soil layers were tested by Mann-Whitney U test, and between the layers within the same treatment by Wilcoxon test.

The relationship between fine root biomass and distance to the nearest tree trunk was fitted by an exponential model ($y = a \exp(-b x^3)$) for each of DBH classes (26-35 cm, 36-45 cm, 46-55 cm, 56-65 cm) of the canopy trees. This model known as Ribbens model was successfully used by Müller and Wagner (2003) or Ammer and Wagner (2002).

Table 1. Description of Douglas fir and beech saplings (height, diameter, and height and diameter increment) per logging types

Parameters (means value with standar error of mean in brackets)	SC		TC	
	Douglas fir	Beech	Douglas fir	Beech
Number of saplings	60	30	60	30
Height 2005, cm	58.5 (2.7)	43.2 (3.1)	49.8 (2.3)	40.2 (2.9)
Diameter 2005, cm	11.9 (0.7)	9.1 (0.5)	7.7 (0.5)	7.5 (0.3)
Height increment 2006, cm	27.4 (3.7)	30.5 (3.9)	14.5 (1.8)	9.1 (1.8)
Height increment 2007, cm	35.9 (3.8)	36.2 (3.9)	12.5 (2.3)	15.3 (2.2)
Diameter increment 2006, mm	4.4 (0.5)	3.3 (0.2)	1.2 (0.3)	1.2 (0.1)
Diameter increment 2007, mm	9.2 (0.9)	4.3 (0.3)	2.2 (0.4)	1.4 (0.2)

SC: strip cutting. TC: target diameter cutting.

Influence of fine root biomass of the canopy spruces and light availability on growth of beech and Douglas-fir saplings was investigated by regression analyses. Diameter and length growth were regressed by fine root biomass and light availability using a general linear model ($y = a + b \text{ Light} + c \text{ Fine root biomass} + d \text{ Light} \times \text{Fine root biomass}$). Model parameters were estimated with least squares methods.

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

Results

Fine root parameters of overstory Norway spruce

The differences in basal area and tree number between the two logging systems were well reflected in various overstory root parameters (Table 2). Fine root density

Table 2. Comparison of fine root attributes (biomass, density, length density, and diameter) and morphological traits (specific root area and specific root length) between the two logging types

Parameter (median with interquartile range in brackets)	Logging type	
	SC	TC
Fine root density, g L^{-1}	0.44 (0.42) ^a	0.62 (0.42) ^b
Fine root biomass, g m^{-2}	137 (130) ^a	184 (135) ^b
Fine root length density, m L^{-1}	2.7 (2.0) ^a	3.6 (2.1) ^a
Specific root area, $\text{cm}^2 \text{g}^{-1}$	230 (98) ^a	217 (87) ^a
Specific root length, m g^{-1}	6.2 (3.4) ^a	5.8 (2.6) ^a
Fine root diameter, cm	0.12 (0.01) ^a	0.13 (0.02) ^a

(SC: strip cutting. TC: target diameter cutting. Significant differences are marked by small letters (Mann-Whitney U test, $p < 0.05$). Basis: data of all layers are pooled by soil profile.

and fine root biomass were significantly higher in TC than in SC. Fine root length density (m L^{-1}) was also greater but the difference lay just under the significant threshold with a probability value of $p = 0.059$. Further parameters of Table 2 like specific fine root area (SRA), specific fine root length (SRL) and fine root diameter did not show significant differences between the two logging types.

Looking at the vertical root distribution pattern, significant differences in fine root density (Fig. 1a), biomass (Fig. 1b), length density (Fig. 1c) and diameter (Fig. 1d) between SC and TC were found only in the organic layer. Although the humus layer of the target diameter plots with an average of 5.5 cm was thinner than on strip cutting plots with 7.0 cm, fine root biomass, density and length density were significantly higher. A significantly smaller mean fine root diameter contributed further to the latter result. In the mineral soil layers, the vertical distribution patterns of root parameters were similar in both cutting types. All root attributes were significantly higher in the humus layer than in mineral layers, whereas any significant differences among mineral layers within the same treatment could not be detected. Particularly, fine root density and length density were strongly concentrated in the humus layer with more than 45% of the total, and more than 60% in the two top layers (humus + 0-5 cm mineral soil). Both densities decreased exponentially in deeper soil layers, down to 10% in the 20-30 cm layer. Moreover, the degree of heterogeneity was greatest in the humus layer, expressed in an interquartile range of root density from 1.23 (SC) and 1.38 (TC) g L^{-1} in the humus layer to 0.35 (SC) and 0.43 (TC) g L^{-1} in the deepest mineral soil layer, or in an interquartile range of fine root length density decreasing from 6.1 (SC) and

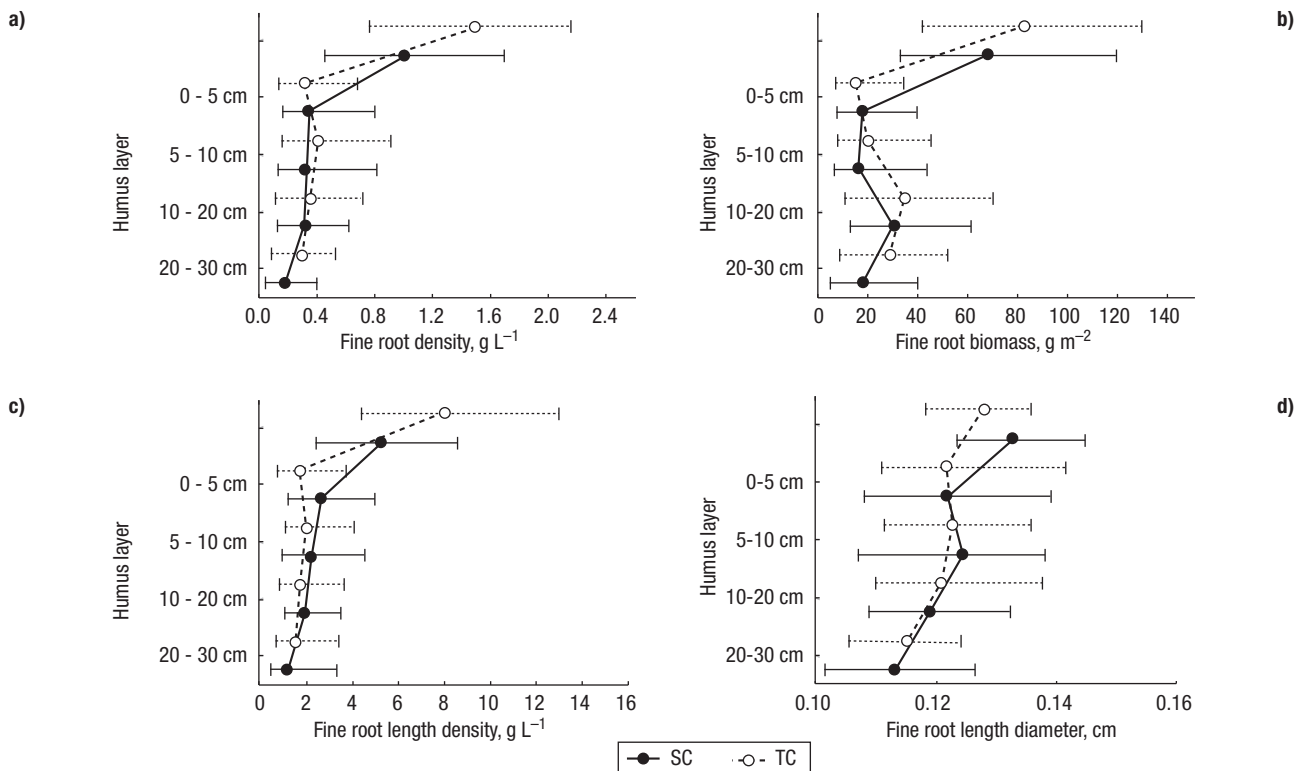


Figure 1. Fine root density (g L^{-1} , a), fine root biomass (g m^{-2} , b), fine root length density (g L^{-1} , c) and fine root diameter (cm, d) per logging system type and soil depth. The significant differences between logging system types (SC and TC) are marked by asterisks (Mann-Whitney U test, $p < 0.05$). SC: strip cutting, TC: target diameter cutting. Depicted are median values with the first and third quartile.

8.4 m L^{-1} (TC) in the humus layer to $2.7\text{-}3.7$ (SC) and $2.5\text{-}2.9$ (TC) in the next four mineral soil layers. Also the variability of fine root biomass was 2-3 times greater in the humus layer than in the mineral layers.

Figure 2 depicts the negative linear relationship between the average diameter of fine roots and specific fine root area (Fig. 2a) and specific fine root length (Fig. 2b). A decreasing root diameter was significantly connected with an increasing surface area (SRA) and length (SRL) per unit root dry weight. These relationships could be based on data merged across the harvest treatments as there were no significant differences in these root characteristics. The data of all layers have been pooled by soil profile.

In Figure 3 we described the relationship between some aboveground parameters of the spruce stand (basal area, DBH) and fine root biomass. We decided to show only the results of fine root biomass modelled as a function of spruce stand parameters because it was the best response variable in relation to the variation of the considered parameters. A significant positive correlation of fine root biomass with overstory basal

area could be detected on the strip cutting plots with their wider range of basal area (Fig. 3a), while a negative relationship appeared between fine root biomass and distance to the nearest tree trunk (Fig. 3b, based on data merged across cutting treatments). We regarded the data merge as appropriate because we found no hints on any influence of the cutting treatments on this relationship. Instead, the diameter of the nearest tree modified this relationship. The bigger the tree, the higher was the fine root biomass in close vicinity up to 2 m distance, and the steeper the decrease with further increasing distance, reaching zero at 8 m. Both regressions are characterized by a considerable scatter around the best-fit curves with fairly low coefficients of correlation or determination, respectively.

Influence of overstory Norway spruce stand on growth of beech and Douglas-fir saplings

Since the variables «fine root biomass» and «light availability» were not inter-correlated (the p-values

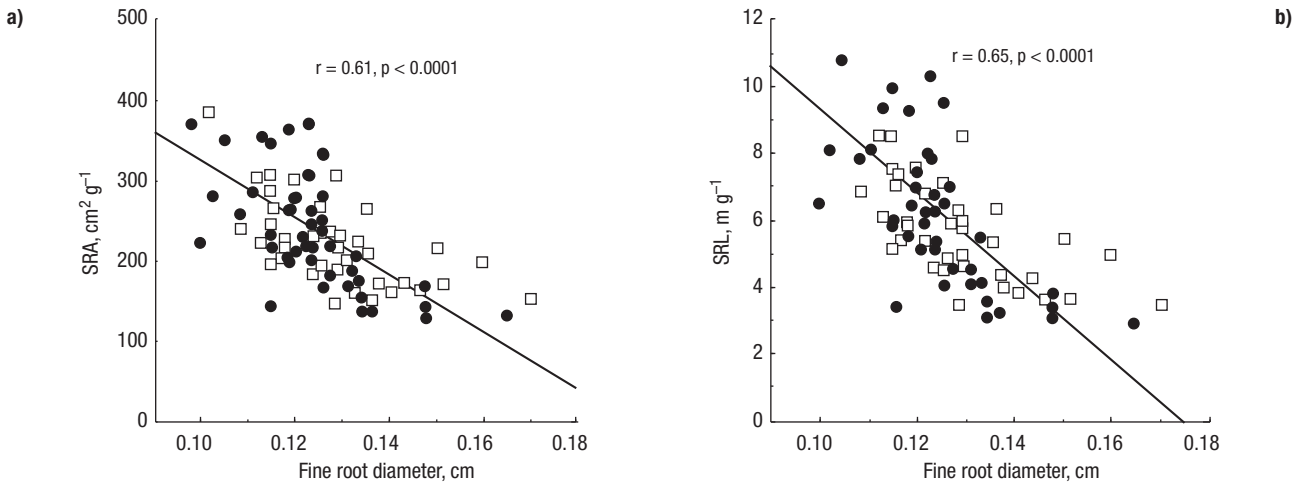


Figure 2. Specific fine root area (SRA, in a) and specific fine root length (SRL, in b) as a function of fine root diameter (linear regressions). TC: open symbols. SC: filled symbols. Because significant differences between the two logging systems were lacking the depicted lines represent the linear regression of merged data. Data of all layers are pooled by soil profile.

associated to the linear regression among fine root biomass and light availability were greater than 0.05), we could use a multiple regression analysis to find out which of the two variables exerted more influence on growth of the underplanted young beeches and Douglas-firs, and whether they interacted significantly. Table 3 and Figure 4 contain the results.

In 2006, light availability alone was the decisive factor for beech saplings, which explained 59% of total variation in diameter growth and 45% in length growth

(Table 3). In Douglas-fir, both growth parameters were also significantly influenced by light availability, but in addition the interaction between light and fine root biomass had a significant effect. With a given light availability, an increasing overstory fine root biomass significantly reduced growth Fig. 4b,d). This model explained 57% of the total variation in diameter growth and 44% in length growth of Douglas-fir. In the following year only light affected significantly diameter and length growth of both species (Table 3).

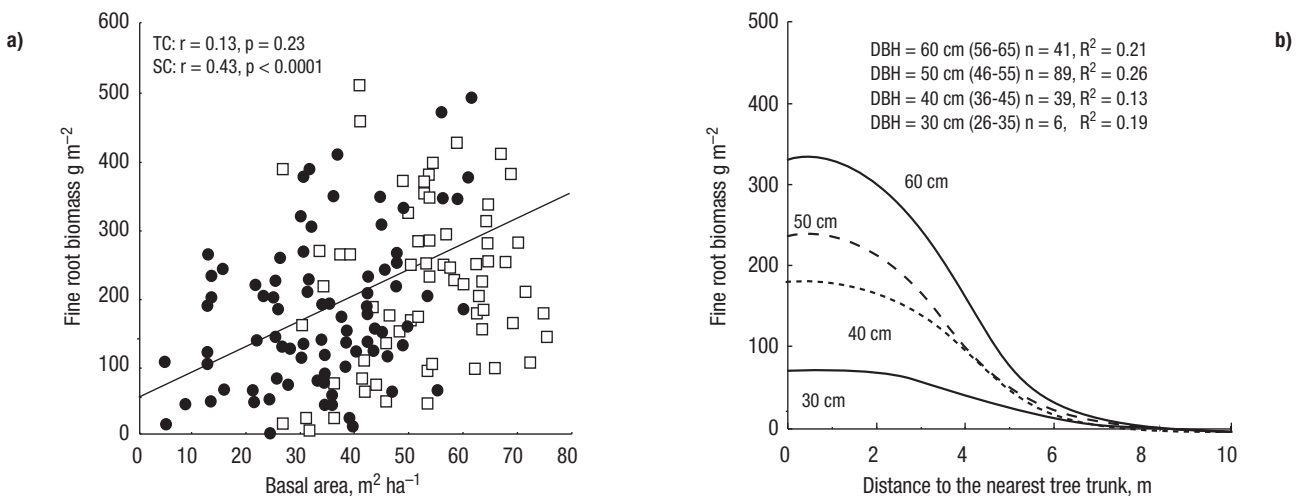


Figure 3. a) Fine root biomass related to basal area of the spruce canopy trees (with TC: open symbols; SC: filled symbols; the line shown represents the linear regression of SC data). b) Fine root biomass modelled by the distance to the nearest canopy tree trunk and its diameter in breast height (DBH). Model: $y = a \exp(-b \cdot x^3)$, with $a = 71, 178, 237, 330$, and $b = -0.0094, -0.0096, -0.0121, -0.0114$ for DBH of 30, 40, 50 and 60 cm, respectively. Basis: Merged data of the two logging systems; Fine root biomass data of all layers are pooled by soil profile.

Table 3. Results of the regression analyses of diameter and length increment in 2006 and 2007 of beech and Douglas-fir saplings as a function of light availability (L) and fine root biomass (FW)

Variable	Species	Year	Model	Coefficients				
				Estimate	SE	t-value	P value	R ²
Diameter increment	Beech	2006	(Intercept)	0.531	0.249	2.13	<0.05	0.59
			L	0.053	0.006	8.68	<0.0001	
		2007	(Intercept)	0.168	0.341	0.491	0.62	0.74
			L	0.074	0.008	8.921	<0.0001	
	Douglas-fir	2006	(Intercept)	-0.433	0.317	-1.36	0.175	0.57
			L	0.118	0.011	10.824	<0.0001	
			L X FW	-0.00012	0.00003	-3.41	<0.0001	
		2007	(Intercept)	-2.287	0.708	-3.234	<0.01	0.71
L	0.232	0.201	11.357	<0.0001				
Length increment	Beech	2006	(Intercept)	3.902	2.927	1.33	0.188	0.45
			L	0.474	0.071	6.58	<0.0001	
		2007	(Intercept)	5.366	4.763	1.126	0.269	0.42
			L	0.506	0.114	4.421	<0.0001	
	Douglas-fir	2006	(Intercept)	6.407	2.37	2.69	<0.01	0.44
			L	0.708	0.078	9.10	<0.0001	
			L X FW	-0.0009	0.0002	-4.50	<0.0001	
		2007	(Intercept)	-2.145	3.370	-0.636	0.59	0.56
	L	0.783	0.092	8.467	<0.0001			

Basis: merged data of the two logging systems. Fine root biomass data of all layers are pooled by soil profile.

Discussion

Fine root parameters of overstory Norway spruce

Fine root biomass in Norway spruce stands can vary from 100 g m⁻² (Schmid, 2002) to 400 g m⁻² (Helmisaari and Hallbäcken, 1999; Schmid and Kazda, 2002). Our values of 137 (86-209) g m⁻² in SC and 184 (116-260) in TC are within this range.

Fine root densities (both biomass and length) were highest in the humus layers (Fig. 1) and declined strongly with increasing soil depth. This is a general pattern which has been observed also in other studies (Parker and Van Lear, 1996; Schmid, 2002; Schmid and Kazda, 2002; Puhe, 2003; Bolte and Villanueva, 2006; Achat *et al.*, 2008; Bakker *et al.*, 2008). According to Schmid and Kazda (2002), more than three-quarters of the fine roots of Norway spruce are located in the upper 30 cm soil zone. Due to this shallow root system, a severe competition for belowground resources is likely to occur between canopy trees and underplanted saplings during the first years after planting when their root system is restricted to the upper soil layers.

Changes in fine root attributes like specific root length and specific root area permit a good adaptation of plants to improve the efficiency of exploiting soil resources (Bauhus and Messier, 1999). After Pregitzer *et al.* (2002) specific root length (SRL) can be interpreted as «index of root benefit to cost» as root length is correlated with the acquisition of resources and root biomass influences root cost, and that differences in SRL between various species are probably a consequence of different root diameters. Ostonen *et al.* (2007) found a strong negative correlation between SRL and the squared mean root diameter for different species including *Picea abies*. They assumed root diameter being of greater importance for SRL than root tissue density, and proposed to calculate SRL as the inverse of the product of squared root diameter and root tissue density. Our results confirm their statement (Fig. 2b). Moreover, specific root area (SRA) —being considered an ecomorphological index for soil quality by Löhmus *et al.* (1989)— exhibited a similar behaviour. It decreased with increasing fine root diameter (Fig. 2a). Trees with greater SRL and SRA —and correspondingly thinner roots— can exploit larger soil volumes per unit of dry

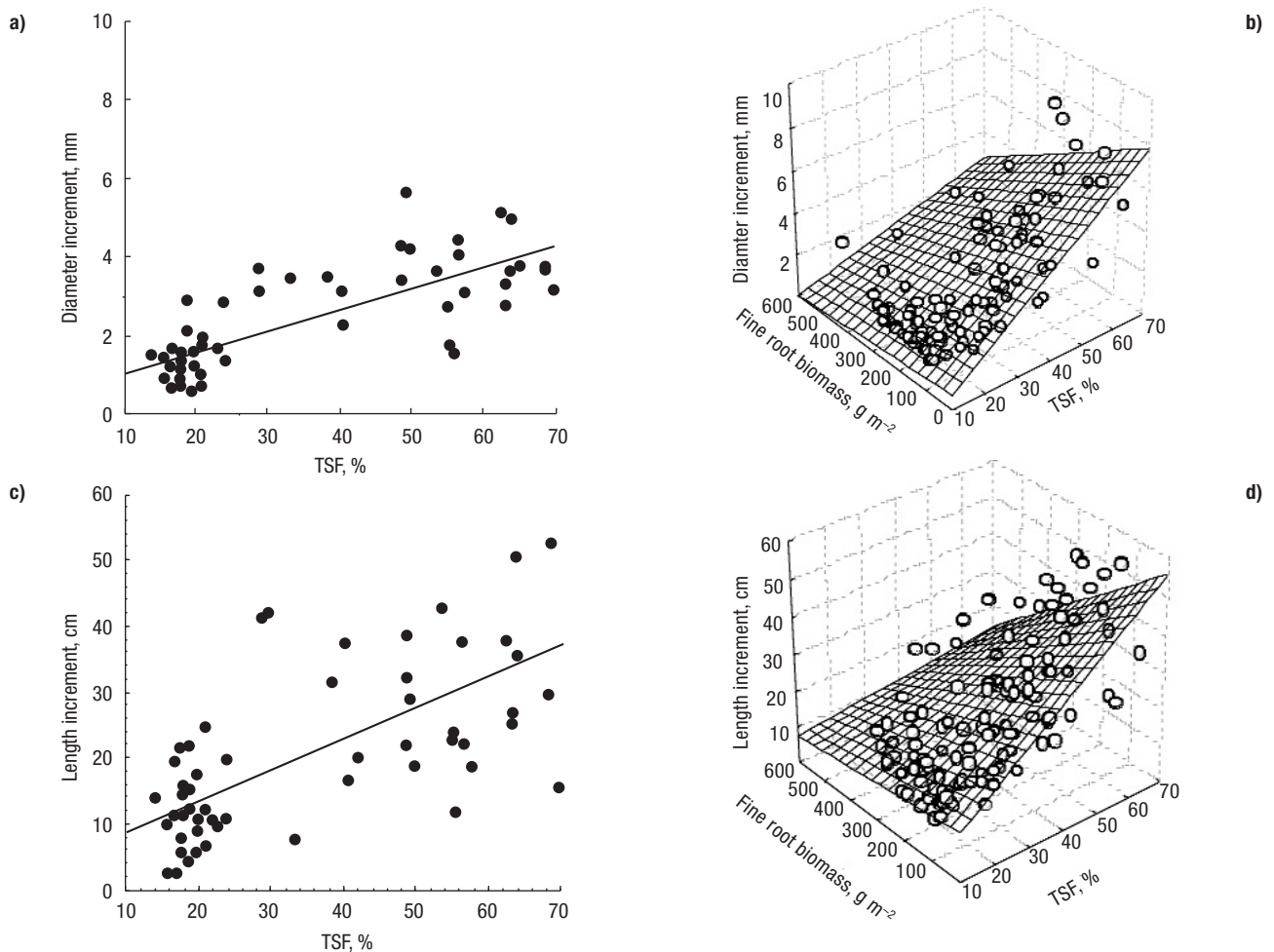


Figure 4. Annual diameter (a, b) and length increment (c, d) as a function of light availability (in % TSF) for beech (a, c: filled symbols) and as a function of light availability and interaction between light availability and fine root biomass of overstory Norway spruce for Douglas fir (b, d: open symbols). The graphs show diameter and length increment in the first study year (2006), when not only light availability but also fine root biomass influences the increment of Douglas fir. Basis: Merged data of the two logging systems; Fine root biomass data of all layers are pooled by soil profile.

mass invested in root construction (Bauhus and Messier, 1999).

Fine root biomass increased with basal area of overstory Norway spruce (Fig. 3a), what is in line with the results of other authors (Nielsen and Mackenthun, 1991; Vanninen and Mäkelä, 1999; Bolte and Villanueva, 2006; Finer *et al.*, 2007). Thus, basal area as an easily measurable indicator for aboveground competition intensity can be used also to predict belowground competition intensity. Further, fine root biomass decreased with increasing distance from the tree stem (Nielsen and Mackenthun, 1991; Rewald and Leuschner, 2009; Meinen *et al.*, 2009) and increased with tree diameter at breast height (Le Goeff and Ottorini, 2001; Ammer and Wagner, 2002; Chen *et al.*, 2004). Both relation-

ships could be found also in our study (Fig. 3a,b). We assessed a maximum horizontal fine root extension of 8 m for all diameter classes. Ammer and Wagner (2002) estimated also 8 m for a 75 years old Norway spruce stand with a density of 545 stems ha^{-1} , and close to 15 m in a stand with 392 stems ha^{-1} . In a boreal 90 years old Norway spruce forest with a density of 450 stems ha^{-1} , Taskinen *et al.* (2003) found a fine root extension zone of about 5 m from the edge of a gap toward the gap centre. Stone and Kalisz (1991) offered an explanation for these variations in observed maximum extension of tree roots in an exhaustive literature review. They stated that the extent of tree roots depends on site type and stand structure, and that it is larger in poor soils and sparse stands than in fertile soils and dense stands

(s. a. Köstler *et al.*, 1968). In our study, the highest fine root biomass occurred in a circle of 2 m radius around the canopy trees. Beyond that it declined steeply (Fig. 3b). As the belowground resources availability decreases with increasing fine root biomass (Coomes and Grubb, 2000), competition of overstory Norway spruce becomes a decisive factor for underplanted saplings particularly within 2 m distance to big trees. To improve the silvicultural success, planting in this zone should be avoided, particularly around spruce trees with more than 40 cm diameter in breast height. However, the often reported (*e.g.*, Müller and Wagner, 2003; Achat *et al.*, 2008) very heterogeneous distribution of fine roots — especially in the humus layer— could to a large extent not be described by models using aboveground and easily to measure variables. For example, our model explained only less than 25% of the total variation in fine root biomass.

Influence of overstory Norway spruce stand on diameter and length growth of beech and Douglas-fir saplings

Our second objective was to investigate the relative importance of above- and belowground resources on growth of underplanted beech and Douglas-fir saplings. To achieve this goal, we used overstory fine root biomass as surrogate for belowground resources availability. Diameter and length growth increased with increasing light availability in both species, and decreased with increasing fine root biomass only in Douglas-fir in 2006 (Table 2). Generally, this observation confirms the findings of other authors regarding the greater importance of aboveground (*i.e.*, above all light) compared to belowground resources (Van Hees, 1997; Coomes and Grubb, 1998; Ammer *et al.*, 2008). As an exception, Ammer *et al.* (2008) found that the availability of belowground resources —also represented by fine root biomass of overstory spruce trees as an inverse proportional surrogate— was more important for height growth of beech seedlings in the first growing season than light availability. But light availability gained more influence in the following years what agrees with our results for five years-old beech saplings.

Douglas-fir proved to be more sensitive to overstory root competition than beech in our study. This became apparent as a significant interaction between light and overstory fine root biomass in the regression analysis

of diameter and length increment in 2006. In 2007 in both species only light was a significant factor (Table 3). As already mentioned above in the site description, 2006 was a year with less rainfall than 2007, receiving about half the amount of 2007. A stronger sensitivity of Douglas-fir to belowground competition accords with the results of a root trenching experiment conducted on the same plots (Petritan *et al.*, 2011), in which Douglas-fir saplings were more responsive to the exclusion of overstory root competition than beech saplings. Again, this response was particularly pronounced in a drier growing season. Also Coomes and Grubb (2000) conclude that root competition of overstory trees has a greater impact in drier conditions.

Also in comparison with other less shade tolerant species, beech saplings proved to be less sensitive to root competition from overstory trees. For example, sessile oak (*Quercus petraea* Liebl.) saplings were more sensitive to beech overstory root competition in a root trenching experiment (Lüpke and Hauskeller-Bullerjahn, 2004), or common ash (*Fraxinus excelsior* L.) as well (Wagner 1999). As an explanation for the relative insensitiveness of young beeches, a higher specific fine root length might be considered like we found in our study. It allows beech to explore a larger soil volume per unit fine root biomass (Petritan *et al.*, 2010). Another explanation might lie in the characteristic of many less shade tolerant species of being generally more affected by limited resources than shade tolerant species which in any way possess slower growth rates and/or higher storage capacities (Chapin, 1980; Messier *et al.*, 1999).

Despite the above described great variability of many features, it might be possible to draw at least the following silvicultural conclusion from our results. For the establishment of a mixed stand beneath the canopy of a mature Norway spruce stand under comparable site conditions we recommend to plant the more sensitive Douglas-fir on central parts of openings where it suffers less from shade and root competition, while the less sensitive beech can be placed below the denser parts of the overstory.

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