

Root overlap and allocation of above- and belowground growth of European beech in pure and mixed stands of Douglas fir and Norway spruce

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ARTICLE INFO

Keywords:

Fine root growth
Stem growth
Trade-off
Cost-benefit ratio
Belowground territoriality
Conspecific neighbors
Heterospecific neighbors

ABSTRACT

Site conditions and species identity have a combined effect on fine root growth of trees in pure and mixed stands. However, mechanisms that may contribute to this effect are rarely studied, even though they are essential to assess the potential of species to cope with climate change. This study examined fine root overlap and the linkage between fine root and stem growth of European beech (*Fagus sylvatica*) growing in pure and mixed stands with Douglas fir (*Pseudotsuga menziesii*) or Norway spruce (*Picea abies*) at two different study sites in northwestern Germany.

The study sites represented substantially different soil and climate conditions. At each site, three stands, and at each stand, three pairs of trees were studied. In the pure beech stand, the pairs consisted of two beech trees, while in the mixed stands each pair was composed of a beech tree and a conifer. Between each pair, three evenly spaced soil cores were taken monthly throughout the growing season. In the pure beech stands, microsatellite markers were used to assign the fine roots to individual trees. Changes in stem diameter of beech were quantified and then upscaled to aboveground wood productivity with automatic high-resolution circumference dendrometers.

We found that fine root overlap between neighboring trees varied independently of the distance between the paired trees or the stand types (pure versus mixed stands), indicating that there was no territorial competition. Aboveground wood productivity (wood NPP) and fine root productivity (root NPP) showed similar unimodal seasonal patterns, peaking in June. However, this pattern was more distinct for root NPP, and root NPP started earlier and lasted longer than wood NPP. The influence of site conditions on the variation in wood and root NPP of beech was stronger than that of stand type. Wood NPP was, as expected, higher at the richer site than at the poorer site. In contrast, root NPP was higher at the poorer than at the richer site.

We concluded that beech can respond to limited resources not only above- but also belowground and that the negative relationship between above- and belowground growth across the study sites suggests an 'optimal partitioning' of growth under stress.

1. Introduction

Climate change will impact European forests dramatically, resulting in modified growth (Pretzsch et al., 2018; Martínez-Sancho et al., 2020; Forzieri et al., 2021; Del Martínez et al., 2022), increased tree mortality rates (Allen et al., 2015; Bosela et al., 2021), and altered species composition (Ammer, 2019). European beech (*Fagus sylvatica* L.) is an example. While this species would dominate Central European forests under natural conditions (Leuschner et al., 2017), it was heavily affected by recent years of severe drought, which could lead to a reduction in its

future competitiveness (Schuldt et al., 2020; Mathes et al., 2023). Defoliation and dieback of both dominant and suppressed trees were observed (Meyer et al., 2022; Mathes et al., 2023). Leuschner et al. (2023) expect that some parts of Germany may even become unfavorable for beech.

Recently, mixing tree species has been discussed as a suitable adaptation to climate change (Ammer, 2019; Ammer and Wagner, 2005). However, the belowground responses of mixed stands to a changing climate are still unclear. While, for example, Zwetsloot et al. (2019) found that beech shifts its root production towards shallower soil layers

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<https://doi.org/10.1016/j.fecs.2024.100217>

Received 26 January 2024; Received in revised form 14 June 2024; Accepted 14 June 2024

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in mixture with Norway spruce, the opposite was reported by Lwila et al. (2021). There, more beech fine roots were allocated to deeper soil layers when mixed with Norway spruce or Douglas fir. However, it appeared that root competition was less intense for beech in mixed stands than in pure stands (Zwetsloot et al., 2019). Several studies have indicated that belowground biomass and its vertical distribution in mixed stands depend on multiple factors such as tree species identity, site conditions, stand age, and stand density (Finér et al., 2007, 2017; Lwila et al., 2021). We found in previous studies that fine root biomass ($\text{g}\cdot\text{m}^{-2}$) and fine root productivity ($\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) in pure and mixed beech stands were higher in nutrient poor and relatively dry soils than at sites with better soil conditions. Moreover, fine root biomass increased with increasing beech percentage on the ‘poor’, but not on the ‘rich’ sites (Lwila et al., 2021, 2023).

Belowground competition is a function of the root system of a tree and the number and identity of neighboring trees. For example, Zeng et al. (2021) found that fine root biomass depends on the interaction between aboveground species richness and stand density. In fact, they found that fine root biomass increased with species richness if stand density was low, but not if stand density was high. However, information is lacking as to the extent that fine root overlaps between competing neighbors determine resource uptake in both monospecific and mixed stands.

In mixed stands, fine roots of different tree species can be identified by their morphological characteristics (Hertel and Leuschner, 2002; Meinen et al., 2009), but in monospecific stands root spreading from individual trees cannot be assessed using the conventional morphometric method. Consequently, little is known about the neighborhood and strength of competition formed by fine roots within monospecific stands. However, the application of molecular methods to identify tree individuals is a promising approach to overcome this methodological limitation. For example, Lang et al. (2010) applied a microsatellite marker to analyze beech territoriality by genotyping beech trees, and Brunner et al. (2004) used plastid microsatellites to identify overlapping root systems of silver fir (*Abies alba* Miller) individuals.

An adaptation of the above- and belowground biomass relationship to different site or competition situations would utilize the “optimal partitioning theory” (Hertel et al., 2013; McCarthy and Enquist, 2007). This theory proposes that plants adjust biomass allocation internally (e.g., investments into leaves versus roots) in order to maintain high growth rates when resources are limited (McCarthy and Enquist, 2007). Higher fine root biomass at the poor as compared to the rich site, found at both stand and tree level in our previous studies (Lwila et al., 2021, 2023), supports this theory. Although belowground biomass and hence growth depend on both above- and belowground processes (Annighöfer et al., 2022), the relationship between the basal area of a tree and its fine root biomass can vary strongly due to differences in site conditions and corresponding plant metabolism. For example, Schall et al. (2012) found that beech is able to increase its proportion of leaf biomass under reduced light conditions and root biomass under drought conditions, resulting in the same total biomass. Thus, beech has a remarkable potential for adjusting fine root biomass to cope with unfavorable conditions. However, it is unclear whether beech can make such adjustments to biomass allocation in species mixtures. Furthermore, belowground biomass allocation not only reflects site conditions (i.e., the availability of nutrients and water (Hutchings and John, 2010), but is also driven by interactions between neighboring trees, which can further limit or enhance resource availability (e.g., by hydraulic lift).

Roots proliferate towards high-nutrient patches; at these hotspots, competition for resources is expected to be intense (O’Brien et al., 2017; Valverde-Barrantes et al., 2015), with a substantial effect on belowground relative abundance and spatial biomass variability in forest stands (Wijesinghe et al., 2005). Schenk et al. (1999) suggested that the benefit of defending space and its resources may be less costly than the overlap of roots in direct competition for resources in a shared soil volume. Nevertheless, it could be that some species do not compete mainly via placing their roots in richer soil patches (and blocking roots of

competitors), but by altering metabolic processes (Schimel and Bennett, 2004), or by using a mix of several strategies (Aidoo et al., 2016).

To assess mechanisms that might influence belowground growth and competitiveness of beech under different sites conditions, this study focused on fine root overlap and the relationship between seasonal and annual fine root and aboveground wood growth of mature beech trees growing at two study sites in northern Germany. We hypothesized that i) fine root overlap between tree pairs is always highest at the center point between the individuals, indicating competition for root space; ii) in pairs of different tree species, beech roots dominate the center point and can be found more frequently close to the heterospecific neighbor, indicating that beech suppresses heterospecific neighbors' roots by occupying rooting space, while in conspecific neighborhoods no differences in the spatial distribution are found; and iii) fine root and stem growth follow opposite patterns in response to site quality, with higher root growth but lower stem growth at the ‘poor’ than at the ‘rich’ site.

2. Materials and methods

2.1. Study sites

The study was conducted in northwestern Germany (the federal state of Lower Saxony, Germany). The study design comprised two ‘clusters’ of stands. One cluster was located in the south of Lower Saxony (‘Winnefeld’, hereafter ‘rich site’ or ‘southern region’), and one in the north (‘Unterlüß’, hereafter ‘poor site’ or ‘northern region’). Each cluster contained two stand types (pure versus mixed stand) and three stands: one monospecific stand of European beech, one mixed stand with beech and Norway spruce and one mixed stand with beech and Douglas-fir. The regions differ in climate, geology, soil texture, and soil type (Table S1, more details can be found at Lwila et al. (2021), and Foltran et al. (2023)). The southern region is in the lower mountain range ‘Solling’. The dominant soil types at this region are Cambisols to Luvisols developed from loess containing material on sandstones, with mean annual precipitation between 839 and 895 mm. The northern region is in the lowland of Lower Saxony. This region is characterized by podsols developed on sand deposits, with mean annual precipitation range from 673 to 747 mm and mean annual air temperature that is nearly 1 °C higher than the south site (Lwila et al., 2021). The southern region contains silty loam soils (23% clay, 57% silt, 20% sand) and has greater water holding capacity than the sandy soils in the north (6% clay, 15% silt, 79% sand) (Foltran et al., 2023).

2.2. Experimental design and soil sampling

We studied even-aged, mature, managed forests (Table 1) that have

Table 1

Stand characteristics of the studied pure and mixed stands at the northern and southern study site. In mixed stands, the value for beech is followed by the value for the respective conifer in parenthesis.

Site and stand type	Stand age (yr)	Stem density ($\text{N}\cdot\text{ha}^{-1}$)	Basal area ($\text{m}^2\cdot\text{ha}^{-1}$)	Average tree height (m)	Average tree dbh (cm)	
South	Beech	89	248	26	33	46
	Beech (Spruce)	94 (86)	158 (35)	18 (7)	32 (33)	50 (53)
	Beech (Douglas-fir)	90 (80)	162 (31)	21 (12)	32 (37)	43 (56)
North	Beech	85	527	24	28	36
	Beech (Spruce)	122 (122)	240 (72)	17 (12)	28 (31)	35 (56)
	Beech (Douglas-fir)	85 (82)	335 (39)	16 (14)	27 (36)	28 (70)

regularly been thinned according to standard forestry practices (selective thinning in order to favor target trees). None of the stands have been thinned within the past 10–15 years. Spruce and Douglas-fir admixtures were planted, while beech originated from natural regeneration.

Three pairs of neighboring mature trees (hereafter termed ‘tree pairs’) were selected at each stand. Each pair consisted of a ‘target tree’, equipped with a dendrometer (see below), and a ‘neighboring tree’ (Fig. 1a). The trees in a pair had comparable diameter at breast height (dbh), and a horizontal distance shorter than that to other surrounding trees of the same size (distance between the paired trees ranged from 2 to 3 m). The pairs were composed of two beech trees in the pure beech stands, and a beech tree and a conifer tree in the mixed stands (for more details see Lwila et al., 2023). Soil cores were taken at three sampling points evenly spaced between the paired trees (Fig. 1a).

The 18 target trees (3 beech trees \times 3 stands \times 2 sites) were equipped with high-resolution circumference dendrometers (Type DC2 and DC3, Ecomatik, Dachau, Germany) for permanent measurements of stem growth at breast height (1.3 m). The instrument measured the circumference by means of a stem-embracing cable wire and a precision linear variable transducer every 10 min from 1st March 2019 to 30th September 2020.

2.3. Fine root sampling

Fine root sampling was conducted monthly (six times) throughout the growing season from March to September 2019. Root sampling was done using the “sequential coring method” (Hertel and Leuschner, 2002; Yuan and Chen, 2013). To avoid interference between the six sequential sampling events, samples per sampling point were randomly located at a minimum distance of 25 cm from each other. To prevent soil compaction and damage to fine roots during coring, we used plastic walking mats. Additionally, we clearly marked the sampling points and filled the holes with white sand to avoid any destruction or depreciation of the sample

area. Each soil core was extracted from the organic layer and the mineral soil (0–30 cm soil depth) using an 8-cm diameter soil corer. The organic layer was sampled as a whole, and the mineral soil was divided into three depth classes (0–10, 10–20, and 20–30 cm). Per depth class, a subsample of 3-cm thickness was taken in the middle of each class. At sampling points where it was impossible to reach the maximum depth of 30 cm because of obstacles (rocks or large roots), the deepest soil depths reached were considered as maximum depths. All samples were collected and stored in plastic bags at 4 °C until further processing in the laboratory (maximum storage time: five months). Earlier root coring studies had shown that the vitality status of tree fine root material stored under these conditions did not change (Leuschner et al., 2001a; Meinen et al., 2009; Jacob et al., 2013).

2.4. Root processing and genotyping

Each root subsample was soaked in tap water overnight to separate roots from the soil and further processed using the floating method (Billings et al., 1979). Visible roots and coarse fragments were hand-sorted, and the remaining floating roots were sieved using a mesh size of 0.1 mm. Washed roots were stored at 4 °C until they were sorted. Fine roots (≤ 2 mm) were selected and live roots were separated from dead roots by examining their turgescence and color, using methods outlined in previous studies (Hertel et al., 2013; Lwila et al., 2021). Live roots were then sorted by species, using their species-specific morphologies. For instance, beech roots are characterized as very firm without much elastic texture, very thin root cortex, and red-brown color. In contrast, spruce and Douglas-fir root are less firm and more elastic, with thick root cortices. The color of spruce roots ranges from light to dark brown, while Douglas-fir roots are dark brown. Coarse tree roots (> 2 mm in diameter) were not further processed. All samples were dried at 60 °C for 72 h and weighed in micrograms.

The simplified decision matrix method was used to estimate fine root production (root NPP) ($\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$). The method was proposed by Yuan and Chen (2013), who modified the original version from Fairley and Alexander (1985). Simplified decision matrices are widely used to estimate fine root dynamics based on living and dead fine root biomass changes during a specific period. The simplified decision matrices method was chosen over the Max-Min method (Hertel and Leuschner, 2002). The Max-Min method was considered to be overly conservative for detecting temporal trends with less reliable estimates of root turnover rates (Fig. S1) (Lwila et al., 2023).

For DNA extraction, we selected all individual fine root fragments with a diameter of > 0.1 mm for each soil depth interval at each soil core (organic, 0–10, 10–20, 20–30 cm) (Fig. 1b). All sampled root fragments were weighed, and the proportion was calculated to refer to the total mass before genotyping. DNA was extracted from fine roots and leaves of all target trees in May 2019 using the DNAeasy Mini Plant Kit by Qiagen. Four highly polymorphic microsatellite loci with the repeat motifs (AG) $_n$ (sfc0018, sfc0161, and sfc1143) and (CT) $_n$ (sfc1063) developed for *Fagus crenata* (Asuka et al., 2004) and successfully transferred to *Fagus sylvatica* were used for genotyping (for detailed information, see Lang et al., 2010). Microsatellite fragments were separated electrophoretically on the ABI Prism Genetic Analyzer 3130xl along with the Applied Biosystems GeneScan 500 ROX internal size standard. Microsatellite size was determined using the GeneMapper v4.0 software package (Applied Biosystems Inc.) (Asuka et al., 2004). About 75% of the fine root samples in the organic layer and the upper 30-cm soil depth of the two mono-specific beech stands were successfully assigned to individual trees by root genotyping.

2.5. Aboveground net primary productivity of wood (wood NPP)

To estimate seasonal (1st March to 30th September) and annual wood NPP of all beech trees in the 10 m-radius neighborhood of the tree pairs, we combined the continuous dendrometer measurements of changes in

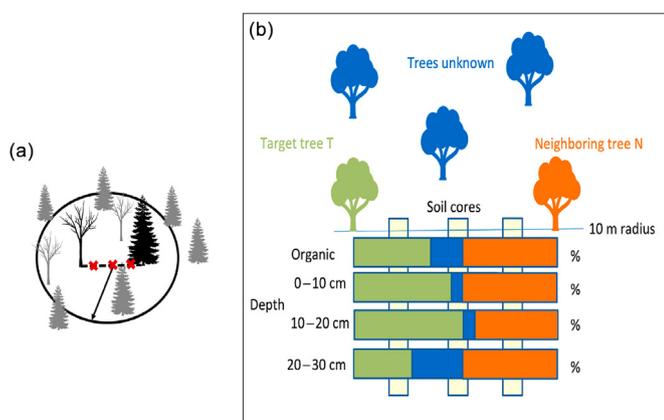


Fig. 1. (a) Scheme of sampling design per stand, here given for the example of a mixed stand. Each pair consisted of a “target (beech) tree” (T) that was equipped with a dendrometer, and a “neighboring tree” (N). The horizontal distance between T and N was always shorter than that between the T or N and other surrounding trees of the same size (distance between T and N ranged from 2 to 3 m). Red Xs show the positions of the soil sampling points. The central sampling point defined the center of the 10 m radius neighborhood. The pairs were replicated three times per stand. Per region (or site), one pure European beech stand and two mixed stands, one with Douglas-fir and one with Norway spruce, were investigated. Considering the two regions, which were characterized by different site conditions, in total 18 tree pairs were selected (3 pairs \times 3 stands \times 2 regions). (b) Schematic vertical and horizontal distribution of root identities resulting from three soil cores taken between a pair of beech trees and subsequent DNA genotyping. The genotyping allowed to assign the roots to the target tree (T; green), the neighboring tree (N; orange) and other, not specified (“unknown”) surrounding trees. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

stem circumference with stand inventory data of the study plots. The stand inventories were conducted in July 2018 and included tree species, position, height, and diameter at breast height (dbh). The dbh was measured with a diameter tape at 1.3 m height. Tree height of at least five beech trees per stand were measured with a TruPulse Laser (Model 360 R, Laser Technology Inc., Centennial, USA). The resulting relationship between dbh and height (tree-height curves) per site was used to estimate the height of the other beech trees in the 10 m-radius neighborhood.

Aboveground wood biomass (AWB) was derived from the following allometric equation (Wutzler et al., 2008).

$$AWB = 0.0523 \text{dbh}^{2.12} h^{0.655} \quad (1)$$

$$\text{Wood_NPP_tree} = t2_AWB - t1_AWB \quad (2)$$

with AWB the total aboveground wood biomass per tree (kg), dbh the diameter at breast height (cm), h the tree height (m), $t1$ the time at the beginning and $t2$ at the end of the considered growth period, and NPP the net primary productivity of aboveground wood biomass ((kg dw)·tree⁻¹). Annual wood NPP equalled the difference between mean AWB of the 1st week of March and the 4th week of September. At the southern site we used a simple linear regression function ($y = b + ax$) derived from the relationship between annual wood NPP and dbh (Fig. 5a) of the target trees to estimate mean wood NPP of the trees without a dendrometer in the 10 m-radius neighborhood of the target trees (Fig. S2). At the northern site there was no significant relationship that could be used for upscaling tree NPP. Here, the mean wood NPP of the target trees was assumed for all trees in the neighborhood.

2.6. Statistical analyses

All statistical analyses were performed using the software environment R, version 3.5.2 (R Core Team, 2018). We treated all soil cores per stand and sampling date (3 cores × 3 tree pairs, $n = 9$) as independent samples (see Lwila et al., 2023 for more details), tree individuals per stand (3 tree pairs, $n = 6$) as random effects, and site properties as influencing factors. We used the TraMineR R-package (Gabadinho et al., 2011) to visualize and calculate diversity indices (based on the relative abundance of fine root biomass per individual tree). TraMineR uses Shannon-Wiener indices. The diversity of individual roots from trees at a specific soil core was calculated by the Shannon entropy with $h(p_1, \dots, p_s) = -\sum_{i=1}^s p_i \log(p_i)$, where p was the relative abundance of the individual tree i ; the log here was the natural (base e) logarithm; and s represented the number of identified markers per individual tree; thus, entropy was 0 when the soil sample contained roots from a single individual tree and was maximally 1 when all individual trees had the same root proportion per soil sample. We used fine root biomass per individual tree to analyze the root overlap in mixed stands, using pairwise comparisons of the sample means using Anova Fisher protected least significant differences at $P \leq 0.05$.

Linear regression analysis was used to analyze the relationship between annual wood NPP and dbh and/or annual root NPP. To compare the course of seasonal stem growth of all target trees, the starting point of growth was set at 1st March. Polynomial regression models were then used to analyze stem growth in the vegetation periods 2019 and 2020 (1st March to 30th September). We used the linear mixed-effects models in the 'lme' package (Bates et al., 2015) to model monthly wood NPP and root NPP. A variable tree was used as random effect, and a second co-variable (south/north) was included in the models to address differences in site properties. The generalized linear hypothesis testing (GLHT) using the 'multcomp' package (Hothorn et al., 2008) was used to predict the differences between months. We applied a pairwise comparison of the sample means using Anova Fisher protected least significant differences at $P \leq 0.05$ and TukeyHSD post-hoc tests using the 'agricolae' package in R (Mendiburu, 2009) to test the differences between the two regions.

3. Results

3.1. Comparison of fine root overlap of beech between sites and stand types

Analysis of the tree pairs in the pure beech stands, consisting of the target tree T (equipped with a dendrometer) and the closest neighboring tree N, revealed an unexpected heterogeneous pattern of fine root distribution and intermixing (Fig. 2a). As indicated by Shannon entropy, fine roots of different individuals do intermix, but the degree of intermixing was not related to the distance to individual tree stems, and it did not differ between stand types. In the monospecific stands, most soil cores contained roots of several individual beech trees. Only one soil core contained roots of a single target tree (Fig. 2a, pair 6), and two samples contained only roots from the paired tree (Fig. 2a, pair 3). Three cores contained roots from one of the paired trees plus unknown "other trees" (Fig. 2a, pairs 3 and 4). Although beech had higher fine root biomass (FRB) than the conifers in mixed stands (Fig. 2b, Table S1), the fine root overlap of the paired trees in mixed stands did not differ by distance.

3.2. Site effect on seasonal stem diameter increment

Differences between the southern region ("richer site") and the northern region ("poorer site") were observed in the seasonal diameter increment of all beech trees in 2019 and 2020. In 2019, mean diameter increment in the south was significantly higher ($P < 0.05$) than in the north, with the highest value of 6.7 ± 0.05 mm·yr⁻¹ recorded in the southern pure stand, while in the north, it reached just 3.4 ± 1.7 mm·yr⁻¹. Mean diameter increment of beech trees in mixture with spruce was 6.1 ± 0.4 mm·yr⁻¹ in the south and 1.2 ± 0.2 mm·yr⁻¹ in the north, and in mixture with Douglas-fir was 7.5 ± 0.9 mm·yr⁻¹ in the south and 1.4 ± 0.5 mm·yr⁻¹ in the north. In 2020, seasonal diameter increment was also significantly higher in the south than in the north, except for beech trees in the pure stands. In general, differences in tree diameter increment between the two sites were smaller in 2020 than in 2019. Mean diameter increment for beech mixed with spruce was 5.9 ± 0.2 mm·yr⁻¹ in the south and 2.0 ± 0.4 mm·yr⁻¹ in the north; when mixed with Douglas-fir it was 5.4 ± 0.01 mm·yr⁻¹ or 2.5 ± 0.4 mm·yr⁻¹ (Table 2). Thus, the lowest diameter increment values of beech were always observed in the mixed stand of beech with spruce. The two polynomial models presenting monthly average diameter increments of all trees showed that the significant differences between the sites resulted mainly from differences in growth in summer (June to September) (Fig. 3).

3.3. Linking seasonal wood and fine root NPP

Over the growing season from March to September 2019, average monthly wood and root NPP of beech showed distinct seasonality at both sites (Fig. 4a), irrespective of stand type (not shown). Monthly wood and root NPP did not increase linearly with time ($P > 0.05$) but exhibited a unimodal distribution. Pairwise analysis indicated significant differences between the months, and these differences were higher for root than for wood NPP. Interestingly, both wood and root NPP peaked in June but production in June contributed differently to total NPP; by 20% for wood NPP and 40% for root NPP. A sharp decline in wood NPP occurred in August, while root NPP had declined in July. Root NPP started earlier and terminated later than wood NPP.

3.4. Linking annual wood and fine root NPP

Mean annual wood NPP and root NPP across all target trees and their 10 m-radius neighbors significantly differed, as expected, between the study sites (Table 2, Fig. 4c). However, these two variables exhibited clear opposite trends; mean annual wood NPP was significantly higher in the south (73 ± 5.4 kg dw·tree⁻¹·yr⁻¹, $P < 0.01$) than in the north (10.8 ± 5 kg dw·tree⁻¹·yr⁻¹), while the reverse was found for annual root NPP

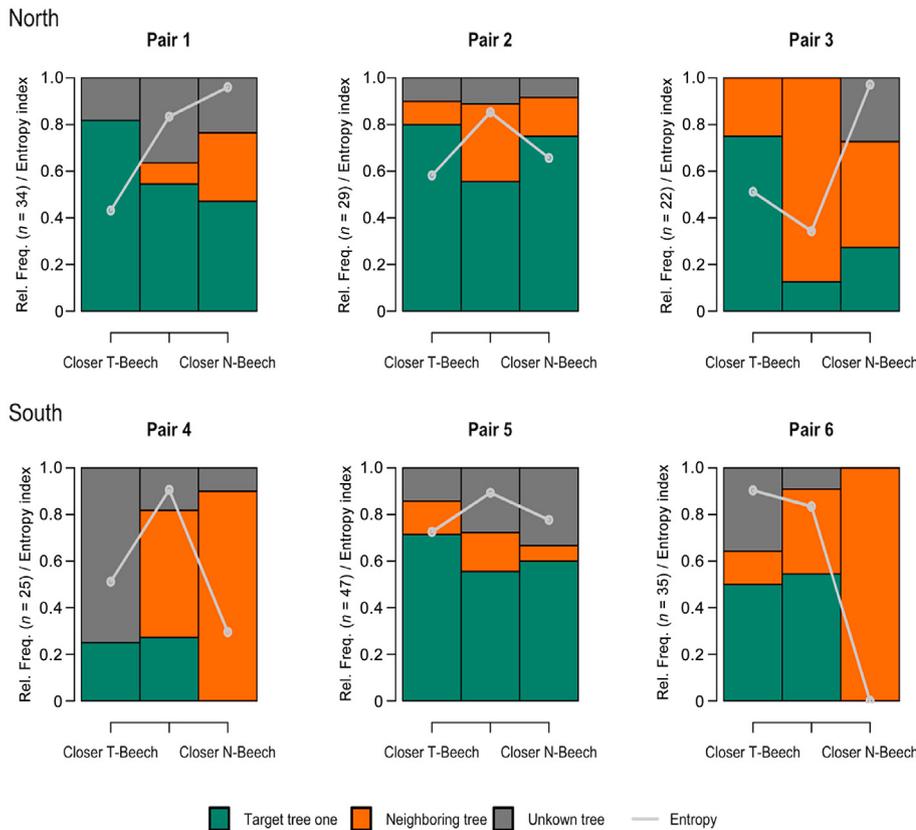


Fig. 2a. Fine root overlap of beech in pure stands. The color refers to the proportion of the individual tree at a specific soil core (in the organic layer and down to 30 cm soil depth) calculated from DNA genotyping. Gray lines show the Shannon entropy of the root distribution. An entropy of 0 indicates that only roots from a single tree are present in the soil core. The maximum 1 would be reached when all trees have the same proportion of roots in each soil core. T: target tree, N: neighboring tree, Unknown trees: Root that was genotyped, but could not be assigned to T or N. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

($215 \pm 12 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in the north, $151 \pm 12 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in the south; Fig. 4c). Also, when looking at the 10 m-neighborhood level there was a significant negative relationship between wood NPP and root NPP across the sites. However, this relationship was weak ($P > 0.05$, $R^2 = 0.26$, Fig. 5), and at the site level these two variables were not significantly correlated (southern region, $P > 0.05$, $R^2 = 0.01$; northern region $P > 0.05$, $R^2 = 0.40$). Furthermore, while wood NPP differed by a factor of 7.7 between the sites, root NPP differed only by a factor of 1.3.

4. Discussion

This study examined fine root overlap and the relationship between fine root and aboveground wood growth of European beech in intra- and interspecific neighborhoods under different site conditions. It was assumed that these variables contributed to the strong species identity effect on root biomass and dynamics observed in our previous studies, which were conducted in part at the same study sites. In those studies, we found that species identity was, after site conditions, the second most important influencing factor, while stand type (pure versus mixed stands) or species mixing had only a relatively weak influence (Lwila et al., 2021, 2023).

4.1. Fine root overlap

Belowground overlap of beech root systems was high, with an average of 60% in all soil cores, and did not differ between the study sites. Furthermore, fine root overlap between neighboring trees varied independently of their distance to the target trees or to stand type. This means that we did not find root territoriality or segregation in European beech stands, similar to the study of Lang et al. (2010). Studies in other ecosystems, such as Jones et al. (2011), Hiiesalu et al. (2012), and Brunner et al. (2004), also did not observe root segregation among conspecific neighbors, suggesting that root systems of conspecific trees do not avoid each other and that they compete for the same resources.

Indeed, a tree that avoids competition with the roots of the same species can be interpreted as having a competitive disadvantage (O'Brien et al., 2017) because it may reduce plant fitness (Schenk, 2006). The finding of extensive root overlap among neighboring trees contradicts our first hypothesis that fine root overlap was related to the distance between individual tree stems, leaving unresolved the question of whether or under what conditions plant roots might be territorial (Schenk et al., 1999).

Similarly, despite the high fine root biomass of beech compared to conifers in mixed pairs, neither beech roots nor conifer roots declined or increased with increasing distance from the stem (Fig. 2b; Table S1). This result is in contradiction to our second hypothesis, theoretical assumptions (Ammer and Wagner, 2005), and results provided by Rewald and Leuschner (2009), all of whom found strong relationships between distance from stems and fine root biomass. However, beech roots in our study dominated all soil cores, indicating that beech can occupy more rooting space than conifers. It could be argued that limited soil depth and/or horizontal space might have influenced our results. In the case of soil depth, we can exclude the possibility that our results were affected by shifts in vertical root distribution. Previous studies by Lwila et al. (2021) as well as Meinen et al. (2009) indicated that 80% of the fine root biomass accumulated in the top 30 cm of soil. Our study design was limited to the small distance scale between tree individuals and their crowns, roughly equivalent to the main rooting zones, (Leuschner et al., 2001b; Ammer and Wagner, 2005; Hendricks et al., 2006). It could be, therefore, that limitations in horizontal space resulted in absence of a relationship between root overlap and distances between individual trees. Indeed, all three species are known to spread their roots beyond their canopy, i.e., maximum horizontal extension of ca. 8 m for beech (Hölscher et al., 2002), ca. 9 m for Douglas-fir (Hendricks et al., 2006), and ca. 10 m spruce (Ammer and Wagner, 2005). However, our results demonstrated that roots of all three species are efficient at exploring horizontal soil compartments around the tree roots' growing zones. Roots of competing trees had similar opportunities to access distributed soil

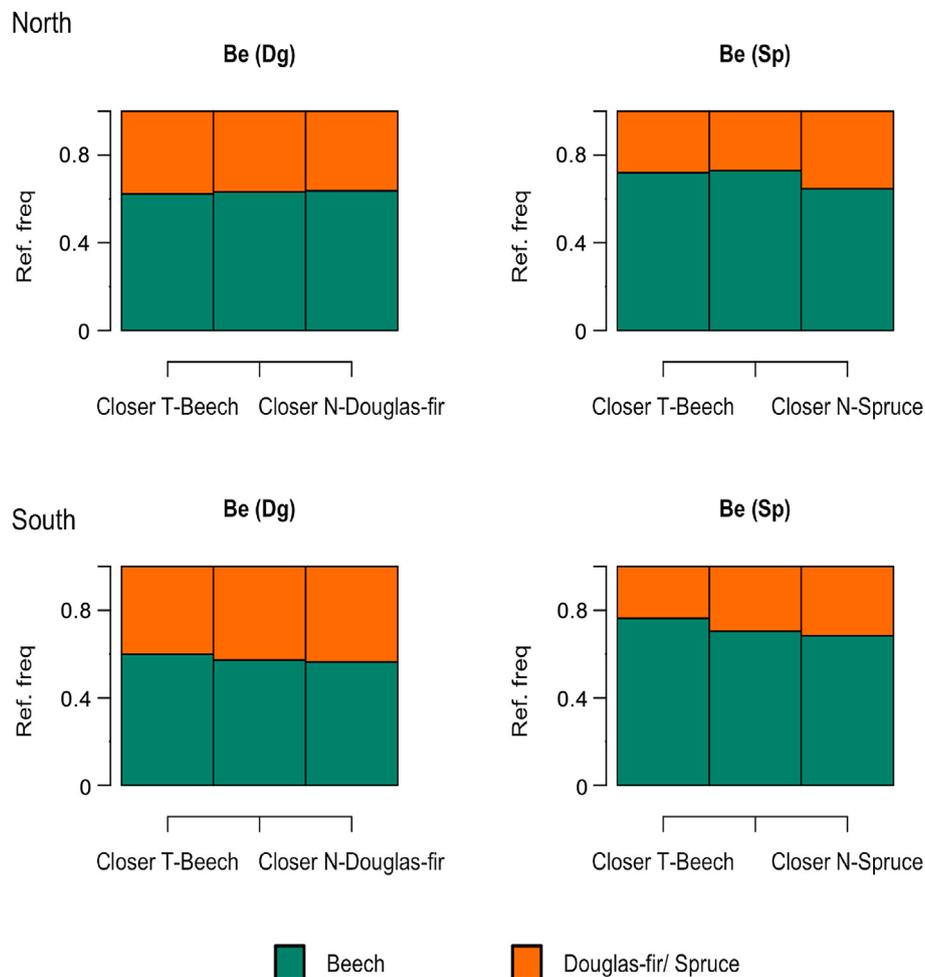


Fig. 2b. Fine root overlap of beech in mixed stands with spruce and/or Douglas-fir. Colors refer to the proportion of individual trees at specific soil cores (calculated from fine root biomass stock). T: target tree, N: neighboring tree; Be: Beech, Sp: Spruce, Dg: Douglas-fir. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

resources, which aligns with our previous conclusion regarding the superior belowground competitiveness of beech. European beech appears to be a strong competitor by producing more FRB than conifers.

Genotyping is essential for the analysis of root overlap in monospecies stands. The genotyping method applied here was successful for beech, where most of the fine roots could be attributed to individual trees, but ineffective for conifers. For the conifers, it failed to assign almost 50% of the fine root fragments to target trees. Thus, an analysis of root overlap was not possible in the pure conifer stands. Some possible reasons for our failure to match the sequences of needles and roots in the conifers are as follows. First, lower genotyping success may have been due to a lower quantity of DNA yield per extraction in fine root tissue than in leaves (Kesanakurti et al., 2011). Bruegmann et al. (2022) found lower DNA quality extraction from cambium than from leaf material in conifers (mainly spruce and pine), while in most deciduous trees the opposite was observed. Second, several studies have observed that DNA concentration declines due to changes in the distribution of root types and/or morphology (Haling et al., 2011; Fisk et al., 2010). For example, Fisk et al. (2010), working in a northern hardwood forest, found differences in DNA per unit root length and diameter despite the common root mass of each species. Root diameter effects on DNA extraction could be due to differences in gene copy numbers and tissue chemistry of larger, more structural, and less metabolically active roots (Fahey and Hughes, 1994; Pregitzer et al., 2002). If so, it is likely that root morphological differences (i.e., specific root length (SRL)) between beech and conifers (Lwila et al., 2021) explain the DNA quality differences between beech and

conifer roots.

Additionally, in spruce, a heavy infestation by bark beetles observed in the sampling year might have been associated with an extraordinarily high content of secondary plant compounds. These might have been produced as a defense reaction by the tree, in turn hampering the later amplification of the DNA extract (Bruegmann et al., 2022). Also, needle loss or fine root dieback due to a dry summer may have impacted DNA quality. Indeed, conifers frequently respond to dry summer by shedding needles (especially as old as 2 years), while beech shedding occurs only during exceptional droughts (Braun et al., 2020).

4.2. Linking annual diameter increment with root growth

Stem increment throughout the growing period was substantially higher in the south compared to the north (Fig. 4), and differences were higher in 2019 than in 2020. Lower stem increment in the northern than in the southern region resulted from less favorable growth conditions in the north. The disproportionately lower growth of beech in 2019 compared to 2020 in the north could have been a reaction to the serious drought in 2018 (Schuldt et al., 2020), which likely had resulted in extreme water deficits in the already drier climate of the northern region (Table S1). It is well known that stem growth of beech responds negatively to low precipitation and high temperatures in a previous year summer (Leuschner, 2020). Our results align with many other findings assessing the impact of the 2018 summer drought on central European forests (Schuldt et al., 2020; Stolz et al., 2021; Schnabel et al., 2022; Diers

Table 2

Mean stem diameter increment and mean aboveground wood NPP of the target trees (beech trees with dendrometers), and fine root NPP (diameter ≤ 2 mm) in the organic layer (OL) and mineral soil (0–30 cm depth) of beech in pure and mixed stands. The root values represent the means \pm standard error of three sampling points and three tree pairs per stand ($n = 9$ cores per stand, $n = 18$ cores per site). Sampling campaign March to September 2019. Significant differences are indicated with letters (Tukey Post-hoc test, $p < 0.05$) based on pairwise comparisons among individual stands and two regions. Upper case and/or lower case letters refer to comparisons within the specific variable and year. ST = Stem increment, Be = Beech, Sp = Spruce, Dg = Douglas-fir, () = Species admitted to beech in the mixed stands.

Stands/ species	ST (mm·yr ⁻¹)		Wood NPP (kg dw·tree ⁻¹ ·yr ⁻¹)		Root NPP (g·m ⁻² ·yr ⁻¹)	
	North	South	North	South	North	South
(a) 2019						
Be, (Dg)	1.4 \pm 0.5 A	7.5 \pm 0.9 C	5.4 \pm 2.2 a	69.3 \pm 11.5 b	164.3 \pm 4.8 AB	125.9 \pm 3.2 A
Be	3.3 \pm 1.6 B	6.8 \pm 0.1 C	21.3 \pm 10.7 a	76.6 \pm 3.4 b	306.6 \pm 6.4 D	218.5 \pm 12.7 C
Be, (Sp)	1.2 \pm 0.2 A	6.1 \pm 0.5 C	5.7 \pm 2.0 a	73.6 \pm 11.9 b	174.2 \pm 10.5 BC	128.1 \pm 7.2 A
(b) 2020						
Be, (Dg)	2.5 \pm 0.1 b	5.4 \pm 0.0 c	15.2 \pm 2.5 A	49.9 \pm 3.0 AB		
Be	5.8 \pm 0.6 c	5.9 \pm 0.1 c	31.3 \pm 8.8 AB	64.2 \pm 2.7 B		
Be, (Sp)	2.0 \pm 0.4 a	5.9 \pm 0.2 c	19.0 \pm 9.9 A	68.9 \pm 8.4 B		

et al., 2023), all of whom found substantial decreases in beech stem growth in most areas. Diers et al. (2023), working in Northern German Lowlands (an area somewhat similar to our northern study sites), found a greater decrease in stem growth of beech compared to pine; beech

growth depended on the weather conditions of the previous summer, while Scots pine growth was primarily influenced by the weather conditions of the current year. The response of stem growth of beech to the previous year's climate conditions (legacy effect) has also been previously reported in different parts of Europe, i.e., across Europe (Dittmar et al., 2003), France (Lebourgeois et al., 2005), the Alps (Di Filippo et al., 2007), and south-western, central, and northern Germany (Dulamsuren et al., 2017; Zimmermann et al., 2015; Diers et al., 2023).

Our data on root NPP refer only to 2019. However, based on previous studies of the effect of drought on root growth Leuschner et al., 2009 it can be assumed that root NPP in 2019 was also strongly negatively affected by the drought in 2018 due to a disruption of growth and/or a dieback of fine roots. It is also possible that the negative effects were more pronounced in the poor, northern than in the rich, southern region. If this was the case, the relatively higher root NPP in the north compared to the south in 2019 might be, at least in part, a 'positive legacy effect'; regeneration of the fine root system after 2018. Furthermore, in our first study (Lwila et al., 2021) on fine root biomass, carried out on a random grid at stand level in spring 2018, before the main growth phase of fine roots and the drought period, fine root biomass of the pure beech stand in the north was nearly twice as high as that in the south. In mixture with Douglas-fir, no significant difference was found, and in mixture with spruce it was 2.8 times higher in the north than in the south. Assuming that the biomass data from 2018 represented the average "basic" fine root biomass for a given stand structure and site conditions, the beech trees in the north would have needed to allocate relatively more growth (or assimilates) to the roots to maintain their basic root biomass than they would have in the south. In 2019, the difference in mean fine root biomass of the two sites, studied at the neighborhood level of the same tree pairs as in this study (Lwila et al., 2023), were much lower (mean factor was about 1.4). Comparison of absolute biomass values from these two studies are limited because of the different spatial scales and sampling

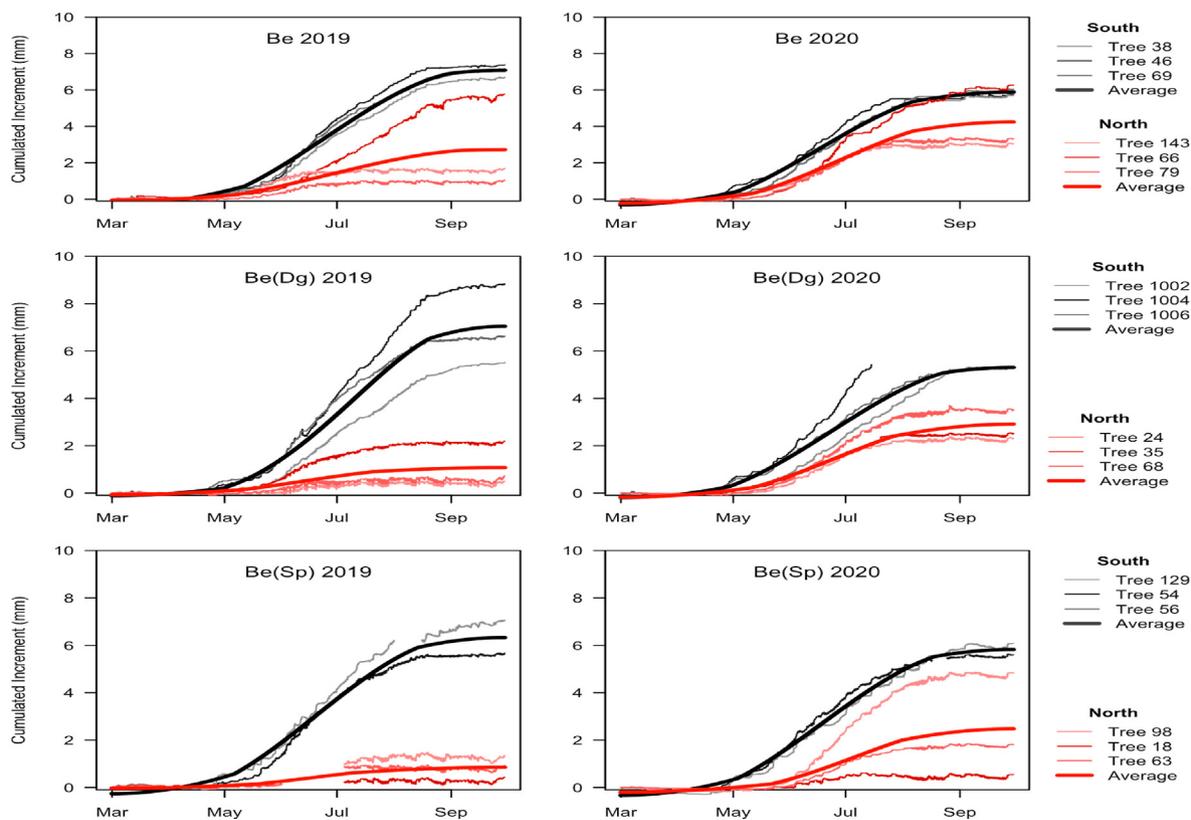


Fig. 3. Seasonal cumulative diameter increment of the target trees (Be) at the pure and the mixed stands with Douglas-fir (Dg) and/or spruce (Sp) at the two sites in 2019 and 2020. The thick lines mark the polynomial function fitted as the average of all measured trees per site. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

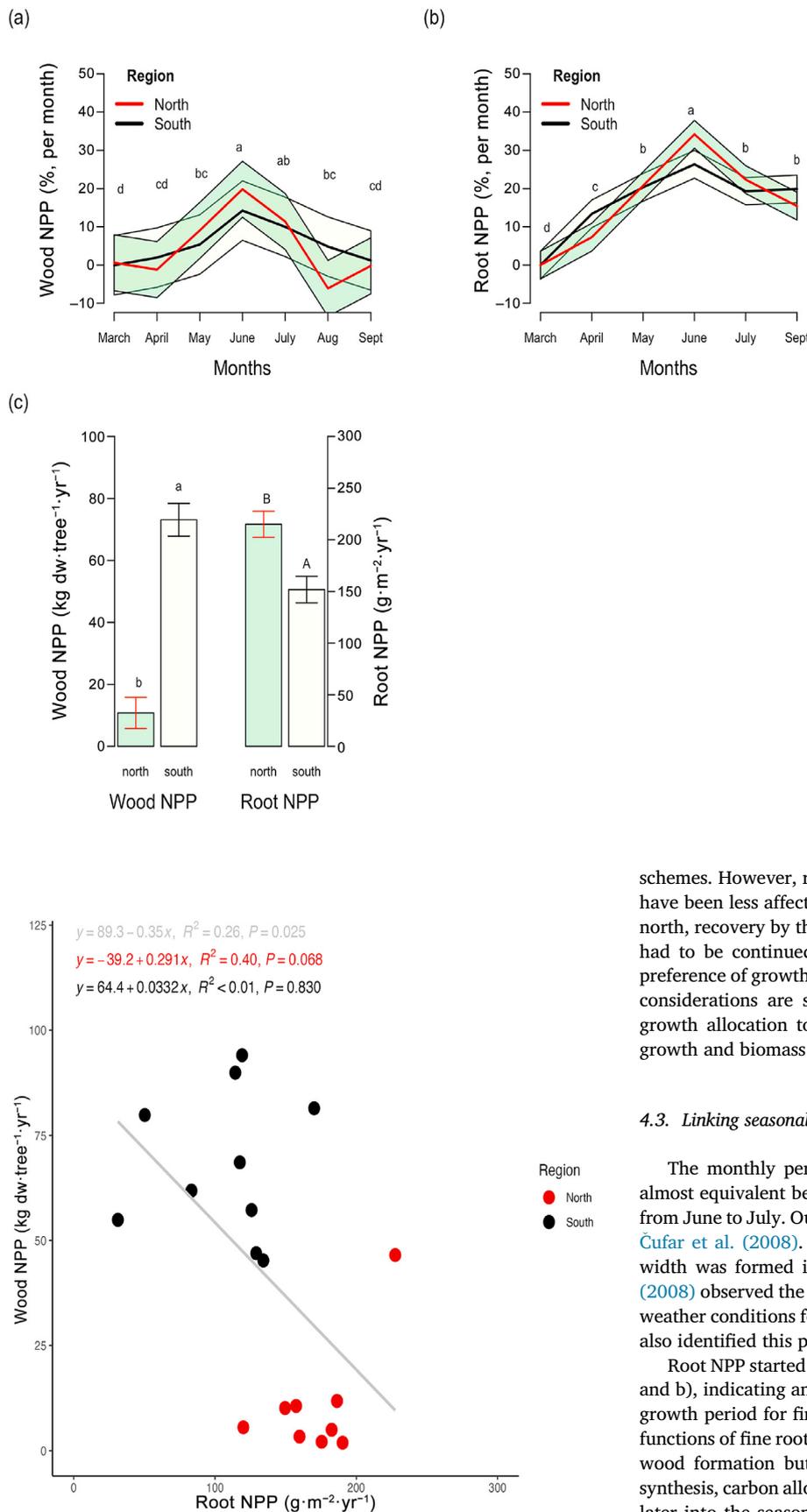


Fig. 4. Relative mean seasonal wood NPP (a) and root NPP (b) in 2019 for the two regions. The letters above the lines indicate significant pairwise differences between different months. The green and the light yellow areas indicate the confidence interval of the polynomial regression model for the north and the south, respectively. The letters above the confidence interval indicate significant pairwise differences between different months. (c) Mean annual wood and root NPP in 2019 of the two regions. The letters above the bars indicate significant pairwise differences between different site conditions (Tukey post-hoc test, $p < 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Fig. 5. Relationship between mean annual wood NPP per tree and mean annual fine root NPP in the two regions. Gray line: Linear regression over both regions. Each data point represents a tree pair ($n = 9$ per site) and its neighboring beech trees within a radius of 10 m.

schemes. However, relative differences between north and south should have been less affected by this limitation and might indicate that in the north, recovery by the fine root biomass was not completed in 2019 and had to be continued in 2020, possibly due to a weaker but ongoing preference of growth allocation to the roots compared to the stem. These considerations are speculative but would correspond with a shift in growth allocation to fine roots at the expense of aboveground wood growth and biomass as a response to unfavorable site conditions.

4.3. Linking seasonal above- and belowground growth

The monthly percentages of wood and/or root NPP of trees were almost equivalent between study sites (Fig. 4a and b), and both peaked from June to July. Our results for stem growth are comparable to those of Čufar et al. (2008). In their study, about 35% of the annual tree ring width was formed in June. Dittmar et al. (2003) and Piovesan et al. (2008) observed the highest sensitivity of annual stem growth to current weather conditions for the period of May to July, and Mund et al. (2010) also identified this period as the main phase of stem growth in beech.

Root NPP started earlier and terminated later than wood NPP (Fig. 4a and b), indicating an extended vegetation period for root NPP. A longer growth period for fine roots seems reasonable with respect to the main functions of fine roots: water and nutrient uptake are needed not only for wood formation but many other processes: leaf development, photosynthesis, carbon allocation and storage etc., that start earlier or continue later into the season than wood formation. How far this result can be generalized, however, remains uncertain. We cannot exclude the possibility that, similar to total root growth (see above), the seasonal growth pattern in 2019 was also affected by extreme drought in 2018. Nevertheless, studies in boreal, arctic, and temperate biomes found similar

seasonal patterns of above- and belowground growth as we did (Abramoff and Finzi, 2015; Blume-Werry et al., 2016).

4.4. Growth partitioning between above- and belowground as a response to site conditions

The opposite responses of wood and root NPP to site conditions (Fig. 4c) and/or the negative relationship between wood and root NPP across our study sites (Fig. 5) support our third hypothesis and the predictions from “optimal partitioning theory” (McConnaughay and Coleman, 1999). The “optimal partitioning theory” suggests that under poor site conditions, plants shift biomass allocation from aboveground to belowground tree compartments. Several previous studies have confirmed that plants increase root NPP to optimize growth under drought conditions, likely resulting from changes in the relative importance of limiting resources (such as water and nutrients).

This finding confirms our previous assumption (see Lwila et al., 2021, 2023) that beech trees tend to allocate more growth or carbon to roots at dry sites where water is the most limiting factor, and to stem wood at rich sites where light is the most limiting factor (Farrior et al., 2013). Several studies have reported the existence of a ‘wood-fine root’ trade-off (i.e., Dybzinski et al., 2011, in theoretical framework stands) and/or ‘root-shoot’ trade-off (i.e., Hertel et al., 2013, in mature beech stand) as potential adaptation mechanisms to changing site conditions.

We interpret the higher root NPP at the northern, poorer site not only as an adaptation mechanism of beech to unfavorable soil conditions, but also as an indicator of plasticity of the root system, by which they allocate more biomass to deeper soil layers in order to better acquire limited resources (Weemstra et al., 2017; Finér et al., 2007). It is likely that this high degree of plasticity in biomass partitioning (see also Schall et al., 2012) is one key factor in the tolerance of this tree species to a wide range of climatic growing conditions (Ellenberg and Leuschner, 2010).

Surprisingly, we did not find relationships between above- and belowground wood NPP at the tree and neighborhood levels, which contrasts somewhat with the optimal partitioning theory. Previous studies have also reported conflicting results of the response of below- and aboveground growth at the tree level. Some reported a strong relationship between above- and belowground tree compartments (Hertel et al., 2013; Meier et al., 2018), but others did not find such a relationship (Friedrichs et al., 2009). Meier and Leuschner (2008) studied carbon partitioning in 14 mature stands across a precipitation gradient. They found that fine root biomass increased with increasing precipitation while leaf biomass remained constant. These seemingly contradictory findings may depend on many factors. One may be the intensity or duration of soil water limitation (Zang et al., 2014). Trees can adapt to moderate water stress in two ways: i) by enhancing root productivity with a surplus of assimilated carbohydrates that are exported to the roots due to allocation changes (Prescott et al., 2020), or ii) by reducing stomatal conductance and photosynthetic enzyme activity (Leuschner et al., 2001a), resulting in a small reduction in wood NPP. Additionally, root growth usually tends to cease if soil water matric potential approaches < -0.1 MPa in mature beech stands (Zang et al., 2014). Beech fine root growth seems to be particularly sensitive to short-term drying in the main growth phase. However, previous studies have found that beech fine root NPP ceased during a short-term drought in July, but new roots produced in August compensated for the earlier drought effect (Leuschner et al., 2001a; Zwetsloot and Bauerle, 2021).

Impacts of previous management practices, specifically selective thinning, could also explain our observed lack of above- and belowground NPP relationships at the tree and neighborhood levels. Depending on the type and intensity of previous thinning and the time lapse since the last thinning, the ratio between above- and belowground growth might reflect more a “man-made”, temporal local resource distribution than average site conditions.

Beyond the temporal variability of growth allocation to roots or shoots caused by variable weather conditions and/or recent

management, small-scale differences in soil properties, which are very common at the studied sites, might lead to great variability in growth allocation within a stand. An example of this can be observed by the single tree no. 98 and its related tree pair in the north, both of which had growth rates nearly the same as the trees and pairs in the south (Figs. 3 and 5). Consequently, significant relationships between above- and belowground growth can be found only when there are substantial, long-lasting site differences at larger scales, such as those between the two regions compared in this study.

4.5. Indications for the potential to deal with increasing drought

Many recent studies have reported contrasting results regarding the drought sensitivity and adaptability of beech, which makes it challenging to predict species responses to future climate change (Schuldt et al., 2020; Schnabel et al., 2022; Rukh et al., 2023). Some studies have reported declining growth rates of beech and broadleaf tree species in the dry continental climate (Piovesan et al., 2008; Weigel et al., 2023; Zimmermann et al., 2015), while others have found successful adaptation (Scharnweber et al., 2011; Stolz et al., 2021). Hackett-Pain et al. (2018) even found increased growth of beech at a climate site that has been relatively dry since the 1990s, suggesting that its climate sensitivity was decreasing, which they interpreted as the drought resistance success of beech. The higher fine root growth at the poorer site than at the richer site observed in our study suggests at least a ‘plastic’ belowground response of European beech to water limitation. The negative relationship between wood and root NPP across our study sites indicates a trade-off between above- and belowground growth (Chapter 4.4). When focusing only on stem growth this might be interpreted as a general limitation of beech growth under existing site conditions in the northern region. But, when considering the entire tree and the basic function of fine roots to supply the tree with water and nutrients, the shift of growth allocation to fine roots – even at the expense of stem growth as in our study – can be interpreted as a mechanism for successfully coping with increasing drought.

5. Conclusions

The observed negative relationship between above- and belowground growth across sites suggests an ‘optimal partitioning’ of growth that corresponds with an optimization of the ‘cost-benefit ratio’ of growth. Trees favor root growth when water or nutrient resources are limited. In fact, aboveground growth reductions that accompany an increase in belowground growth and biomass due to reduced belowground resource availability should not be interpreted only as a sign of vulnerability to stress. Instead, such a shift in growth allocation could also be seen as a suitable adaptation to stress, and thus, may be a reasonable mechanism by which beech can cope with increasing drought under climate change. Beech exhibited no indication of fine root territorial competition in the presence of both conspecific and heterospecific neighbors. This means beech that has the capacity to respond to limited resources not only above- but also belowground and maintain its competitiveness even in mixture with the highly productive non-native Douglas-fir. This confirms the conclusion from our previous study on fine root dynamics that mixed beech-Douglas fir stands could become a reasonable alternative to the mixture of beech and spruce since spruce is seriously affected by drought and bark beetle attacks.

From a methodological point of view, the present study demonstrates that application of molecular techniques can be used in the future to investigate how environmental drivers such as nutrient availability, spacing, light, and other factors influence conspecific root competition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

CRedit authorship contribution statement

Amani S. Lwila: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christian Ammer:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Oliver Gailing:** Writing – review & editing, Resources, Methodology, Investigation. **Ludger Leinemann:** Methodology, Data curation. **Martina Mund:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Acknowledgements

The study was conducted as part of the Research Training Group 2300, funded by the German research funding organization (Deutsche Forschungsgemeinschaft –DFG) Grand id: 316045089. We gratefully acknowledge the administrative support by Serena Müller and the indispensable help of Andreas Parth, Michael Unger, Karl-Heinz Heine, Julian Meyer and Ulrike Westphal during soil core sampling. We thank Dirk Hölscher, Torsten Vor, and Dietrich Hertel for their advice on root sampling. We also thank the numerous student helpers for carefully washing the soil samples and extracting fine roots. We are grateful to Jonas Glatthorn for the advices and assisting in calculating beech APA. We also thank Christina Hackmann for preparation of dendrometer data and Kathleen Regan (USA) for linguistic corrections.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2024.100217>.

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