



Heavy thinning from above affects growth and coarse root-stem allometry of mature Scots pine (*Pinus sylvestris* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) in monospecific and mixed-species stands

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Abstract

Key message Heavy thinning from above promotes coarse root and stem diameter growth in both Scots pine and sessile oak. Coarse root-stem allometry indicates a greater allocation of resources to coarse roots relative to the stem in both species.

Abstract The effects of heavy thinning from above on stem and coarse root growth, as well as on coarse root–stem allometry, were investigated in mature Scots pine (*Pinus sylvestris* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) growing in monospecific and mixed stands in Bavaria, Germany. Thinning was conducted in autumn 2017, and growth was analyzed over a five-year pre-thinning (2013–2017) and post-thinning (2018–2022) period using replicated thinned and unthinned plots. Thinning substantially enhanced diameter growth in both species. On average, stem increments increased by 26–61% and coarse root increments by 2–77% relative to unthinned controls, with the relative growth between stems and coarse roots varying among variants. Coarse root–stem allometry showed species-specific responses: in Scots pine, thinning intensity had the strongest effect, whereas in sessile oak, variation was more closely linked to precipitation and water availability. Across all variants, allometric exponents ranged from 1.59 to 7.14, with sessile oak exhibiting higher values than Scots pine, reflecting greater proportional investment in coarse roots among species and thinning regimes. Overall, heavy thinning from above promoted growth and altered biomass partitioning between stems and coarse roots in both species. Stimulated coarse root development likely improved anchorage, water and nutrient uptake, and resilience to climatic stress, thereby strengthening stand stability. These findings highlight the importance of adapting thinning strategies to species-specific traits and site conditions to enhance forest productivity and adaptability under changing climatic conditions.

Keywords Thinning · Root growth · Stem growth · Root-stem allometry · Scots pine · Sessile oak

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Introduction

Ongoing climate change presents major challenges for European forests (Seidl et al. 2011, 2017; Stojanović et al. 2014; Madritsch et al. 2019; Černý et al. 2024). In Central Europe, mean temperatures are projected to rise by 1.5–2 °C during the 21st century relative to pre-industrial levels (Winkler et al. 2008; Kjellström et al. 2018). Together with elevated atmospheric CO₂ and longer growing seasons, this warming may stimulate tree growth (Boisvenue and Running 2006; Pretzsch et al. 2014a). At the same time, increasingly frequent and severe heatwaves and droughts are expected to reduce forest stability and increase tree mortality risk (Dobbertin et al. 2007; Allen et al. 2010; Choat et al. 2018; Anderegg et al. 2020). Because of their long lifespans, trees

have limited capacity to adapt rapidly to such changes (Lindner et al. 2010; Schuldt et al. 2020). Although species have evolved diverse strategies to cope with environmental shifts (Kremer et al. 2012; Valladares et al. 2014), drought sensitivity varies considerably among taxa (Häberle et al. 2012; Pretzsch et al. 2013a, 2014b, 2020a). Phenotypic plasticity, local adaptation, ecological versatility, and site conditions play key roles in determining drought resistance and distribution patterns (Pedlar and McKenney 2017; Fréjaville et al. 2020). Ultimately, species' capacity to adjust to changing conditions will be critical for persistence under future climate scenarios (Bréda et al. 2006; Bisbing et al. 2021).

Scots pine (*Pinus sylvestris* L.) is among Europe's most widespread and economically important conifers. It is valued for timber production, reforestation, and its ecological resilience, thriving even in nutrient-poor soils and harsh climates across boreal and temperate regions from Spain to Siberia. Sessile oak (*Quercus petraea* (Matt.) Liebl.) is a key broadleaved species, prized for its high-quality timber, its role in supporting biodiversity, and its contribution to drought tolerance, stand stability, and productivity in mixed forests. It occurs widely across Europe, from western France to eastern Ukraine, particularly on well-drained hilly and mountainous soils (Ellenberg 1988; Ellenberg and Leuschner 2010; Eaton et al. 2016; Houston Durrant et al. 2016). Together, Scots pine and oaks (sessile and common oak, *Quercus robur* L.) currently occupy ~1.3 million ha in mixed stands in Europe, with a potential distribution of 35 million ha (Pretzsch et al. 2020b; Brus et al. 2012). This species combination is expected to gain importance because they are economically valuable, well-suited to adaptive management, and more resilient to climate change than Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.) (Obladen et al. 2021). Their broad ecological range allows tolerance to fluctuating water supply and drought (Fischer 1995; Annighöfer et al. 2015), making them crucial for sustainable forest management and biodiversity conservation. As climate change alters competitive dynamics, Scots pine and oaks are projected to gain advantage due to their higher drought resilience compared to other widespread species (Spellmann et al. 2011; Bouwman et al. 2021; Hallingbäck et al. 2021).

Mixed-species forests often surpass monocultures in productivity, biodiversity, stability, and resistance to pests and pathogens, thereby providing broader ecological and socioeconomic benefits (Knoke et al. 2008; Pretzsch et al. 2013b, 2015; Jactel et al. 2017; Gamfeldt et al. 2013). Studies show that mixing Scots pine with oaks reduces drought susceptibility and enhances productivity compared to monocultures, with effects depending on site water availability and fertility (Steckel et al. 2019, 2020). Under climate change, mixed stands are better able to buffer extreme events through

complementary resource use and reduced host density for specialized pests (Forrester 2014; Pardos et al. 2021). Species diversity and functional complementarity further strengthen resilience, as above- and belowground interactions enhance biodiversity, productivity, and stability (Forrester et al. 2016; Vitali et al. 2018; Grossiord 2020; Liu et al. 2018; Jing et al. 2021). As aridity intensifies, promoting mixed-species stands will be essential for maintaining forest health and functioning (Puettmann et al. 2012; Brang et al. 2014; Pretzsch and Zenner 2017). For example, in Central Europe, competition between European beech and sessile oak is expected to shift toward sessile oak due to the higher drought sensitivity of European beech (Mette et al. 2013), while in the Netherlands, Scots pine–common oak mixtures are projected to outperform monocultures, with Scots pine gaining an advantage on resource-poor soils (Bouwman et al. 2021). At larger scales, Scots pine–oak mixtures show complementary growth across Europe, with Scots pine performing better on nutrient-rich sites and oaks on nutrient-poor sites, fostering productive and climate-resilient forests (Pretzsch et al. 2020b).

Stand density and species composition strongly affect growth efficiency in mixed forests, with stocking degree shaping tree interactions (Condés et al. 2013; Forrester 2017). Alongside species selection, thinning remains a key silvicultural practice, reducing competition to enhance growth, drought resilience, and carbon storage (Bréda et al. 1995; Aldea et al. 2017; Montwé et al. 2022; Zhang et al. 2024). Thinning also improves stability by modifying stem architecture, stimulating root development, and fostering structurally complex, species-rich stands (Cremer et al. 1982; Nyland 2016; Li et al. 2021). In mixed stands, effects depend on species traits and thinning regime, with potential to increase resilience and productivity through greater heterogeneity and moderated interactions (Chen et al. 2014; Aldea et al. 2023). Effective management requires calibrating thinning intensity, species selection, and timing to sustain health and long-term resilience (Puettmann et al. 2012; Del Río et al., 2017). In contrast, thinning responses in monocultures often diverge from those in mixtures (Bartelink 2000; Zamora-Pereira et al. 2021). Generally, thinning intensity strongly modulates tree growth and drought responses, with most studies reporting increased DBH and improved drought tolerance proportional to intensity and frequency (Cescatti and Piutti 1998; Sohn et al. 2013, 2016a, b; Aldea et al. 2023). Moderate thinning (20–40% basal area removal) typically enhances soil infiltration, water retention, and climate resilience, though effects may diminish after 30–40 years (Chen et al. 2014; Ameztegui et al. 2017). Conversely, overly intensive thinning can compromise wood quality, reduce yield, delay canopy closure, and increase mortality risk (Mäkinen and Isomäki 2004; Del

Río et al., 2017; Bréda et al. 2006), while light thinning may provide insufficient drought and pest protection (Hood et al. 2016; Castagneri et al. 2022). Site conditions strongly mediate outcomes: in moist, high-elevation forests, thinning mitigates drought stress by improving resource availability (Giuggiola et al. 2013), whereas in arid regions it may reduce growth and exacerbate drought stress by accelerating soil drying (Del Río et al. 2008). These findings highlight the need for adaptive, site-specific thinning strategies to sustain productivity and resilience under climate change (Zamora-Pereira et al. 2021; Zhang et al. 2022, 2024). While aboveground responses such as stem growth and canopy expansion are well documented (Han et al. 2014; Drew and Downes 2018; Li et al. 2023), belowground dynamics remain less explored (Leuschner et al. 2001; Freschet et al. 2021). In particular, the effects of thinning on root development are poorly understood (Wang et al. 2019), despite the crucial role of roots in stability, resource acquisition, and belowground carbon storage in forest ecosystems (Coutts 1983; George and Marschner 1996; Brunner and Godbold 2007; Kalliokoski et al. 2008).

This study extends previous research by examining how thinning from above and water availability influence coarse root–stem allometry in Scots pine and sessile oak across monospecific and mixed stands. Tree biomass allocation is shaped by intrinsic strategies and external drivers, balancing resource distribution among organs in response to biotic and abiotic factors (Niklas 1994, 2004; Weiner 2004; Weiner et al. 2009; Nikolova et al. 2011). While allocation patterns are generally consistent across species, research highlights their plasticity, enabling acclimation to changing environments

(Comeau and Kimmins 1989; Hulshof et al. 2015; Qiu et al. 2021). Two major frameworks underpin this field: (i) the balanced growth hypothesis, which posits that resources are allocated to the most limiting organ (Bloom et al. 1985; Shipley and Meziane 2002), and (ii) allometric partitioning, where allocation scales with plant size following predictable scaling laws (Niklas 1994; West et al. 1999; Poorter et al. 2012). Allometric relationships are species-specific and influenced by stand composition, climate, competition, and age (Pretzsch 2009a; Genet et al. 2011; Forrester et al. 2017; Zhang et al. 2019, 2020). Incorporating intra- and interspecific competition into allometric models has accordingly been recommended to better capture variability across tree organs (Del Río et al. 2019). Although thinning effects on growth (Peltola et al. 2007; Kerr and Haufe 2011; Pretzsch 2020) and stand composition (Pretzsch and Forrester 2017; Pretzsch 2018, 2019) have been widely studied, their impact on allometry remains insufficiently explored (Deng et al. 2019). Some studies have analyzed coarse root–stem allometry (e.g., Drexhage et al. 1999; Nikolova et al. 2011; Pretzsch et al. 2012a, b; Ulbricht et al. 2025), yet the role of environmental conditions and species mixing remains unclear (Nikolova et al. 2011). Understanding how composition, thinning intensity, and water availability govern biomass allocation is therefore essential for optimizing silviculture and enhancing carbon sequestration under climate change (Dutcă et al. 2018).

In summary, this study evaluates how intra- and interspecific competition affect above- and belowground growth by comparing monospecific and mixed stands of Scots pine and sessile oak. It further investigates the effects of heavy thinning from above on stem and coarse root growth, and specifically assesses how thinning influences (Q1) stem growth, (Q2) coarse root growth, and (Q3) coarse root–stem allometry, with emphasis on thinning intensity and annual water availability. By addressing these aspects, the study contributes to a deeper understanding of growth responses across different stand compositions and management regimes.

Materials and methods

Experimental area

Two experimental sites were selected in the Franconian region of Bavaria, Germany: one near Baunach (49°56′48.1″N, 10°50′44.0″E) and the other near Triesdorf (49°13′39.8″N, 10°33′28.0″E), both characterized by similar climatic conditions but differing in geology (Table 1).

Table 1 Climate data and location characteristics of the Baunach and Triesdorf experimental sites (PRECIP: precipitation, precipveg: precipitation within vegetation period, T: temperature and tveg: temperature within vegetation period)

Metric	Unit	Baunach	Triesdorf
PRECIP	[mm]	574	573
PRECIPVeg	[mm]	288	323
T	[°C]	10.1	9.6
TVeg	[°C]	15.6	15.0
Altitude	[m]	370	480
Geology		Keuper	Shell Limestone
Soil type		Loess-derived Cambisols	Terra Fusca, brown earths, calcareous brown earths, and colluvial soils
Soil texture		Sandy loam topsoil overlain by a silt layer	Sandy loam containing varying proportions of clay and silt
Humus form		Moder and mull under oak, mor humus under pine	Moder and mull under oak, mor humus under pine
Forest type		Galio-Carpinetum	Galio-Carpinetum

Experimental design

At each site (Baunach and Triesdorf), six plots were selected, consisting of one triplet of Scots pine (hereafter also “pine”) stands and one triplet of sessile oak (hereafter also “oak”) stands. These plots were further categorized by stand type (monospecific vs. mixed) and treatment (unthinned vs. thinned). Across both sites (12 plots total), this design yielded eight stand type variants: pine monospecific unthinned (PPU), pine monospecific thinned (PPT), pine mixed unthinned (PMU), pine mixed thinned (PMT), oak monospecific unthinned (OPU), oak monospecific thinned (OPT), oak mixed unthinned (OMU), and oak mixed thinned (OMT). In autumn 2017, heavy thinning from above was implemented to reduce competition by selectively removing dominant and co-dominant trees (data are shown in Tables 3 and 4, Sect. “Local Stand Density Index (SDI), Δ SDI (delta SDI), and Basal Area (BA) (Q3)”). The average stand ages by variant were as follows: PPU=70 years, PPT=70 years, PMU=75 years, PMT=75 years, OPU=90 years, OPT=90 years, OMU=75 years, and OMT=75 years — classifying this as a mature stand thinning. In autumn and winter 2022, 10 dominant trees were selected from each of the four unthinned stand type variants based on Kraft’s social classes 1 and 2 (Kraft 1884), representing trees that would have been designated as crop trees under thinning practices. Similarly, 10 crop trees from Kraft’s social classes 1 and 2 were also selected from each of the four thinned stand type variants. This resulted in 80 sample trees per site, totaling 160 sample trees across the experiment. Diameter at breast height (DBH, cm) and total tree height (m) were measured for each

sample tree. Increment cores were collected following standard techniques described by Nikolova et al. (2011). Two stem cores were extracted at DBH (1.3 m), one from the north and one from the east. Coarse root core sampling was conducted on a reduced subset of 5–8 trees per stand type variant due to difficult soil conditions and deep root growth at both sites. Two coarse roots per tree were exposed at a minimum distance of 0.5 m from the trunk edge, and their diameters were measured. Two increment cores were taken per coarse root, drilled obliquely from above and rotated by 90° to minimize bias from elliptical root cross-sections. To enable reconstruction of stem and coarse root growth from 2022 back to 2013, increment cores were taken to reach the pith whenever possible. A schematic of the core sampling method is provided in Pretzsch et al. (2012b). Annual radial increments were measured using a Digitalposiometer Type 2, following the method described by Johann (2000) and Biritz GmbH (2012). Tree-ring sequences for each stem and the two coarse roots were synchronized and averaged per tree, resulting in a single increment sequence for each tree’s stem and one for its coarse roots. The increment data were normalized to serve as the foundation for analyzing the effects of thinning on coarse root and stem growth (see Chap. 2.3). Additionally, diameter measurements were log-transformed for use in coarse root–stem allometric analyses (see Chap. 2.7). Table 2 summarizes the averaged dendrometric coarse root and stem increment data at the single-tree level by stand type variant (PPU, PPT, PMU, PMT, OPU, OPT, OMU, OMT) for 2013–2022, as well as averaged tree height, DBH, and coarse root diameter measured in autumn and winter 2022. For further information on the

Table 2 Averaged heights, coarse root and stem diameters, and radial increment data of cored sample trees from Baunach and Triesdorf, categorized by stand type variants: pine monospecific unthinned (PPU), pine monospecific thinned (PPT), pine mixed unthinned (PMU), pine mixed thinned (PMT), oak monospecific unthinned (OPU), oak monospecific thinned (OPT), oak mixed unthinned (OMU), and oak mixed thinned (OMT) within the period 2013–2022. Abbreviations: N=Number of sample trees, H=Tree height, DBH=Diameter at breast height, D=Coarse root diameter, i=radial increment, norm i=normalized radial increment

Stand type	N (stem)	H (min. - max.) [m]	DBH (min. - max.) [cm]	i stem (min. - max.) [mm]	norm i stem (min. - max.) [mm]	N (root)	D (min. - max.) [cm]	i root (min. - max.) [mm]	norm i root (min. - max.) [mm]
PPU	20	21.20 (19.30–22.60)	32.56 (23.00–38.80)	1.84 (0.26–5.28)	1.84 (0.26–5.28)	12	11.12 (8.15–15.55)	1.08 (0.17–3.15)	1.08 (0.17–3.15)
PPT	20	21.24 (19.10–23.80)	32.65 (23.10–48.50)	2.10 (0.61–4.85)	2.36 (0.67–5.22)	11	9.19 (7.45–11.45)	1.08 (0.20–3.72)	1.33 (0.20–5.13)
PMU	20	23.93 (22.00–25.90)	33.69 (26.70–40.10)	1.36 (0.23–4.13)	1.36 (0.23–4.13)	13	9.61 (6.75–14.60)	0.70 (0.12–2.33)	0.70 (0.12–2.33)
PMT	20	23.73 (21.80–25.80)	31.57 (25.40–39.00)	1.84 (0.16–5.60)	1.68 (0.18–4.56)	10	9.07 (5.40–11.35)	1.19 (0.15–4.19)	0.92 (0.14–3.00)
OPU	20	20.70 (16.30–25.4)	30.73 (16.20–51.70)	1.93 (0.26–5.00)	1.93 (0.26–5.00)	11	10.96 (7.30–19.40)	2.42 (0.19–8.48)	2.42 (0.19–8.48)
OPT	20	20.75 (18.40–22.30)	28.14 (18.70–35.80)	2.19 (0.56–6.62)	2.41 (0.58–7.87)	11	11.10 (9.15–13.80)	3.19 (0.27–9.59)	2.44 (0.12–8.25)
OMU	20	22.52 (21.30–24.00)	33.13 (26.70–42.60)	2.01 (0.74–4.32)	2.01 (0.74–4.32)	11	11.02 (7.70–16.90)	3.18 (0.56–8.09)	3.18 (0.56–8.09)
OMT	20	21.67 (19.90–24.10)	31.58 (24.60–45.00)	2.25 (0.58–6.19)	2.28 (0.61–6.13)	10	10.41 (9.30–11.60)	3.16 (0.74–8.85)	4.32 (0.78–13.54)

experimental sites in Baunach and Triesdorf, as well as the experimental design, refer to Pretzsch et al. (2020b).

Normalized radial increments (Q1 and Q2)

To assess the impact of thinning on the radial increments of stem and coarse root compartments while accounting for pre-thinning growth rates, the growth trend method described by Pretzsch and Utschig (1989) was applied. The analysis covered the period from 2013 to 2022, constrained by the challenging soil conditions and the limited accessibility of oak roots for coring prior to 2013. Radial increments from unthinned plots, categorized by tree species and stand type, during the pre-thinning period (2013–2017) served as the reference, with 2017 marking the year of thinning. For this reference period, average radial increments for stem and coarse root compartments were calculated for the respective stand type variant pairs: PPU vs. PPT, PMU vs. PMT, OPU vs. OPT, and OMU vs. OMT, based on the radial increments of individual trees. To quantify the thinning effect, the average radial increments of the thinned stand type variants (PPT, PMT, OPT, and OMT) were compared with their corresponding unthinned counterparts (PPU, PMU, OPU, and OMU) by calculating ratios. This normalization process isolates the pure effect of thinning on stem and coarse root growth during the post-thinning period (2018–2022), as differences in mean stem and coarse root growth between the stand type variant pairs in the pre-thinning period (2013–2017) were mathematically equalized. Consequently, the main focus is on the post-thinning period. Statistical tests for significant effects of the factors stand type and thinning, as well as for differences between the respective stand type variant pairs in the pre-thinning period, are therefore not appropriate, since the mean growth values between these variant pairs have been standardized by the normalization process. Equation 1 illustrates this calculation, using the PPU and PPT stand type variants as an example for determining the normalization factor for the PPT stand type variant.

$$Q_{i_{PPT}} = \frac{\overline{i_{PPT}}}{\overline{i_{PPU}}} \quad (1)$$

$Q_{i_{PPT}}$: Normalization factor for the annual radial increment of the PPT stand type variant.

$\overline{i_{PPT}}$: Average annual radial increment (mm) of the PPT stand type variant 2013–2017.

$\overline{i_{PPU}}$: Average annual radial increment (mm) of the PPU stand type variant 2013–2017.

For both compartments, the annual normalized radial increments (i_{norm}) for individual trees over the entire observation period (2013–2022) were computed by dividing

the corresponding absolute radial increments (i_{abs}) by their respective normalization factors (Q_i). This calculation is exemplified for the PPT stand type variant in Eq. 2. The analysis of the ratio between i_{norm} of the coarse root compartment and i_{norm} of the stem compartment is provided in the supplementary section (see Results S1).

$$i_{norm_{PPT}} = \frac{i_{abs_{PPT}}}{Q_{i_{PPT}}} \quad (2)$$

$i_{norm_{PPT}}$: Normalized annual radial increment (mm) of the PPT stand type variant 2013–2022.

$i_{abs_{PPT}}$: Absolute annual radial increment (mm) of the PPT stand type variant 2013–2022.

$Q_{i_{PPT}}$: Normalization factor for the annual radial increment of the PPT stand type variant.

Standardized precipitation evapotranspiration index (SPEI) (Q3)

Annual water availability at the experimental sites Baunach and Triesdorf from 2013 to 2022 was assessed using the Standardized Precipitation Evapotranspiration Index (Vicente-Serrano et al. 2010), with average water availability calculated for each site based on this index. To capture microclimatic differences among stand type variants, distinct GPS coordinates were used for each variant to extract location-specific climate data from a high-resolution climate product (1 km × 1 km grid). Monthly precipitation and potential evapotranspiration were obtained for the corresponding grid cells, with interpolation applied when coordinates fell between grid points. SPEI was computed separately for the Franconian sites of Baunach and Triesdorf, ensuring that each stand type variant was represented by the climate conditions specific to its exact location. This approach can result in minor differences in SPEI values among stand type variants within the same site, reflecting local variations in climate exposure and grid positioning. The SPEI is a statistical measure that quantifies periods of aridity (water deficit) and humidity (water surplus) by evaluating the local climatic water balance, defined as the difference between precipitation and potential evapotranspiration (PET). To analyze water availability over extended periods, moving averages of 3, 6, or 12 months are typically used (SPEI3, SPEI6, and SPEI12, respectively). The 6-month SPEI for September (SPEI6) was selected, representing the water balance for the growing season from April to September across the observation period (2013–2022).

Based on Table S1, the mean, minimum, and maximum SPEI6 values were calculated for each stand type variant (PPU, PPT, PMU, PMT, OPU, OPT, OMU, and OMT). For the graphical illustration of root–stem allometry in Scots

Table 3 Averaged values of pre-thinning and post-thinning SDI, along with the mean, minimum, and maximum of SDI, and the overall mean of the pre- and post-thinning SDI values, categorized by stand type variants (PPU, PPT, PMU, PMT, OPU, OPT, OMU, OMT)

Stand type variant	SDI Pre-thinning	SDI Post-thinning (%)	Δ SDI (min., max.) (%)	Mean SDI
PPU	1000	1000 (100)	0 (0)	1000
PPT	1144	482 (42.1)	-662 (-279, -1086) (-57.9)	813
PMU	844	844 (100)	0 (0)	844
PMT	726	412 (56.7)	-314 (-221, -480) (-43.3)	569
OPU	761	751 (98.7)	-10 (0, -44) (-1.3)	756
OPT	910	494 (54.3)	-416 (-150, -868) (-45.7)	702
OMU	863	863 (100)	0 (0)	863
OMT	921	566 (61.5)	-355 (-231, -760) (-38.5)	743

pine and sessile oak, SPEI6 values from the Baunach and Triesdorf sites were combined and averaged (Figs. 3, 4, 5 and 6).

Local stand density index (SDI), Δ SDI (delta SDI), and basal area (BA) (Q3)

To evaluate the effects of thinning intensity on tree growth, the stand density index (SDI) established by Reineke (1933) served as the primary metric (see Equation S1 in the supplementary section). Using individual stem coordinates and corresponding tree heights from 2017, local pre-thinning and post-thinning SDI values were calculated for each living tree within the experimental plot variants (PPU, PPT, PMU, PMT, OPU, OPT, OMU, and OMT). An algorithm implemented in R Statistics was applied for this purpose. Around each stem base, a virtual circular area with a radius equal to half the tree height was projected, within which all living trees were counted as competitors for both unthinned and thinned stand type variants. In thinned plots, trees removed during the 2017 thinning from above were also included as competitors. The radius, standardized to half the tree height, was used in the R algorithm to calculate local SDI values per tree, consistently capturing the neighboring trees that represent the primary competitors of each sample

Table 4 Averaged pre- and post-thinning basal area (BA) per hectare, BA, and the percent of BA, categorized by thinned stand type variants (PPT, PMT, OPT, OMT)

Stand type variant	BA Pre-thinning [m ²]	BA Post-thinning [m ²]	Δ BA [m ²]	Δ BA [%]
PPT	42.3	22.5	-19.8	46.7
PMT	41.6	24.3	-17.3	42.0
OPT	36.0	21.3	-14.8	41.4
OMT	41.6	24.3	-17.3	42.0

tree. Assigning a local SDI to each tree allowed quantification of within-stand variation and increased the sample size, thereby enabling more robust statistical analyses of the relationship between thinning intensity and root-stem allocation. This approach follows common practice in computing local SDI values and ensures that the most relevant competitive interactions are represented, whereas larger radii would include more distant trees with negligible influence on local competition. Local SDI values per tree were then extrapolated to local SDI values per hectare. The mean, minimum, and maximum Δ SDI values per hectare and per tree were calculated by subtracting the local pre-thinning SDI from the corresponding post-thinning SDI. For both tabular and graphical illustration, SDI and Δ SDI values from the experimental sites in Baunach and Triesdorf were combined and averaged (Table 3). The slight SDI reduction in the unthinned OPU variant was attributed to natural mortality. Additionally, Table 4 presents the basal area (BA) per hectare of the thinned stand type variants (PPT, OPT, PMT, and OMT) before and after thinning to illustrate thinning intensity, with data from both sites combined and averaged.

Statistical analyses of the normalized radial stem and coarse root increments (Q1 and Q2)

For the statistical analysis of the dependent variables—normalized coarse root and stem increments—as functions of the predictor variables (stand type and treatment), two linear mixed-effects models with identical structure were fitted (Models 1 and 2). This approach enabled the assessment of the individual and interactive effects of stand type and thinning treatment on the dependent variables for Scots pine and sessile oak separately. The ratio of normalized coarse root increment to normalized stem increment (hereafter also referred to as the coarse root-stem quotient) is presented in Model S1 in the supplementary section. A random effect was specified at the site level (Baunach and Triesdorf) to account for the grouped data structure and capture site-specific variability when estimating overall effects, following standard practice in mixed-effects modeling (e.g., Mehtätalo and Lappi 2020). For both tree species, treatment (unthinned=0, thinned=1) and stand type (monospecific=0, mixed=1) were included as dummy variables, with

interactions considered up to the second degree. The analysis focused on the impact of the 2017 thinning intervention. Based on the fitted linear mixed models (Model 1 and 2), post hoc simultaneous tests for general linear hypotheses were performed in R using the multcomp package, following the methodology of Hothorn et al. (2008), which serves as the package reference. These tests were conducted to assess significant differences in normalized root and stem increments, as well as in root-to-stem ratios (as detailed in the supplementary section) across the following stand type pairs: PPU vs. PPT, PMU vs. PMT, PPU vs. PMU, PPT vs. PMT, OPU vs. OPT, OMU vs. OMT, OPU vs. OMU, and OPT vs. OMT. Comparisons across years and species were derived by subsetting the data accordingly, with contrasts focused on stand type and treatment.

Model 1 (normalized stem increment) (Q1).

$$\text{norm}_{i, \text{stem}, j_l} = a_0 + a_1 \times \text{stand type}_j + a_2 \times \text{treatment}_j + a_3 \times \text{stand type}_j \times \text{treatment}_j + c_j + \epsilon_{jl}$$

Model 2 (normalized coarse root increment) (Q2)

$$\text{norm}_{i, \text{root}, j_l} = a_0 + a_1 \times \text{stand type}_j + a_2 \times \text{treatment}_j + a_3 \times \text{stand type}_j \times \text{treatment}_j + c_j + \epsilon_{jl}$$

$\text{norm}_{i, \text{stem}, j_l}$; $\text{norm}_{i, \text{root}, j_l}$: Annual normalized stem and coarse root increments (mm) of individual trees, analyzed separately by species (Scots pine and sessile oak) for each year of the post-thinning period (2018–2022).

a_0 : Intercept

$a_1, \dots, a_3$: Model parameters based on the predictor variables stand type, treatment and interaction between stand type and treatment.

c : Random effects.

j : Experimental site.

l : Single observation.

ϵ : i.i.d. errors.

Statistical analyses of the coarse root-stem allometry (Q3)

The statistical models applied for coarse root-stem allometry are based on a double-logarithmic representation of an allometric relationship (Eq. 3).

$$\log(d_{\text{root}}) = a + b \times \log(d_{\text{stem}}) \quad (3)$$

d_{root} : Average root diameter (cm).

d_{stem} : Average DBH (cm).

a : Allometric factor (i.e. allometric intercept).

b : Allometric exponent (i.e. allometric slope).

Based on Eq. 3, linear mixed models were developed for each tree species, Scots pine and sessile oak, with the logarithm of coarse root diameter ($\log(d_{\text{root}})$) as a function of the logarithm of stem diameter ($\log(d_{\text{stem}})$), incorporating stand type (monospecific=0, mixed=1) and treatment (unthinned=0, thinned=1) as dummy variables. ANOVA pre-tests revealed significant effects of SPEI6 and Δ SDI on both the allometric factors and exponents of the allometric coarse root-stem diameter lines (referred to as allometric lines) for both species. Consequently, these covariates were included in the allometric coarse root-stem models. Interactions among stand type, treatment, SPEI6, and Δ SDI were examined for their statistical significance, including all combinations up to the third-order interaction.

For the allometric factor, random effects were specified at the experimental site (Baunach and Triesdorf) and individual tree levels for both pine and oak. The random effect for the allometric exponent was tested at the individual tree level for both species. Comparing models with and without this effect, the pine model (Model 3) showed a lower AIC, indicating a better fit, whereas the oak model (Model 4) had a slightly higher AIC. Thus, the random effect was included only in the pine model. Based on the fitted linear mixed models (Models 3 and 4), post hoc simultaneous tests for general linear hypotheses were performed according to Hothorn et al. (2008), employing the multcomp package in R Statistics.

Model 3 (coarse root-stem allometry for Scots pine) (Q3)

$$\begin{aligned} \log(d_{\text{root}})_{jkl} = & (a_0 + a_1 \times \text{type}_j + a_2 \times \text{treat}_j + a_3 \times \text{spei6}_j \\ & + a_4 \times \Delta \text{SDI}_j + a_5 \times \text{type}_j \times \text{treat}_j + a_6 \times \text{type}_j \\ & \times \text{spei6}_j + a_7 \times \text{type}_j \times \Delta \text{SDI}_j + a_8 \times \text{treat}_j \\ & \times \text{spei6}_j + a_9 \times \text{spei6}_j \times \Delta \text{SDI}_j + a_{10} \times \text{type}_j \\ & \times \text{treat}_j \times \text{spei6}_j + a_{11} \times \text{type}_j \times \text{spei6}_j \times \Delta \text{SDI}_j) \\ & + \log(d_{\text{stem}})_{jkl} \times (b_0 + b_1 \times \text{type}_j + b_2 \times \text{treat}_j + b_3 \\ & \times \text{spei6}_j + b_4 \times \Delta \text{SDI}_j + b_5 \times \text{type}_j \times \text{treat}_j + b_6 \\ & \times \text{type}_j \times \Delta \text{SDI}_j) + c_j + c_{jk} + d_{jk} \times \log(d_{\text{stem}})_{jkl} + \epsilon_{jkl} \end{aligned}$$

$\log(d_{\text{root}})$: Logarithmic coarse root diameter.

$\log(d_{\text{stem}})$: Logarithmic stem diameter.

$a_0, \dots, a_{11}$: Components of the allometric factor a .

$b_0, \dots, b_6$: Components of the allometric exponent b .

c : Random effects (Allometric factor).

d : Random effects (Allometric exponent).

j : Experimental site (Baunach, Triesdorf).

k : Tree.

l : Single observation.

Type: Stand type (pure (=0) and mixed (=1)).

Treat: Treatment (unthinned (=0) and thinned (=1)).

spei6: SPEI within vegetation period by stand type variant.

Δ SDI: DeltaSDI, difference of SDI between pre-thinning and post-thinning by stand type variant.

ε : i.i.d. errors.

Model 4 (coarse root-stem allometry for sessile oak) (Q3)

$$\begin{aligned} \log(d_{root})_{jkl} = & (a_0 + a_1 \times type_j + a_2 \times treat_j + a_3 \times spei6_j \\ & + a_4 \times \Delta SDI_j + a_5 \times type_j \times treat_j + a_6 \\ & \times type_j \times spei6_j + a_7 \times type_j \times \Delta SDI_j \\ & + a_8 \times treat_j \times \Delta SDI_j) + \log(d_{stem})_{jkl} \\ & \times (b_0 + b_1 \times type_j + b_2 \times treat_j + b_3 \times \\ & spei6_j + b_4 \times \Delta SDI_j + b_5 \times type_j \times \\ & treat_j + b_6 \times treat_j \times \Delta SDI_j) + c_j + c_{jk} + \epsilon_{jkl} \end{aligned}$$

$\log(d_{root})$: Logarithmic coarse root diameter.

$\log(d_{stem})$: Logarithmic stem diameter.

$a_0, \dots, a_8$: Components of the allometric factor a .

$b_0, \dots, b_6$: Components of the allometric exponent b .

c : Random effects (Allometric factor).

j : Experimental site (Baunach, Triesdorf).

k : Tree.

l : Single observation.

Type: Stand type (pure (=0) and mixed (=1)).

Treat: Treatment (unthinned (=0) and thinned (=1)).

spei6: SPEI within vegetation period by stand type variant.

ΔSDI : DeltaSDI, difference of SDI between pre-thinning and post-thinning by stand type variant.

ε : i.i.d. errors.

Linear mixed-effects model assumptions—linearity, normality and homogeneity of residuals, independence of observations (conditional on random effects), and normality of random effects—were assessed using diagnostic plots such as residuals versus fitted values and Q–Q plots of residuals and random effects. Random effects were assumed to be independent across sites and trees, and residuals were assumed independent and identically distributed (i.i.d.) with mean zero, constant variance, and no correlation among errors (ϵ_{jl} in Models 1 and 2, and ϵ_{jkl} in Models 3 and 4).

All calculations and graphical illustrations were performed using R 4.1.0 (R Core Team 2021), specifically employing the packages nlme (Pinheiro et al. 2023), ggplot2 (Wickham 2016), grid (R Core Team 2023), and plyr (Wickham 2011).

Results

Classification of the normalization factor (Q1 and Q2)

For the stem and coarse root compartments, the normalization factor for the unthinned stand type variants (PPU, PMU, OPU, and OMU) was set to 1. For the stem compartment, the normalization factors for the thinned stand type

variants were 0.90 (0.93 in Baunach and 0.87 in Triesdorf) for PPT, 1.06 (0.88 in Baunach and 1.23 in Triesdorf) for PMT, 0.96 (1.08 in Baunach and 0.84 in Triesdorf) for OPT, and 0.98 (0.95 in Baunach and 1.01 in Triesdorf) for OMT. In the coarse root compartment, the normalization factors were 0.86 (0.99 in Baunach and 0.73 in Triesdorf) for PPT, 1.28 (1.05 in Baunach and 1.51 in Triesdorf) for PMT, 1.69 (2.21 in Baunach and 1.16 in Triesdorf) for OPT, and 0.80 (0.94 in Baunach and 0.65 in Triesdorf) for OMT.

Normalized stem increment (Q1)

The statistical analysis showed that thinning, stand type, and their interactions influenced normalized stem increments in both species, with varying significance, magnitude, and timing across the post-thinning period. Thinning generally enhanced stem increments in both Scots pine and sessile oak; however, significant effects of the 2017 thinning emerged only in the later post-thinning years (2020–2022) for Scots pine, while for sessile oak they were consistent throughout 2018–2022. For Scots pine, the mixed stand factor had significant effects in 2018, 2021, and 2022, while no significant effects were detected for sessile oak in individual post-thinning years. The mixed stand factor and its interaction with thinning influenced stem increments in both enhancing and reducing ways, with significant effects observed for Scots pine in 2021 and 2022 and for sessile oak in 2019. Table S3 in the supplementary section summarizes the results of the statistical analysis of normalized stem increments for Scots pine and sessile oak across stand type variants. Table S4 reports the standard deviations of the random effects for intercepts and residuals, categorized by species and individual post-thinning years (2018–2022).

Due to normalization, differences in normalized stem increments between thinned (OPT, OMT, PPT, PMT) and unthinned (OPU, OMU, PPU, PMU) stand type variants remained minimal before thinning (2013–2017) (Fig. 1). In Scots pine, monospecific variants (PPU, PPT) showed higher increments than mixed variants (PMU, PMT), peaking in 2014 and 2017. For sessile oak, increments remained similar across variants except in 2016, when mixed stands (OMU, OMT) exceeded monospecific ones (OPU, OPT); the lowest increments occurred in 2015 and 2017. Throughout the pre-thinning period, Scots pine mixed stands (PMU, PMT) consistently showed the lowest increments. The average normalized increments ranked as follows: OMT (2.02 mm)=OMU (2.02 mm)>PPT (1.99 mm)=PPU (1.99 mm)>OPT (1.86 mm)=OPU (1.86 mm)>PMT (1.50 mm)=PMU (1.50 mm).

During the post-thinning period (2018–2022), normalized stem increments were consistently higher in thinned stand variants (OPT, OMT, PPT, PMT) than in their

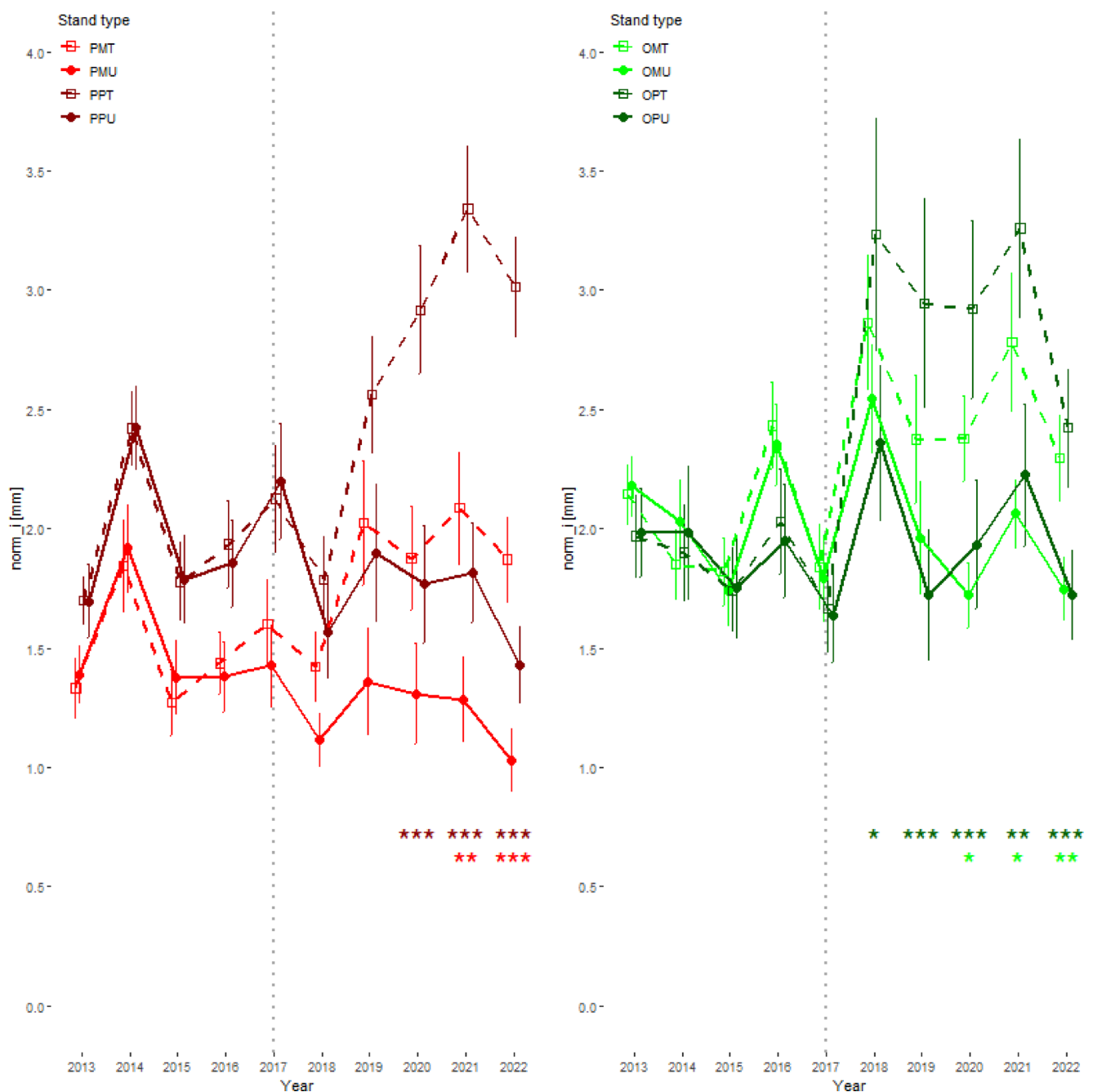


Fig. 1 Average normalized stem increment (norm_i) from 2013 to 2022 for pine stand type variants (PPU, PPT, PMU, PMT) and oak stand type variants (OPU, OPT, OMU, OMT). The dotted vertical line indicates thinning in autumn 2017. Significant differences between the

unthinned counterparts (OPU, OMU, PPU, PMU). While sessile oak and Scots pine followed similar trends, their increments occurred at different levels. Sessile oak showed an increase in 2018, more pronounced in thinned variants (OPT, OMT), whereas Scots pine exhibited a decline. Monospecific variants (OPU, OPT, PPU, PPT) generally had higher increments than mixed stands (OMU, OMT, PMU, PMT), with OPT, PPT, and OMT highest, PMU lowest, and

unthinned variants (PPU, PMU, OPU, OMU) and their thinned counterparts (PPT, PMT, OPT, OMT) during the post-thinning period are indicated by coloured asterisks (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$)

others intermediate. Average normalized increments followed this order: OPT (2.96 mm) > PPT (2.72 mm) > OMT (2.54 mm) > OMU (2.01 mm) > OPU (1.99 mm) > PMT (1.86 mm) > PPU (1.70 mm) > PMU (1.22 mm). Compared to their unthinned counterparts, stem increments in the thinned variants were higher by approximately 61% (PPT vs. PPU), 52% (PMT vs. PMU), 48% (OPT vs. OPU), and 26% (OMT vs. OMU).

Pairwise comparisons of normalized stem increments between thinned and unthinned variants revealed significant differences among stand types and years. For Scots pine, significant differences occurred between monospecific variants (PPU and PPT) in 2020–2022 and between mixed variants (PMU and PMT) in 2021–2022. For sessile oak, differences between mixed variants (OMU and OMT) were significant in 2020–2022, while those between monospecific variants (OPU and OPT) remained significant throughout the entire post-thinning period (2018–2022). Significant differences between monospecific and mixed variants appeared only among the thinned Scots pine variants (PPT and PMT) during the later post-thinning years (2020–2022). Table S5 in the supplementary section presents the detailed statistical results of these pairwise comparisons.

Normalized coarse root increment (Q2)

Compared to normalized stem increments, thinning, stand type, and their interaction generally had weaker effects on normalized coarse root increments. Thinning tended to increase coarse root increments in both Scots pine and sessile oak, except for sessile oak in 2020 and 2022, with significant effects observed only for Scots pine in the later post-thinning years (2021–2022). The mixed stand factor showed opposing trends: it reduced coarse root increments in Scots pine but increased them in sessile oak across the entire period, though without statistical significance. The interaction between stand type and thinning enhanced coarse root increments in Scots pine (2018, 2022) and in sessile oak throughout the study period, with significant effects for sessile oak in 2020–2022. Table S6 in the supplementary section summarizes the results of the statistical analysis of normalized coarse root increments for Scots pine and sessile oak across stand type variants. Table S7 presents the standard deviations of random effects for intercepts and residuals, grouped by tree species and individual post-thinning years (2018–2022).

Similar to the stem compartment, normalized coarse root increments for thinned (OPT, OMT, PPT, and PMT) and unthinned (OPU, OMU, PPU, and PMU) stand type variants remained nearly identical during the pre-thinning period (2013–2017) due to normalization (Fig. 2). Throughout this period, sessile oak variants (OPU, OPT, OMU, and OMT) consistently showed higher normalized coarse root increments than Scots pine variants (PPU, PPT, PMU, and PMT). Among sessile oak stands, mixed variants (OMU and OMT) exceeded monospecific ones (OPU and OPT), whereas monospecific Scots pine variants (PPU and PPT) surpassed mixed Scots pine variants (PMU and PMT). Leading up to the 2017 thinning, normalized coarse root increments increased in monospecific sessile oak and Scots pine

variants (OPU, OPT, PPU, and PPT) but remained stable in mixed Scots pine variants (PMU and PMT), while mixed sessile oak variants (OMU and OMT) showed a decline. The average normalized coarse root increments during this period followed the order: OMT (3.81 mm) > OMU (3.64 mm) > OPT (2.47 mm) = OPU (2.47 mm) > PPU (1.01 mm) > PPT (0.98 mm) > PMT (0.66 mm) > PMU (0.65 mm).

During the post-thinning period (2018–2022), sessile oak variants (OPU, OPT, OMU, and OMT) consistently showed higher normalized coarse root increments than Scots pine variants (PPU, PPT, PMU, and PMT), peaking in 2021. Among thinned variants, OMT, PPT, and PMT had higher increments than their unthinned counterparts (OMU, PPU, and PMU), while monospecific sessile oak variants (OPT and OPU) remained similar. OMT exhibited the highest annual coarse root increment among sessile oak stands. Scots pine variants (PPU, PPT, PMU, and PMT) and OMT showed an upward trend, whereas OPU, OPT, and OMU declined, with OMU experiencing the steepest drop. Average normalized coarse root increments followed the order: OMT (4.82 mm) > OMU (2.72 mm) > OPT (2.41 mm) > OPU (2.37 mm) > PPT (1.68 mm) > PMT (1.18 mm) > PPU (1.16 mm) > PMU (0.74 mm). Compared to unthinned variants, thinned variants had higher coarse root increments by approximately 77% (OMT vs. OMU), 58% (PMT vs. PMU), 46% (PPT vs. PPU), and 2% (OPT vs. OPU).

Pairwise comparisons between the thinned and unthinned variants revealed significant differences for monospecific Scots pine variants (PPU and PPT) in 2021–2022, mixed Scots pine variants (PMU and PMT) in 2022, and mixed sessile oak variants (OMU and OMT) in 2020–2022. Significant differences between monospecific and mixed variants were observed only for oak variants (OPT and OMT) throughout the entire post-thinning period (2018–2022). Table S8 in the supplementary section provides detailed statistical results of these pairwise comparisons. Additional information on the coarse root-stem quotient is presented in Results S1, together with Tables S9–S11 and Figure S1, and further discussed in Discussion S1.

Classification of SPEI6 (Q3)

SPEI6 values remained within the normal range in 2013, 2014, 2016, 2017, and 2021, while they indicated arid conditions in 2015, 2018, 2019, 2020, and 2022, with the most severe aridity observed in 2018. For tabular representation, the SPEI6 values for Baunach and Triesdorf were combined and averaged (Table S1 in the supplementary section). The mean SPEI6 values by stand type variant were −0.8938 for PPU, −0.8903 for PPT, −0.8826 for PMU, −0.8862 for PMT, −0.8957 for OPU, −0.8957 for OPT, −0.8820 for OMU, and

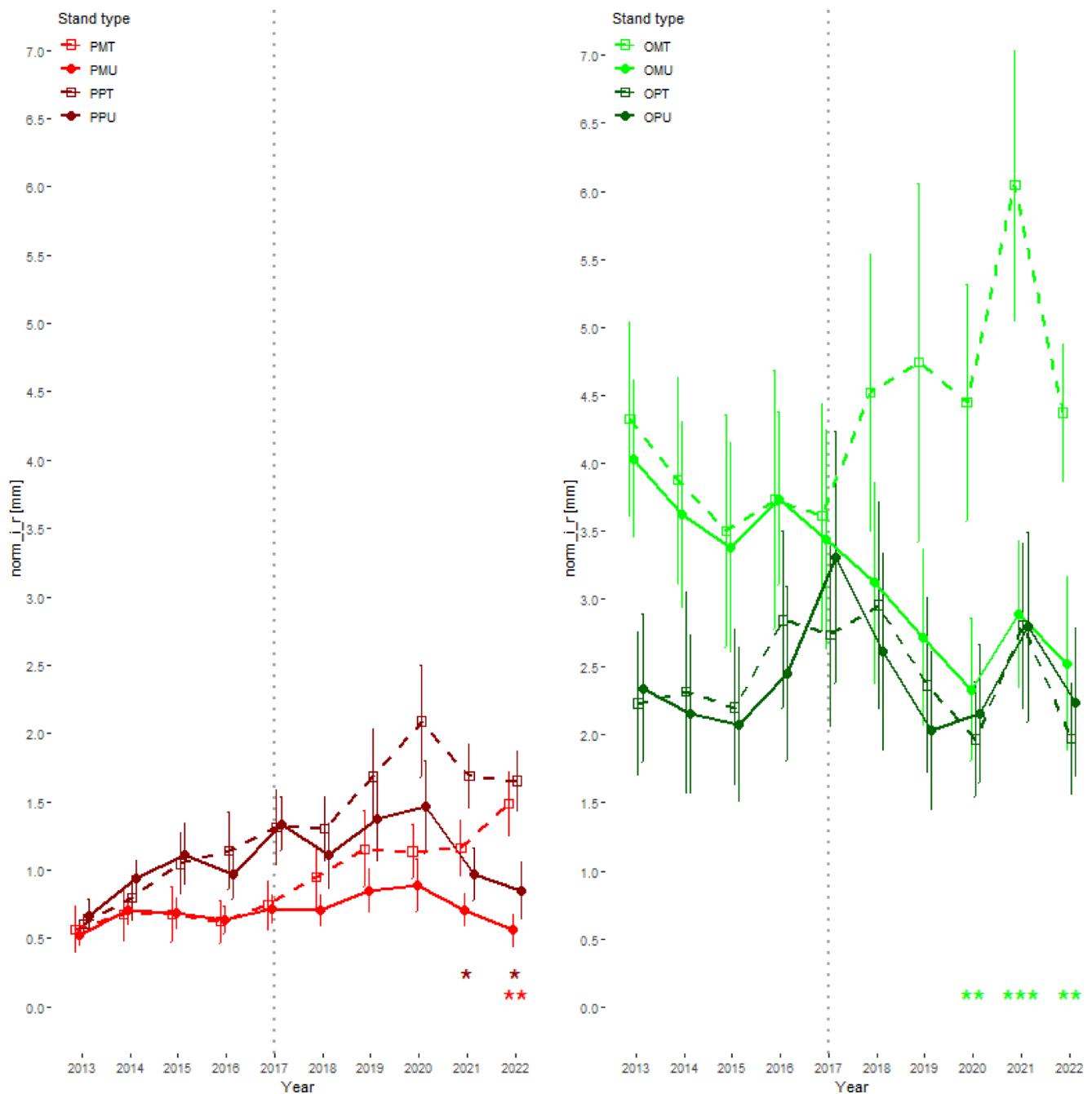


Fig. 2 Average normalized coarse root increment (norm_i_r) from 2013 to 2022 for pine stand type variants (PPU, PPT, PMU, PMT) and oak stand type variants (OPU, OPT, OMU, OMT). The dotted vertical line indicates thinning in autumn 2017. Significant differences

–0.8862 for OMT. The minimum and maximum SPEI6 values across all stand type variants were –2.3349 and 1.0355, respectively. The corresponding Table S2 can be found in the supplementary section.

between the unthinned variants (PPU, PMU, OPU, OMU) and their thinned counterparts (PPT, PMT, OPT, OMT) during the post-thinning period are indicated by coloured asterisks (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$)

Coarse root-stem allometry of Scots pine (Q3)

The statistical analysis of coarse root-stem allometry showed that thinning in PPT and PMT, as well as the interaction between mixed stand and Δ SDI in PMT, significantly reduced the allometric factors (Table 5). In contrast, Δ SDI in PPT and PMT, and the interaction between mixed stand and

Table 5 Components of the allometric factor and the allometric exponent for Scots pine by stand type and treatment (Model 3). The “×” represents an interaction between two or three predictors. Abbreviations: *dstem* = stem diameter at breast height, *Para.comp.* = Parameter component, *Para.est.* = Parameter estimate, *Std.error* = Standard error, *Sig.* = Level of significance. Significant estimates are marked with asterisks (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, n.s.: not significant)

	Para. comp.	Para.est.	Std.error	p-value	Sig.
<i>Allometric factor</i>	a_0	-3.5675	0.9422	0.0002	***
<i>log(dstem)</i>	b_0	1.5922	0.2592	0.0000	***
<i>mixed</i>	a_1	0.1980	1.0929	0.8563	n.s.
<i>thinning</i>	a_2	-8.2891	3.4136	0.0156	*
<i>spei6</i>	a_3	-0.0194	0.0130	0.1365	n.s.
<i>ΔSDI</i>	a_4	-0.0083	0.0036	0.0203	*
<i>log(dstem) × mixed stand</i>	b_1	0.1350	0.3165	0.6699	n.s.
<i>log(dstem) × thinning</i>	b_2	2.4344	0.9613	0.0117	*
<i>log(dstem) × spei6</i>	b_3	0.0056	0.0038	0.1402	n.s.
<i>log(dstem) × ΔSDI</i>	b_4	0.0025	0.0010	0.0138	*
<i>mixed × thinning</i>	a_5	18.5965	5.9572	0.0019	**
<i>mixed × spei6</i>	a_6	0.0012	0.0017	0.4711	n.s.
<i>mixed × ΔSDI</i>	a_7	0.0565	0.0139	0.0001	***
<i>thinning × spei6</i>	a_8	-0.0005	0.0038	0.8912	n.s.
<i>spei6 × ΔSDI</i>	a_9	-0.000003	0.000005	0.5942	n.s.
<i>log(dstem) × mixed × thinning</i>	b_5	-5.5977	1.6781	0.0009	***
<i>log(dstem) × mixed × ΔSDI</i>	b_6	-0.0165	0.0039	0.0000	***
<i>mixed × thinning × spei6</i>	a_{10}	0.0227	0.0070	0.0013	**
<i>mixed × spei6 × ΔSDI</i>	a_{11}	0.0001	0.000019	0.0000	***

thinning in PMT, had a significant positive effect. A third-order interaction between mixed stand, thinning, and SPEI6 indicated that drier conditions lowered allometric factors in PMT, while wetter conditions increased them. Conversely, the interaction between mixed stand, SPEI6, and ΔSDI had a positive effect under drier conditions but a negative effect under wetter conditions. Thinning significantly increased allometric exponents in PPT and PMT, but this effect was outweighed by the significantly negative impact of the mixed stand-thinning interaction in PMT. In contrast, ΔSDI had a significantly negative effect on the allometric exponents in PPT and PMT, but the mixed stand-ΔSDI interaction had a significantly positive effect, counteracting the negative impact of ΔSDI in PMT. Overall, ΔSDI's influence on allometric factors and exponents intensified with greater thinning intensity. For the allometric factor, the standard deviation of random effects was 0.3224 at the experimental site level and 3.9669 at the tree-in-experimental-site level. For the allometric exponent, the standard deviation was 1.1143 at the tree-in-experimental-site level, with a residual standard deviation of 0.0117.

Table 6 Differences between the allometric factors for pine stand type pairs (PPU – PPT, PMU – PMT, PPU – PMU, PPT – PMT), and between the allometric exponents for pine stand type pairs (PPU – PPT, PMU – PMT, PPU – PMU, PPT – PMT) (Model 3). Abbreviations: *Para.est.* = Parameter estimate, *Std.error* = Standard error, *Sig.* = Level of significance. Significant differences are marked with asterisks (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, n.s.: not significant)

	Stand type pairs	Para.est.	Std.error	p-value	Sig.
<i>Allometric factor</i>	PPU – PPT	2.8014	1.0833	0.0354	*
<i>Allometric factor</i>	PMU – PMT	4.8238	1.2995	<0.001	***
<i>Allometric factor</i>	PPU – PMU	-0.1967	1.0931	0.9974	n.s.
<i>Allometric factor</i>	PPT – PMT	1.8258	1.4887	0.5580	n.s.
<i>Allometric exponent</i>	PPU – PPT	-0.7914	0.3056	0.0346	*
<i>Allometric exponent</i>	PMU – PMT	-1.2485	0.3637	0.0025	**
<i>Allometric exponent</i>	PPU – PMU	-0.1351	0.3165	0.9678	n.s.
<i>Allometric exponent</i>	PPT – PMT	-0.5922	0.4182	0.4348	n.s.

Pairwise comparisons of allometric factors in Scots pine revealed that unthinned variants (PPU and PMU) significantly exceeded their thinned counterparts (PPT and PMT) (Table 6). Among unthinned stands, PMU had higher allometric factors than PPU, while among thinned stands, PPT exceeded PMT. However, differences between monospecific and mixed stand pairs (PPU vs. PMU and PPT vs. PMT) were not statistically significant. For allometric exponents, thinned variants (PPT and PMT) consistently exceeded unthinned variants (PPU and PMU), and mixed stand variants (PMU and PMT) surpassed monospecific variants (PPU and PPT). Significant differences were observed only between PPU vs. PPT and PMU vs. PMT.

The coarse root-stem diameter trajectories for all Scots pine trees are shown on a double-logarithmic scale in Fig. 3 for monospecific stands and in Fig. 4 for mixed stands, alongside the allometric lines predicted by the fitted Model 3. This model incorporated the factors stand type and treatment, as well as the covariates SPEI6 and ΔSDI. The predictions were based solely on the model's fixed effects. For the graphical representation of the applied linear mixed model, the mean values of SPEI6 and ΔSDI, as shown in Sect. "Classification of SPEI6", Table S2 in the supplement, and Table 3 in Sect. "Local Stand Density Index (SDI), ΔSDI (delta SDI), and Basal Area (BA) (Q3)", respectively, were used.

After summing the components of the allometric factors and exponents, allometric factors followed the order: PMU (-3.3535) > PPU (-3.5502) > PPT (-6.3517) > PMT (-8.1774), while allometric exponents declined as follows:

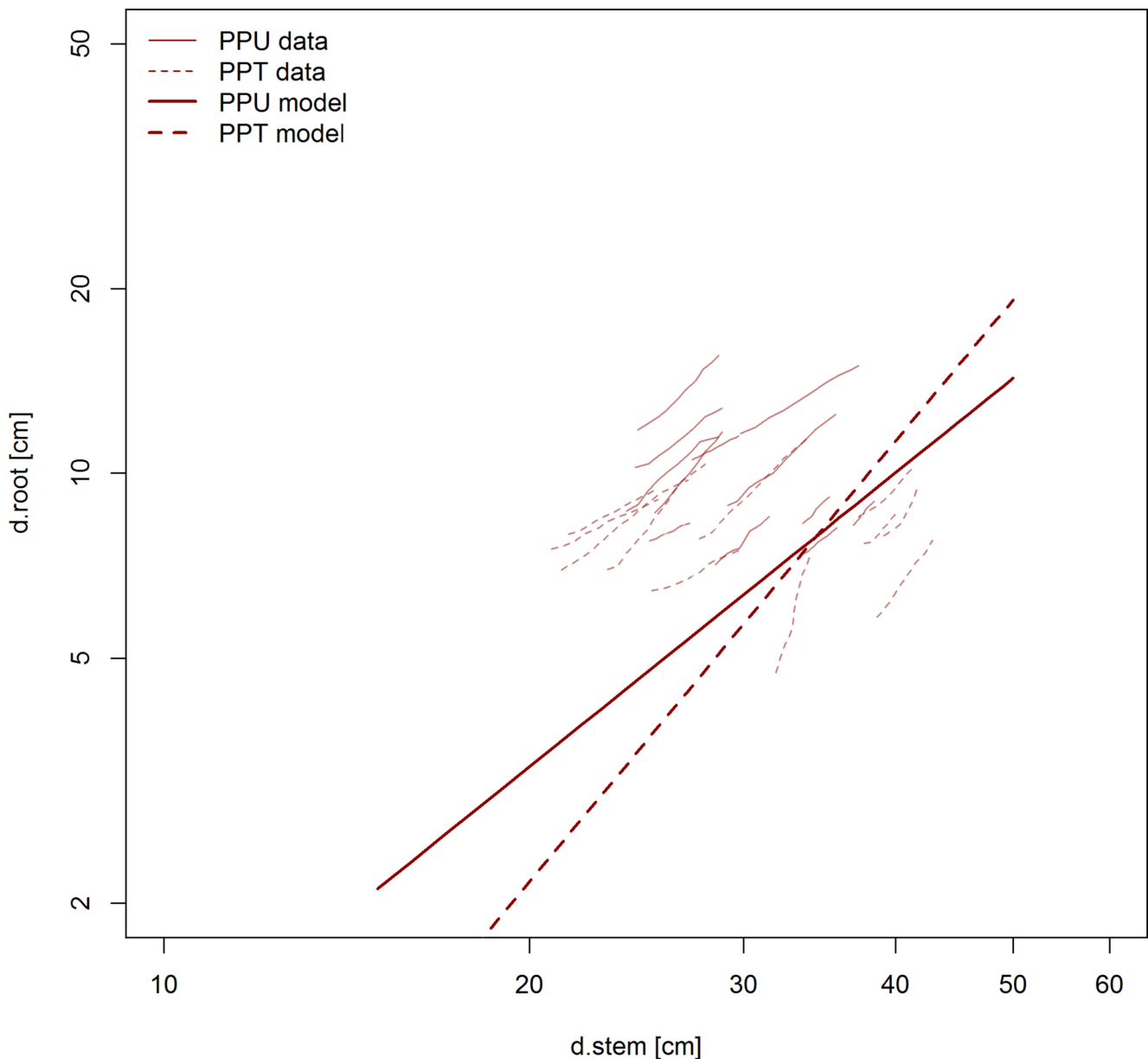


Fig. 3 Coarse root-stem diameter trajectories for Scots pine trees in monospecific stands, categorized by treatments (unthinned and thinned), as a function of SPEI6 and Δ SDI. The straight lines represent predictions based on the fitted Model 3, including only the fixed effects

PMT (2.9707) > PPT (2.3785) > PMU (1.7223) > PPU (1.5872). Unthinned variants (PPU and PMU) exhibited higher allometric lines than their thinned counterparts (PPT and PMT), with shifts occurring around 35 cm DBH between PPU and PPT and around 50 cm DBH between PMU and PMT, driven by higher allometric exponents in PPT and PMT. Additionally, mixed stand variants (PMU and PMT) showed higher allometric lines than their monospecific counterparts (PPU and PPT), with a shift between PPT and PMT occurring at approximately 23 cm DBH due to the higher allometric exponent of PMT. The differences between PPU vs. PMU and PPT vs. PMT became more

pronounced with increasing DBH due to steeper trajectories in PMU and PMT.

Coarse root-stem allometry of sessile oak (Q3)

The statistical analysis of coarse root-stem allometry showed that thinning significantly reduced allometric factors in OPT and OMT, while the mixed stand factor had a similar negative effect on OMU and OMT (Table 7). However, the interaction between mixed stand and thinning partially offset this negative impact for OMT. SPEI6 significantly influenced allometric factors across all variants (OPU, OPT, OMU,

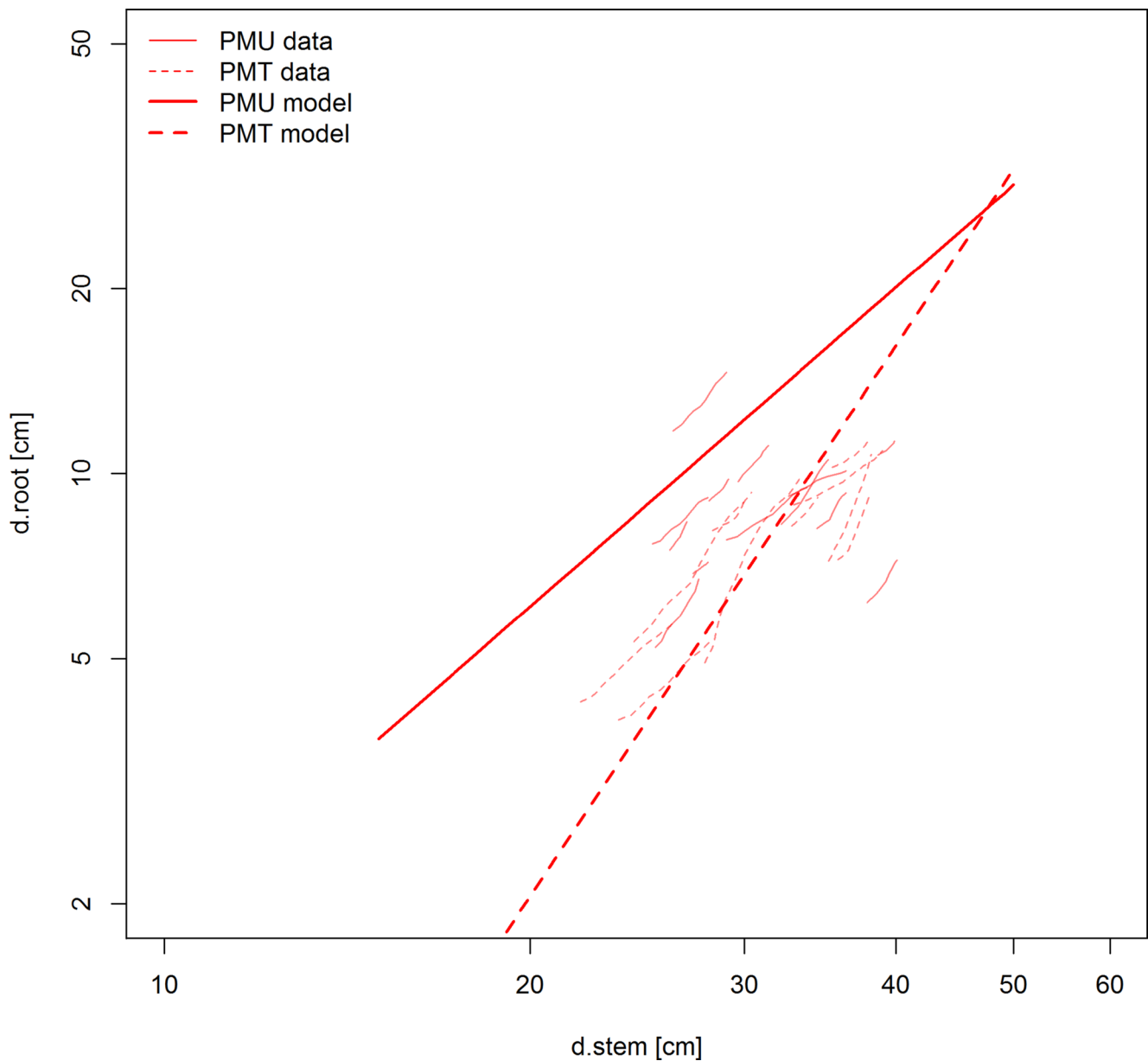


Fig. 4 Coarse root-stem diameter trajectories for Scots pine trees in mixed stands, categorized by treatments (unthinned and thinned), as a function of SPEI6 and Δ SDI. The straight lines represent predictions based on the fitted Model 3, including only the fixed effects

and OMT), with drier conditions associated with higher factors and wetter conditions associated with lower factors. For allometric exponents, the mixed stand factor had a significantly positive effect on OMT and OMT. Thinning also increased the allometric exponents of OPT and OMT, but this effect was reversed by a significant negative interaction between mixed stand and thinning in OMT. Unlike the trend for allometric factors, SPEI6 had an opposite effect on allometric exponents, with drier conditions leading to lower values and wetter conditions to higher values. Although Δ SDI and its interaction with thinning did not reach conventional significance thresholds, they approached weak

significance. Δ SDI negatively affected the allometric factor but positively influenced the allometric exponent, while its interaction with thinning had the opposite effects. For the allometric factor, the standard deviation of random effects was 0.6684 at the experimental site level and 0.6329 at the tree-in-experimental-site level, with a residual standard deviation of 0.2293.

Pairwise comparisons of allometric factors among sessile oak stand type variants showed that the unthinned variant OPU had a significantly higher allometric factor than the thinned variant OPT (Table 8). Additionally, monospecific variants (OPU and OPT) exhibited significantly higher

Table 7 Components of the allometric factors and the allometric exponents for sessile oak by stand type and treatment (Model 4). The “×” represents an interaction between two or three predictors. Abbreviations: *dstem*=stem diameter at breast height, *mixed*=mixed stand type variants, *thinning*=thinned stand type variants, *Para.comp.* = Parameter component, *Para.est.* = Parameter estimate, *Std.error*=Standard error, *Sig.* = Level of significance. Significant estimates are marked with asterisks (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, n.s.: not significant)

	Para.comp.	Para.est.	Std.error	p-value	Sig.
<i>Allometric factor</i>	a_0	-7.1322	1.6514	0.0000	***
<i>log(dstem)</i>	b_0	2.8367	0.4563	0.0000	***
<i>mixed</i>	a_1	-16.2626	2.5101	0.0000	***
<i>thinning</i>	a_2	-5.5903	2.4999	0.0259	*
<i>spei6</i>	a_3	-0.7126	0.2231	0.0015	**
ΔSDI	a_4	0.1183	0.0667	0.0768	n.s.
<i>log(dstem) × mixed stand</i>	b_1	4.4926	0.7206	0.0000	***
<i>log(dstem) × thinning</i>	b_2	1.9539	0.7136	0.0065	**
<i>log(dstem) × spei6</i>	b_3	0.2100	0.0672	0.0019	**
<i>log(dstem) × ΔSDI</i>	b_4	-0.0380	0.0198	0.0552	n.s.
<i>mixed × thinning</i>	a_5	9.2505	3.1551	0.0036	**
<i>mixed × spei6</i>	a_6	-0.0446	0.0271	0.1000	n.s.
<i>mixed × ΔSDI</i>	a_7	0.0017	0.0015	0.2526	n.s.
<i>thin-ning × ΔSDI</i>	a_8	-0.1151	0.0668	0.0858	n.s.
<i>log(dstem) × mixed × thinning</i>	b_5	-2.7348	0.8957	0.0024	**
<i>log(dstem) × thin-ning × ΔSDI</i>	b_6	0.0376	0.0198	0.0582	n.s.

allometric factors than mixed variants (OMU and OMT). In contrast, the pattern was reversed for allometric exponents: OPU had a significantly lower exponent than OPT, and monospecific variants (OPU and OPT) had significantly lower exponents than mixed variants (OMU and OMT). No significant differences were found between OMU and OMT for either the allometric factor or exponent.

The coarse root-stem diameter trajectories for all sessile oak trees are presented on a double-logarithmic scale in Fig. 5 for monospecific stands and in Fig. 6 for mixed stands, alongside the allometric lines predicted by the fitted Model 4. This model incorporated the factors stand type and treatment, as well as the covariates SPEI6 and ΔSDI . The predictions were based solely on the model's fixed effects. For the graphical representation of the applied linear mixed model, the mean values of SPEI6 and ΔSDI , as shown in Sect. "Classification of SPEI6", Table S2 in the supplement, and Table 3 in Sect. "Local Stand Density Index (SDI),

Table 8 Differences between the allometric factors for oak stand type pairs (OPU – OPT, OMU – OMT, OPU – OMU, OPT – OMT), and between the allometric exponents for oak stand type pairs (OPU – OPT, OMU – OMT, OPU – OMU, OPT – OMT) (Model 4). Abbreviations: *Para.est.* = Parameter estimate, *Std.error*=Standard error, *Sig.* = Level of significance. Significant differences are marked with asterisks (*: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, n.s.: not significant)

	Stand type pairs	Para.est.	Std.error	p-value	Sig.
<i>Allometric factor</i>	OPU – OPT	5.6890	1.5850	0.0010	**
<i>Allometric factor</i>	OMU – OMT	-1.9270	2.4850	0.8325	n.s.
<i>Allometric factor</i>	OPU – OMU	15.0060	2.2690	<0.001	***
<i>Allometric factor</i>	OPT – OMT	7.3890	1.9810	<0.001	***
<i>Allometric exponent</i>	OPU – OPT	-1.7299	0.4634	<0.001	***
<i>Allometric exponent</i>	OMU – OMT	0.6361	0.7154	0.7696	n.s.
<i>Allometric exponent</i>	OPU – OMU	-4.1009	0.6571	<0.001	***
<i>Allometric exponent</i>	OPT – OMT	-1.7349	0.5786	0.0105	*

ΔSDI (delta SDI), and Basal Area (BA) (Q3)", respectively, were used.

After summing the components of the allometric factors and exponents, allometric factors decreased in the order: OPU (-7.7213)>OPT (-13.4106)>OMT (-20.8001)>OMU (-22.7269), while allometric exponents followed the opposite pattern: OMU (7.1440)>OMT (6.5078)>OPT (4.7729)>OPU (3.0431). The allometric line for the unthinned monospecific variant OPU remained above that of the thinned monospecific variant OPT until approximately 27 cm DBH, after which the higher exponent of OPT caused its line to rise above OPU's. In contrast, the unthinned mixed stand variant OMU consistently remained above the thinned mixed variant OMT, with both running nearly parallel but OMU having a slightly higher allometric exponent. Around 38 cm DBH, OMU's higher allometric exponent led it to cross above the unthinned monospecific variant OPU. Despite its higher allometric exponent, the thinned mixed variant OMT remained below the thinned monospecific variant OPT. Compared to Scots pine stand variants (PPU, PPT, PMU, and PMT), sessile oak variants (OPU, OPT, OMU, and OMT) consistently exhibited lower allometric factors and higher exponents.

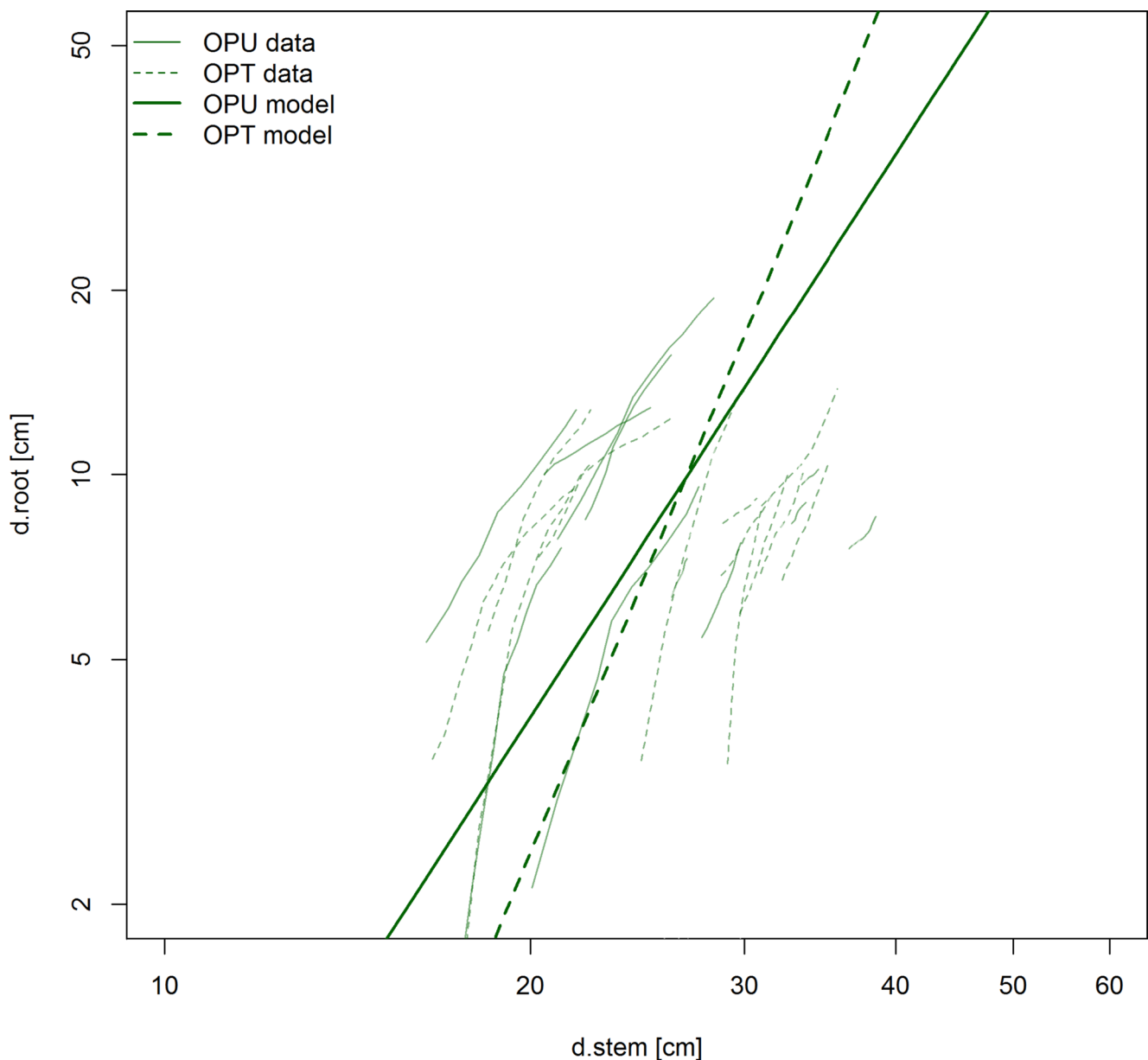


Fig. 5 Coarse root-stem diameter trajectories for sessile oak trees in monospecific stands, categorized by treatments (unthinned and thinned), as a function of SPEI6 and Δ SDI. The straight lines represent predictions based on the fitted Model 4, including only the fixed effects

Discussion

Effects of thinning on stem growth (Q1)

Across all variants, DBH increments were consistently higher in thinned stands (OPT, OMT, PPT, PMT) than in unthinned controls (OPU, OMU, PPU, PMU) throughout the entire post-thinning period, supporting previous findings on the positive effects of thinning (e.g., Valinger et al. 2019; Ara et al. 2023; Li et al. 2023). However, species responses differed, reflecting contrasting ecological and physiological traits (Ellenberg 1988; Lyr et al. 1992).

Sessile oak exhibited an immediate and pronounced post-thinning increase, particularly in the first year, consistent with its capacity to rapidly allocate additional light, water, and nutrients to stem and foliage growth (Adamec et al. 2014; Fedorová et al. 2016). In contrast, Scots pine showed an initial decline in 2018 followed by gradual recovery. This delayed response is linked to its foliage dynamics: Scots pine typically retains four to six older needle cohorts that demand substantial maintenance resources (Jalkanen 1998; Valinger et al. 2000). Consequently, it cannot immediately reinvest released resources after thinning, but instead benefits progressively as competition declines. Despite this lag,

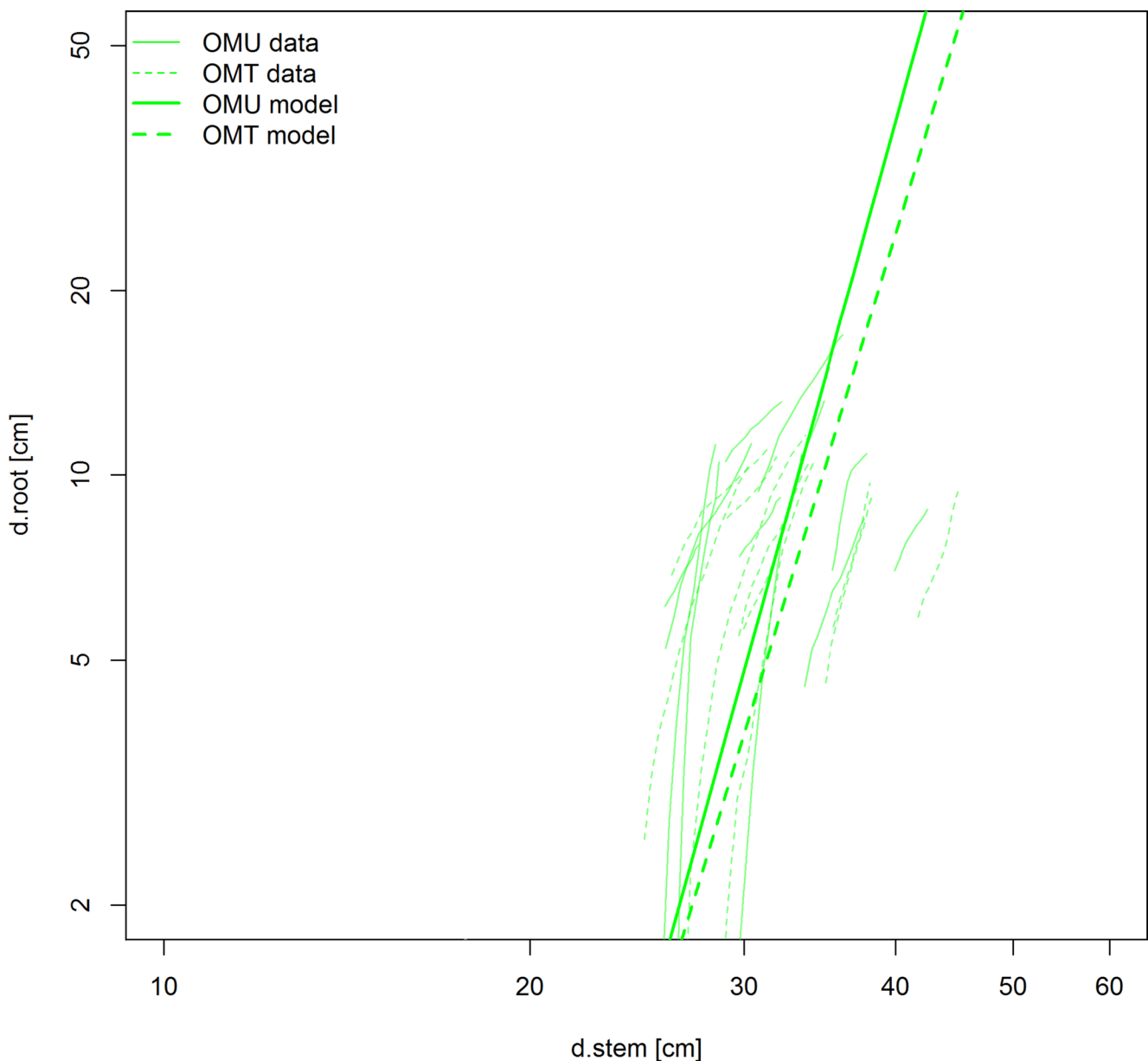


Fig. 6 Coarse root-stem diameter trajectories for sessile oak trees in mixed stands, categorized by treatments (unthinned and thinned), as a function of SPEI6 and Δ SDI. The straight lines represent predictions based on the fitted Model 4, including only the fixed effects

Scots pine ultimately displayed a strong growth response—a pattern also documented for lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) after partial cutting in dry conifer forests of central British Columbia (Kneeshaw et al. 2002).

The exceptionally hot and dry conditions in 2018, combining drought and heat stress, further contributed to the initial decline in Scots pine growth, reflecting its well-known drought sensitivity (Rebetez and Dobbertin 2004; Poyatos et al. 2008; Zang et al. 2012; Senf and Seidl 2021; Haberstroh et al. 2022). A thinning shock, as described in Douglas-fir (Harrington and Reukema 1983), Corsican pine

(*Pinus laricio*) (Picchio et al. 2011, 2018), and ponderosa pine (*Pinus ponderosa*) (Dore et al. 2012), appears unlikely, since reductions were less pronounced in thinned than in unthinned stands. Instead, heavy thinning from above likely mitigated drought stress by reducing stand density and competition, consistent with findings for Scots pine in Switzerland (Giuggiola et al. 2013) and Spain (Navarro-Cerrillo et al. 2019). In contrast, sessile oak showed no decline in 2018, reaffirming its higher drought tolerance (Ellenberg 1988; Aas 1998). Thinned oak stands (OPT, OMT) exhibited enhanced growth, further confirming the beneficial effects of thinning for this species.

Lagged responses in Scots pine also align with findings for white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.)), where significant growth gains emerged only several years after treatment (Urban et al. 1994; Vincent et al. 2009). In the present study, substantial increments appeared three years post-thinning in PPT, PMT, and OMT, whereas monospecific oak (OPT) responded rapidly within the first year. This difference likely reflects species- and stand-specific strategies for capitalizing on reduced competition. Favorable precipitation in 2021 further amplified thinning effects, as all oak variants and thinned pine stands showed another peak in DBH growth.

The magnitude of growth response also differed between species. Sessile oak showed moderate increases (+48% in OPT, +26% in OMT), in agreement with Mayor and Rodà (1993), though lower than their reported gains in holm oak (*Quercus ilex* L.), likely due to site and species differences. Scots pine exhibited stronger gains (+61% in PPT, +52% in PMT), consistent with Peltola et al. (2002), Aldea et al. (2017), and Pape (1999), who found that heavy thinning maximizes conifer growth even under drought conditions. These results emphasize that while sessile oak benefits immediately, Scots pine exhibits a delayed but substantial response, reinforcing heavy thinning from above as an effective strategy for promoting DBH growth and resilience in both species.

Comparative studies further show that thinning intensity largely determines the magnitude of growth response, whereas tree size influences its timing—a relationship consistent across species and regions (Mehtätalo et al. 2014). Similarly, Franklin et al. (2009) reported overlapping near-optimal density ranges among species, suggesting that thinning principles can be broadly generalized. The present results support this view: heavy thinning from above consistently enhanced DBH growth in both species. Growth surges are typically strongest shortly after thinning (Gonçalves 2021), although crown thinning may induce delayed but more sustained effects (Bella and Franceschi 1974). While benefits diminish as stands reclose, positive effects can persist for decades (Assmann 1970; Pretzsch 2009b; Ameztegui et al. 2017). Overall, thinning remains a key silvicultural tool for enhancing forest growth and resilience across species.

Effect of thinning on stem growth: monospecific vs. mixed stand types (Q1)

Monospecific stands (OPU, OPT, PPU, PPT) exhibited consistently higher DBH increments than mixed counterparts (OMU, OMT, PMU, PMT), with the strongest growth in thinned monospecific stands (OPT, PPT) and the lowest in unthinned mixed stands (OMU, PMU). Thinning effects

were particularly pronounced in monospecific Scots pine, where reduced intraspecific competition enhanced access to light, water, and nutrients, in line with classical thinning theory (Assmann 1970; Oliver et al. 1996; Pretzsch 2009b). In mixed stands, growth responses were more complex due to interspecific interactions, which can be either competitive or facilitative depending on site conditions and species composition (Pretzsch 2005; Forrester and Bauhus 2016; Primicia et al. 2016; Ammer 2019). In the unthinned mixture (PMU), sessile oak suppressed Scots pine, resulting in the lowest growth, whereas thinning mitigated this effect and promoted recovery in PMT during 2021–2022. Nevertheless, thinned monospecific stands (OPT, PPT) consistently outperformed mixed variants (OMT, PMT). In unthinned stands, by contrast, species composition exerted limited influence, with growth not differing significantly between monospecific and mixed plots.

These patterns suggest that while thinning reduces intra-specific competition in both species, the benefits of lowered interspecific competition in mixtures are less pronounced due to persistent resource partitioning. This interpretation aligns with Condés et al. (2013), who noted that species composition may outweigh stand density in determining thinning outcomes. Although certain mixtures can enhance productivity (Pretzsch et al. 2012c), interspecific competition in Scots pine–sessile oak stands appears to constrain post-thinning gains. Comparable results were reported by Houtmeyers and Brunner (2020) in Norway spruce–Scots pine mixtures, where growth responses were driven mainly by release from competition rather than species composition. Overall, these results highlight the need for stand type-specific management: heavy thinning from above is highly effective in monospecific Scots pine and sessile oak stands, whereas its success in mixed stands depends largely on interspecific dynamics and site conditions.

Effect of thinning on coarse root growth (Q2)

Coarse root increments were consistently higher in sessile oak variants (OPU, OPT, OMU, OMT) than in Scots pine (PPU, PPT, PMU, PMT) during 2018–2022. All oak variants peaked in 2021, paralleling stem growth, likely in response to favorable precipitation. Thinned stands (OMT, PPT, PMT) generally exceeded unthinned counterparts (OMU, PPU, PMU), reflecting reduced competition for water and nutrients (Da-Lun et al. 2010). However, thinning had only a minor effect in monospecific oak (OPT vs. OPU), suggesting lower sensitivity to intraspecific belowground competition or a more conservative allocation strategy. Among oak variants, OMT exhibited the highest coarse root increment, indicating benefits from interspecific interactions with Scots pine, potentially through niche complementarity in soil

resource use (Hendriks and Bianchi 1995; Brassard et al. 2011; Pardos et al. 2021). In contrast, Scots pine responded most strongly in the thinned monospecific variant (PPT), consistent with a greater reliance on reduced intraspecific competition.

Coarse root responses lagged behind stem growth, with substantial increases emerging after four years in PPT and five in PMT, while OMT showed a three-year delay and OPT no clear response. This trend mirrors the findings of Vincent et al. (2009), who observed delayed post-thinning root growth in black spruce. The weaker and slower coarse root responses relative to stems likely reflect carbon allocation priorities, with resources initially directed toward stem expansion to maintain canopy dominance, followed by root system adjustment to enhance resource uptake and stability. Since crop trees were already dominant, light competition was likely less relevant, pointing instead to species-specific allocation strategies and belowground dynamics as drivers of root responses.

Overall, mixed oak stands (OMU, OMT) outperformed monospecific ones (OPU, OPT), suggesting that sessile oak benefits from interspecific interactions, whereas mixed pine stands (PMU, PMT) generally lagged behind monospecific variants (PPU, PPT), indicating stimulated Scots pine root development under reduced intraspecific competition. These contrasting patterns underscore species-specific physiological strategies and highlight the importance of considering both above- and belowground processes when evaluating thinning and mixture effects.

Coarse root-stem allometry of Scots pine and sessile oak (Q3)

Both Scots pine and sessile oak allocated proportionally more biomass to coarse roots than to stems, with Scots pine characterized by higher allometric factors and sessile oak by higher allometric exponents. This pattern mirrors results from Ulbricht et al. (2025), who reported comparable contrasts between Norway spruce and European beech. Coarse root allocation was enhanced in PPT, PMT, and OPT through the combined effects of thinning and crop-tree dominance, whereas dominance alone increased coarse root growth in PPU, PMU, OPU, OMU, and OMT, with no detectable thinning effect in OMT. According to the balanced growth hypothesis (Bloom et al. 1985; Tilman 1988; Shipley and Meziane 2002; McCarthy and Enquist 2007), light availability is rarely limiting for dominant crop trees. Occupying favorable canopy positions, these trees expand their root systems to maximize water and nutrient uptake and to improve anchorage against windthrow (Ulbricht et al. 2025), thereby enhancing long-term stability, resilience,

and ecosystem biodiversity (Kimmins 2004; Grebner et al. 2021).

Sessile oak consistently exhibited lower allometric factors but higher exponents than Scots pine, indicating proportionally stronger coarse root allocation. These interspecific differences were reflected both in coarse root–stem ratios (see Results S1 in the Supplementary Section) and in coarse root–stem allometry, consistent with broadleaf–conifer contrasts reported by Bolte et al. (2004), Wang et al. (2008), and Qi et al. (2019). Such variation likely results from species-specific genetic control, site conditions, and belowground competition for resources (Enquist et al. 1999; Delucia et al., 2000; Copenhaver and Tinker 2014; Dutcă et al. 2018). With increasing age, declining root efficiency necessitates greater biomass investment (Shipley and Meziane 2002), a trend particularly evident in dominant crop trees. Thinning amplifies these dynamics by enhancing canopy light availability and photosynthesis (Vincent et al. 2009), while simultaneously increasing transpiration and wind exposure (Pothier and Margolis 1990, 1991; Urban et al. 1994; Ruel et al. 2003). To restore root–shoot balance, trees may therefore prioritize belowground growth to offset greater water demand and nutrient uptake requirements (Kneeshaw et al. 2002).

Despite distinct physiological traits, both species share structural similarities, including deep taproots and extensive lateral roots that provide anchorage and access to deeper soil layers (Leuschner and Meier 2018). Crown architecture, however, diverges: sessile oak develops broad, spreading crowns suited to open habitats, whereas Scots pine forms narrow, conical crowns adapted to dense stands (Richardson 2000). Biomass partitioning also differs: sessile oak allocates approximately 20–30% to roots and 50–60% to stems, compared with 15–20% and 55–65% in Scots pine (Helmisaari et al. 2002; Mokany et al. 2006; Finér et al. 2007; Qi et al. 2019). The broad oak crown likely increases transpiration and wind exposure, promoting greater root allocation, while Scots pine invests more in stem biomass to remain competitive under light-limited conditions.

Coarse root-stem allometry in monospecific vs. mixed stands (Q3)

Contrasting biomass partitioning between coarse roots and stems was observed in Scots pine and sessile oak, with all stand type variants allocating proportionally more biomass to coarse roots than stems. Sessile oak exhibited a stronger coarse root allocation response than Scots pine. In Scots pine, unthinned stands showed higher allometric factors (PMU>PPU) than thinned stands (PPT>PMT), whereas thinned stands exhibited higher allometric exponents (PMT>PPT) than unthinned ones (PMU>PPU). In

sessile oak, monospecific stands displayed higher allometric factors (OPU > OPT) than mixed stands (OMT > OMU), while mixed stands showed higher allometric exponents (OMU > OMT) than monospecific ones (OPT > OPU).

Thinning markedly altered both intra- and interspecific competition in Scots pine but primarily affected intraspecific competition in sessile oak. These findings indicate that Scots pine coarse root–stem allometry is more responsive to thinning in mixed stands, whereas sessile oak coarse root–stem allometry is less sensitive to thinning under interspecific competition. Competition type influenced allocation patterns in sessile oak across stand types, whereas species composition exerted only a minor effect on Scots pine, highlighting species-specific responses to thinning and competition dynamics. Similar patterns were reported by Ulbricht et al. (2025), who found no significant differences in coarse root–stem allometry between monospecific and mixed stands of Norway spruce and European beech. This supports the results for Scots pine but contrasts with those for sessile oak, suggesting that conifers tend to maintain stable coarse root–stem allocation regardless of species composition, while broadleaved trees exhibit more plastic, species-specific allocation strategies that vary with competition intensity and stand structure.

Coarse root-stem allometry modulated by Δ SDI and SPEI6 (Q3)

Water availability (SPEI6) exerted stronger control over coarse root–stem allometry in sessile oak, whereas thinning intensity, expressed as changes in stand density index (Δ SDI), had a greater influence in Scots pine. In Scots pine, thinning generally reduced allometric factors (PPT, PMT) and increased exponents, promoting coarse root growth, with effects varying according to thinning intensity and moisture conditions. Responses were most pronounced in mixed stands under wetter conditions, while the direct impact of water availability was minimal. This pattern suggests that Scots pine prioritizes structural stability over plasticity in biomass allocation, partly deviating from the balanced growth theory (Bloom et al. 1985; Tilman 1988; Shipley and Meziane 2002; McCarthy and Enquist 2007). Sessile oak, by contrast, exhibited a more flexible allocation strategy. In monospecific oak (OPT), thinning reduced the allometric factor but increased the exponent, enhancing coarse root allocation under higher thinning intensity. Conversely, mixed oak (OMT) showed the opposite response: thinning increased the factor but reduced the exponent, although both effects weakened with intensity. Across all oak stands, allometric factors increased in dry years and declined in wet years, whereas exponents decreased under drought and rose with higher moisture availability. This pattern indicates

stronger coarse root investment under favorable growing conditions and reduced allocation during water stress, again diverging from balanced growth predictions.

Comparisons with other species support these contrasting strategies. Norway spruce, for instance, allocated more biomass to coarse roots only under extreme drought (Nikolova et al. 2011), consistent with the relatively low sensitivity of Scots pine to moderate moisture variation. In contrast, Pretzsch et al. (2012a) observed that drought in Monterey pine (*Pinus radiata*) and maritime pine (*Pinus pinaster*) reduced exponents but increased factors—a pattern resembling sessile oak in this study, possibly reflecting greater fine-root vulnerability to water deficits. Pretzsch et al. (2012b) further documented stable coarse root–shoot allometry in lodgepole pine, with shifts occurring only on nutrient-poor, water-limited sites. Together, these studies reinforce that root–stem allocation adjustments are highly species-specific and shaped by prevalent growth conditions.

Broader syntheses highlight the combined influence of climate and ontogeny. Stem and root biomass generally increase with stand age and precipitation (Zhang et al. 2015), while root–stem ratios tend to decline with rising temperature and precipitation but increase with elevation and latitude (Mokany et al. 2006; Wang et al. 2008; Lim et al. 2013; Qi et al. 2019). However, other research found no consistent correlations (Cairns et al. 1997; Wang et al. 2012) or reported near-isometric allocation across environments (Hui et al. 2014; Easdale et al. 2019). Reich et al. (2014) identified temperature as a stronger driver of biomass allocation than water availability. In line with previous research, the present findings demonstrate that coarse root–stem allocation patterns vary markedly among species and are contingent on stand structure and site conditions, with Scots pine responding primarily to thinning and competition release, and sessile oak more sensitive to water availability and species composition.

Critique and generalisability

Due to differences in data acquisition and experimental plots, the Scots pine and sessile oak sample trees exhibited variation in root and stem growth, despite efforts to ensure comparable age, stand structure, and growth conditions. These trees represent forests with typical light, water, and nutrient availability found across much of Central Europe. Growth patterns can vary with tree species, management regime, and resource availability, as documented by Jactel et al. (2009); Forrester et al. (2016); Grossiord et al. 2014a, b; Nikolova et al. (2011). As the analysis focused on dominant mature trees, species-specific growth responses may partly reflect competitive status rather than intrinsic physiological traits. Variability within the same species, driven

by age, size, site conditions, and competition, has also been reported by Drexhage et al. (1999), Peichl and Arain (2007), Genet et al. (2011), Schall et al. (2012), and D'Amato et al. (2013).

While heavy thinning from above can initially promote diameter growth, it may also influence long-term stand structure, species composition, and forest dynamics, thereby affecting growth rates beyond the immediate post-thinning period. Consequently, the results presented here may not be directly transferable to forests under different climatic, geological, or management conditions, or to other tree size classes. Moreover, the stems and coarse roots analyzed represent only part of the total above- and belowground biomass. Branch, twig, and fine-root growth may differ substantially from stem and coarse-root dynamics (Zerihun and Montagu 2004; Coyle et al. 2008). Therefore, the root–stem allometry examined in this study captures only a subset of overall biomass allocation patterns (Santantonio et al. 1977), even though coarse organs are functionally and structurally linked to finer components (Pretzsch et al. 2012a).

Conclusions

This study highlights the complex, species-specific responses of Scots pine and sessile oak to heavy thinning from above and to environmental drivers such as water availability. While heavy thinning from above generally promoted tree growth, its effects on coarse root–stem allometry differed between species: in Scots pine, allometry was primarily influenced by thinning intensity, particularly in mixed stands, whereas in sessile oak it responded more strongly to precipitation, with thinning intensity playing a secondary role. Enhanced coarse root allocation in dominant trees of both species—most pronounced in unthinned mixed oak stands but generally elevated under thinning—suggests potential benefits for belowground carbon sequestration, stand stability, and resilience, thereby contributing to climate change mitigation.

These findings underscore the importance of integrating both environmental factors and stand structure when predicting forest growth responses to thinning and climate variability. Forest management should be tailored to species-specific traits and dynamics, for example by applying graduated thinning to maintain structural heterogeneity, promoting mixed-species stands to enhance resource complementarity, and adjusting thinning intensities according to site conditions and future climate projections. Nevertheless, the mechanisms governing biomass allocation between coarse roots and stems remain insufficiently understood, highlighting the need for further research. Expanding understanding of coarse root–stem allometry across stand types and environmental gradients will be crucial for improving

silvicultural strategies that support long-term forest stability, productivity, and adaptive capacity under changing climatic conditions.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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