



Competitive disadvantage of *Quercus petraea* seedlings in mixtures with *Fagus sylvatica* and *Carpinus betulus* can be explained by different biomass allocation patterns

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Abstract

Natural regeneration of *Quercus petraea* is often inferior in height growth compared to shade-tolerant companion species. As a result, frequent removal of competing vegetation is typically required to promote *Q. petraea* for successful regeneration. Here we examined whether differences in species' biomass allocation, biomass density, and total leaf area are responsible for inferior competitiveness of *Q. petraea*. For this purpose, 37 four-year-old *Q. petraea* seedlings and 15 and 17 seedlings of the shade-tolerant *Fagus sylvatica* and *Carpinus betulus*, respectively, were excavated along a radiation gradient within a mixed *Q. petraea* forest. Solar radiation above each seedling ranged from 1 to 70% of open field conditions. Annual shoot lengths and total heights of *F. sylvatica* and *C. betulus* were higher than in *Q. petraea* across the radiation gradient. Total biomass was comparable among the species at any level of radiation, but aboveground woody mass fraction in *Q. petraea* (34%) was always significantly lower than in *F. sylvatica* (47%) and *C. betulus* (52%), while its root mass fraction was significantly higher at 47% compared to 34% and 26%, respectively. At the same time, *Q. petraea* had a significantly lower average height-to-root collar diameter ratio (56) than *F. sylvatica* (71) and *C. betulus* (105). In contrast, biomass density of *Q. petraea* roots and shoots was significantly higher than in *F. sylvatica* and *C. betulus*. Owing to different biomass allocation patterns between *Q. petraea* and companion species, there are no light levels at which *Q. petraea* regeneration does not require control of competition to survive.

Keywords *Quercus petraea* · Natural regeneration · Interspecific competition · Light availability · Biomass allocation

Introduction

At most sites where *Q. petraea* (Mattuschka) Liebl. is cultivated in Central Europe, its natural regeneration typically competes with more shade-tolerant tree species such as *F. sylvatica* L. and *C. betulus* L. (Annighöfer et al. 2015; Mölder et al. 2019; Kohler et al. 2020; Kuehne et al. 2020; Govedar et al. 2021). Shade-tolerant tree species differ from

more light-demanding species such as *Q. petraea* in morphological and physiological leaf traits that enable their survival and growth under low light conditions (Valladares and Niinemets 2008). They generally have a higher specific leaf area (SLA) and a lower light compensation point, allowing them to achieve a positive photosynthetic rate and to assimilate carbon even at low radiation intensity. At high radiation intensity, however, shade-tolerant species typically have a lower maximum photosynthetic rate and are more susceptible to photoinhibition than light-demanding species (Valladares and Niinemets 2008).

Inferior height growth of *Q. petraea* seedlings and saplings was found in almost all studies that compared it to *F. sylvatica* and/or *C. betulus* (e.g., Tobisch 2010; Ligot et al. 2013; Annighöfer et al. 2019; Modrow et al. 2020; Tinya et al. 2020; Govedar et al. 2021). In particular, at prolonged low light conditions, regeneration of *Q. petraea* is usually overgrown and outcompeted by *F. sylvatica* and *C. betulus*

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(von Lüpke and Hauskeller-Bullerjahn 1999; Valladares et al. 2002; Ligot et al. 2013; Modrow et al. 2020). These light conditions are characterised by long-lasting indirect radiation of low intensity and short phases of direct radiation of medium to high intensity, i.e. lightflecks (Modrow et al. 2025b). Lightflecks can contribute between 10% and 80% of the total daily radiation reaching the forest floor, even though they may occur for only about 10% of the day (Chazdon 1988; Pfitsch and Pearcy 1989; Leakey et al. 2005). This specific light regime favours *F. sylvatica* and *C. betulus* over *Q. petraea*, as the former species - in contrast to *Q. petraea* - can quickly acclimate to variable light conditions and have a higher photosynthetic efficiency during lightflecks (Modrow et al. 2025a). However, even under elevated light conditions at which its leaves have a higher photosynthetic capacity (Modrow et al. 2020, 2025a) than those of *F. sylvatica* and *C. betulus*, *Q. petraea* generally displays inferior height growth performance (Bobiec et al. 2018; Modrow et al. 2025a). Other studies indicated that the growth inferiority of *Q. petraea* may be attributable to differences in biomass allocation, but they have not provided data on the biomass allocation of *Q. petraea*, *F. sylvatica*, and *C. betulus* at an identical site. These studies suggested that seedlings of *Q. petraea* have a lower aboveground woody mass fraction and a higher root mass fraction (Humphrey and Swaine 1997; Rodríguez-Calcerrada et al. 2008; Vernay et al. 2016) compared to those of *F. sylvatica* (Welander and Ottosson 1998; Pastorella and Paletto 2014; Bebre et al. 2022) and *C. betulus* (Kawaletz et al. 2014; Kuehne et al. 2014; Konôpka et al. 2023). Since biomass allocation of tree species can be influenced by seedling age (Pastorella and Paletto 2014; Le Goff and Ottorini 2022), site conditions (Poorter and Nagel 2000; Poorter et al. 2012) and tree species composition (Audisio et al. 2024; Paligi et al. 2024), it is not possible to directly compare the results of these studies, which did not control for these factors. Another explanation for the inferior competitiveness of *Q. petraea* may result from differences in the species-specific height to diameter ratio (HD ratio) (Bebe et al. 2021). Individuals or species with a higher HD ratio reach a greater height with the same aboveground woody mass compared to those with a low HD ratio. Differences in wood density of aboveground mass could also lead to differences in height growth (Kooyman and Westoby 2009). Furthermore, the higher photosynthetic performance of leaves of *Q. petraea* compared to *F. sylvatica* and *C. betulus*, especially under high light conditions, may be compensated by a larger total leaf area of *F. sylvatica* and *C. betulus* at the plant level (cf. Kuehne et al. 2014).

In addition to tree species competition, ground vegetation plays a decisive role in the success of *Q. petraea* natural regeneration (Annighöfer et al. 2015; Mölder et al. 2019;

Kohler et al. 2020; Kuehne et al. 2020; Govedar et al. 2021). The height and cover of ground vegetation increase substantially with increasing radiation (Gálhidy et al. 2006; Tobisch 2010; Kelemen et al. 2012; Kollár 2017). High light conditions in the initial establishment phase can cause *Q. petraea* seedlings to be overgrown by dense ground vegetation due to their low height (Harmer et al. 2005; Harmer and Morgan 2007; Kuehne et al. 2020).

Although there are studies describing light ecology of *Q. petraea*, it is still unclear under which light conditions *Q. petraea* is outcompeted by ground vegetation. However, this knowledge is essential for deriving silvicultural interventions creating optimal light conditions in the initial establishment phase of *Q. petraea*.

The morphological and physiological variables that may be decisive for the competition among the tree species have unfortunately been studied mostly for individual species but not in a comparative design. This of course limits the comparability between the species due to differences in site conditions, including light microclimate, and ontogenetic stage of studied individuals. This study aims to fill this knowledge gap by examining biomass allocation, height-to-diameter ratio, biomass density and total leaf area of 4-year-old seedlings of *Q. petraea*, *F. sylvatica*, and *C. betulus* under varying light conditions at a single site. To take competition from ground vegetation into account, its height and cover were also recorded. The following hypotheses were addressed:

1. Competition intensity between seedlings of *Q. petraea* and other tree species as well as ground vegetation is highly dependent on radiation,
2. *Q. petraea* has a lower aboveground woody mass fraction and a lower height-to-diameter ratio than *F. sylvatica* and *C. betulus*,
3. The biomass density of *Q. petraea* is higher than that of *F. sylvatica* and *C. betulus*, and
4. For seedlings of the same age growing under similar light conditions, *Q. petraea* has a smaller total leaf area than *F. sylvatica* and *C. betulus*.

Methods

Study site

The study site is located in the northern part of Bavaria, Germany, near the city of Lohr am Main (49° 56' 53" N, 9° 29' 33" E), on a plateau 330 m above sea level. The area has a slope of 10% with a southern exposure and a mean annual temperature of 7.3 °C and average annual rainfall of 960 mm (1991–2020, LWF 2021). The soil is a brown earth

derived from sandy top layers of the Lower Sandstone. The potentially natural forest community is mapped as a *Luzulo-Fagetum*, i.e. *F. sylvatica* forest with individual admixed *Q. petraea* trees (Ellenberg 2009).

The concrete study site is dominated by approximately 250-year-old *Q. petraea* trees with a single-stem admixture of *F. sylvatica* in the overstorey. Understorey and midstorey is formed by *F. sylvatica* and *C. betulus*. After the mast year of 2018, a shelterwood cut was conducted on an area of approximately 1.6 hectares. All understorey and midstorey trees as well as all *F. sylvatica* and individual *Q. petraea* from the overstorey, were removed. After tree harvesting, the area was fenced. Natural regeneration of *Q. petraea*, *F. sylvatica* and *C. betulus* as well as understorey species consisting mainly of raspberry and blackberry had established on the site. Until the time of measurements, no tending to promote *Q. petraea* regeneration had taken place. Measurements were carried out in the shelterwood stand described above in August 2022, after completion of leaf flush.

Data collection

To capture variable site conditions, line transects were established at 10 m intervals in a North-South direction across the study site. Circular sample plots with a radius of 2 m were systematically placed within these transects at 10 m intervals, assuming that at this distance, the studied relationships between radiation and growth variables were spatially independent from those at neighbouring points. However, since we did not vary the distance between sampling points, we could not analyse whether the distance between seedlings had an influence on the analysed relationship.

In each sample plot, the tallest individual of *Q. petraea*, *F. sylvatica* and *C. betulus* was recorded and light availability was measured directly above its terminal bud. Solar radiation was quantified using a Solariscope instrument, which contains a camera with fisheye lens (Solariscope Behling SOL 300B contact: hb.messtechnik@gaia.de). Photos were taken under overcast sky conditions or just before sunrise or after sunset. The Solariscope calculates average light availability in relation to light availability under open field conditions (indirect site factor (ISF), direct site factor (DSF), total site factor (TSF) by automated analysis of the hemispherical photos according to seven threshold values (cf. Pryor 2010). ISF and DSF are the relative amount of diffuse and direct radiation that penetrates the forest canopy during one growing season. The growing season was defined as the period from 01.05 to 30.09. The share of diffuse radiation in total radiation is 50% in the long-term average (1957–2020) at the weather station Würzburg (station ID=05705, DWD 2021), which is representative for Germany, due to the

reduction of direct radiation by cloud cover. Therefore, ISF and DSF were equally weighted for the calculation of TSF.

Of the recorded individuals, a total of 36 *Q. petraea*, 17 *F. sylvatica* and 17 *C. betulus* were selected based on their TSF values, ensuring an even distribution along the radiation gradient. Two of the original 17 *F. sylvatica* individuals were subsequently removed from the dataset after a tree-ring analysis revealed they were two years older than the others. The analyses therefore comprised only 15 individuals of *F. sylvatica*. Total height, annual shoot length and root collar diameter (measured twice in rectangular positions) of the selected individuals were measured. To assess the competition for each individual, we recorded the height of the five tallest competitors, and the coverage (%) and height of the ground vegetation within a 0.5 m radius around each individual. All leaves were collected from the individuals and frozen to -18°C until analysed. The individual seedlings were excavated carefully to capture their complete root system. The roots and the aboveground woody mass were then separated at the root collar. The roots were frozen to -18°C , while the aboveground woody mass was oven-dried at 70°C for 72 h.

Five undamaged leaves were systematically selected from each individual to represent the observed range of leaf size variation. Their leaf area was measured using a scanner and the WinRHIZO software (Regent Instruments, Québec, Canada). The leaves, along with the remaining leaf sample from each individual, were then dried for 48 h at 40°C and weighed. The average specific leaf area (SLA) was calculated from the dry weight and leaf area of the five representative leaves. Total leaf area per seedling was then determined as the product of SLA and dry weight of the entire leaf sample.

The oven dry density of aboveground woody mass was calculated based on their dry weight and dry volume. The latter was determined using the water displacement method. Previously frozen roots were washed to remove adhering soil. The volume of the fresh roots was measured using the water displacement method, after which the roots were oven-dried at 70°C for 72 h. The root tissue density was calculated from the oven dry weight and the fresh volume.

Data analysis

Generalised linear models (GLMs) were used to evaluate and model the effect of total site factor (TSF) on the response variables studied. The quasibinomial family with a logit link was used to predict cover of ground vegetation due to the proportional data structure. Cover of ground vegetation was transformed, i.e. divided by 100, to obtain values between 0 and 1 prior to analysis. For total mass, total leaf area, annual shoot length, total height and root collar diameter of all

juvenile trees, the identity link was used to link the predictor to expected values of the gamma-distributed response variables (Zuur et al. 2009). For all other modelled relationships between TSF and the gamma-distributed response variables, as well as for the global models, the log link was used. Tree species was included as a categorical variable in global GLMs to compare the impact of TSF on growth variables across species. Owing to collinearity between TSF and the height of the five tallest competitors, as well as between TSF and the cover and height of ground vegetation, only TSF was included as a predictor.

In global GLMs, the influence of aboveground woody mass fraction, height-to-diameter-ratio at the root collar, and oven dry density of aboveground woody mass on the total seedling height was analysed. Owing to the collinearity among these predictor variables, they were analysed in three separate models. To make the influence of the three variables comparable, the independent variables were standardised using the scale function, resulting in a mean of 0 and a standard deviation of 1 (Zuur et al. 2009).

Model performance was evaluated using residual deviance, mean absolute bias (MAB, absolute value of observed-predicted), mean bias (MB) and root mean square error (RMSE) for the proportional response variables and additionally Akaike's information criterion (AIC) for the continuous response variables. Because model development aimed at optimising model performance, explanatory variables were transformed where appropriate to maximise prediction accuracy. Residuals of all models were checked for fit and concurrence with model assumptions.

All statistical analyses were performed with a significance level of $P < 0.05$ using the R programming software (version 4.4.1, R Core Team 2024).

Results

Growth of oak and competing tree species

Annual shoot length, total height and root collar diameter of *Q. petraea*, *F. sylvatica*, and *C. betulus* increased with increasing TSF. The increase was more continuous in *C. betulus* than in *Q. petraea* and *F. sylvatica* and also stronger in the former species for the variables annual shoot length and total height (Fig. 1a–c; Table 2, Appendix). In contrast, height and diameter growth of *Q. petraea* and *F. sylvatica* mainly increased within the radiation ranges of 1–20% and 50–70% TSF. *C. betulus* had significantly higher annual shoot length over the entire radiation range compared to *Q. petraea* and *F. sylvatica* (Fig. 1a). Seedlings of *C. betulus* were significantly taller than those of *Q. petraea* above a TSF of 15%, with the differences increasing with increasing

TSF. However, annual shoot length and total height of *Q. petraea* and *C. betulus* slightly converged again above 60% TSF. Annual shoot length and total height of *F. sylvatica* were generally higher than those of *Q. petraea*, but differences were not significant. Root collar diameter did not differ significantly between *Q. petraea*, *F. sylvatica*, and *C. betulus* (Fig. 1c).

The ratio of total height to diameter at the root collar (HD ratio) was significantly higher in *C. betulus* than in *F. sylvatica* and *Q. petraea*, averaging 105 compared to 71 and 56 respectively, and increased slightly with increasing TSF in *C. betulus* and *Q. petraea*, while remaining constant in *F. sylvatica* (Fig. 1d).

Growth of competing ground vegetation

Height and cover of the ground vegetation increased with increasing TSF. While height of ground vegetation increased mainly at $TSF < 30\%$, the increase in coverage was most pronounced at $TSF > 30\%$ (Fig. 2b). The height difference between *Q. petraea* and ground vegetation decreased strongly with increasing TSF and became negative at approx. 40% TSF, i.e. from this point onwards the ground vegetation was taller than *Q. petraea* (Fig. 2a).

Biomass and its allocation

Total biomass of *Q. petraea*, *F. sylvatica* and *C. betulus* increased with increasing TSF though at different rates. While total biomass of *C. betulus* increased continuously with TSF, total biomass of *Q. petraea* and *F. sylvatica* increased mainly within the radiation ranges of 1–20% and 50–70% TSF, although this pattern was less pronounced for *F. sylvatica* than for *Q. petraea* (Fig. 3a). Interestingly, there were no significant differences in total biomass between species along the radiation gradient. Total biomass of *Q. petraea* and *F. sylvatica* was almost equal, whereas that of *C. betulus* tended to be generally higher than that of *Q. petraea* and *F. sylvatica*. This difference became even more pronounced in the radiation range of 30–60% TSF, where total biomass diverged between *C. betulus* and the other two species. However, total biomass levels of the three tree species converged again above 60% TSF (Fig. 3a).

Significant differences in biomass allocation were observed between species. As indicated by the average root mass fraction (RMF) of 47%, *Q. petraea* allocated a significantly greater proportion of biomass to roots compared to *F. sylvatica* and *C. betulus*, which had an average RMF of 34% and 26%, respectively (Fig. 3b). Correspondingly, the average aboveground woody mass fraction (AMF) of 34% in *Q. petraea* was significantly lower than in *F. sylvatica* (47%) and *C. betulus* (52%) (Fig. 3c). Whereas RMF slightly

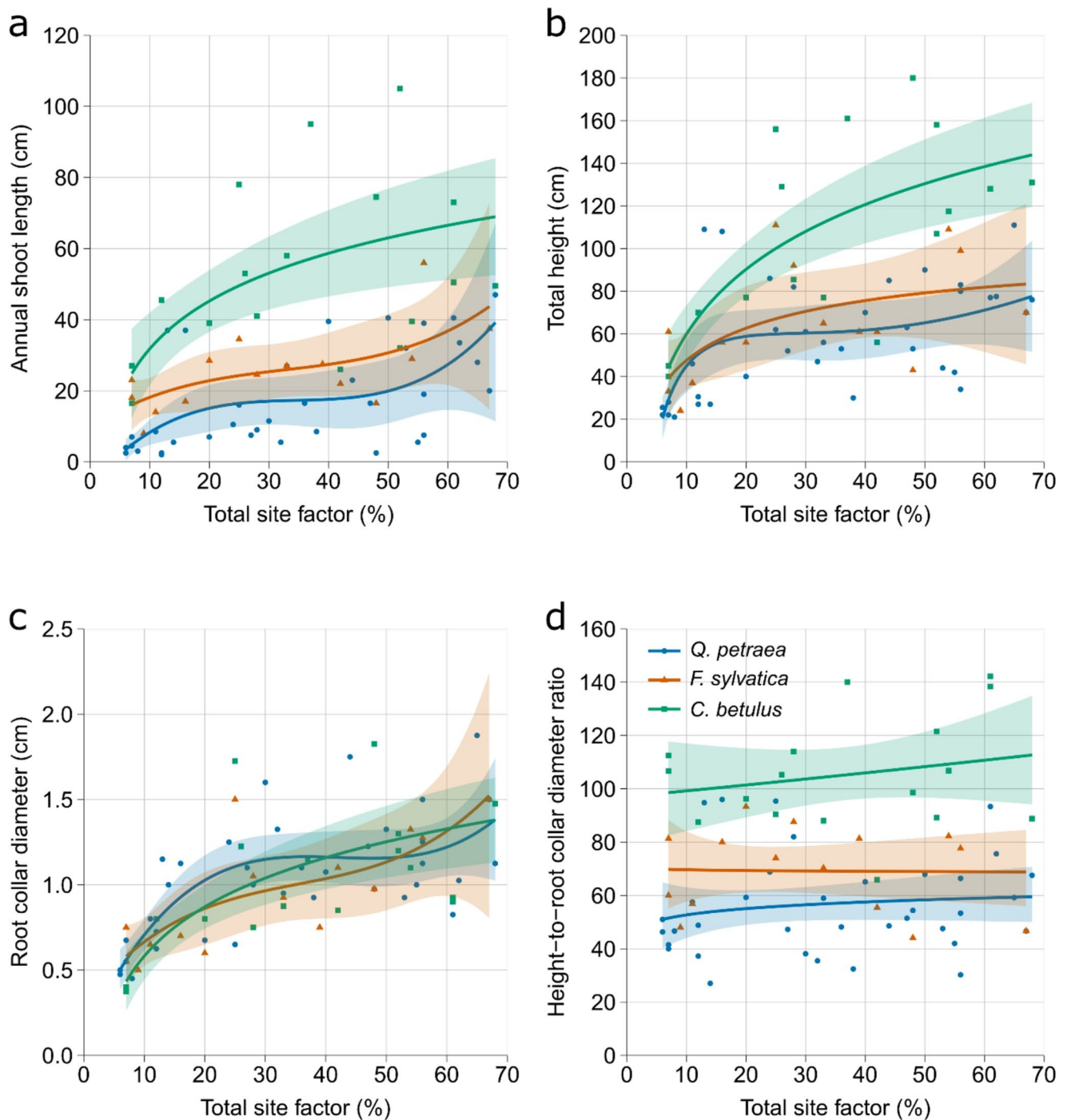


Fig. 1 Model predictions for **a** annual shoot length, **b** total height, **c** root collar diameter and **d** height-to-root collar diameter ratio of *Q. petraea* ($N=37$), *F. sylvatica* ($N=15$) and *C. betulus* ($N=17$) in rela-

tion to total site factor (TSF). Solid lines represent model fits and shaded areas indicate the 95% confidence intervals

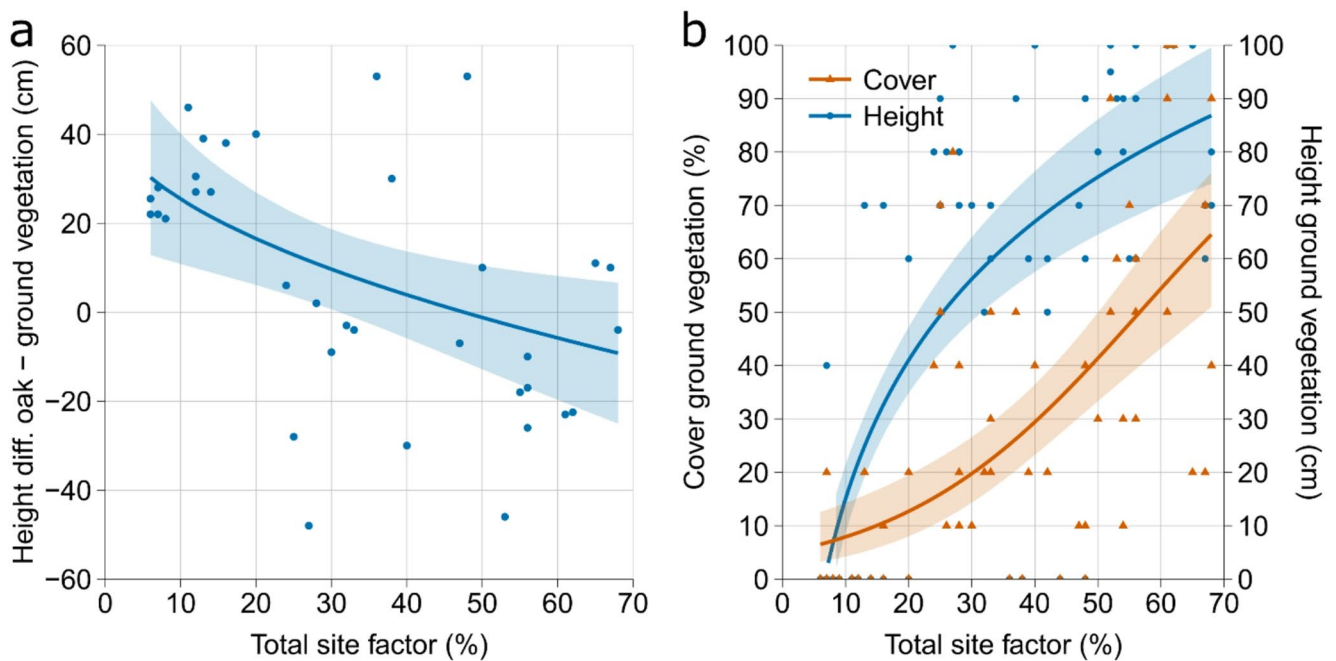


Fig. 2 Model predictions for **a** height difference between *Q. petraea* and ground vegetation ($N=37$) and **b** cover and height of ground vegetation ($N=69$; recorded in 10% and 10 cm classes, respectively) in

relation to total site factor (TSF). Solid lines represent model fits and shaded areas indicate the 95% confidence intervals

decreased, AMF increased with increasing TSF in all species. The average leaf mass fraction (LMF) was comparable in *Q. petraea* and *F. sylvatica* (19%), but slightly higher in *C. betulus* (22%). This difference was significant only at $TSF < 30\%$. The LMF of *Q. petraea* remained constant along the radiation gradient, whereas it decreased slightly in *F. sylvatica* and *C. betulus* (Fig. 3d).

Biomass density

The root tissue density of *Q. petraea*, *F. sylvatica* and *C. betulus* remained almost constant along the radiation gradient, averaging 1.03, 0.92 and 0.84 g cm⁻³, respectively (Fig. 4a). Differences between species were statistically significant over almost the entire radiation range. A similar pattern was observed for oven dry density of aboveground woody mass (AM) of *Q. petraea*, *F. sylvatica* and *C. betulus*, averaging 0.85, 0.8 and 0.74 g cm⁻³, respectively (Fig. 4b). Oven dry density of aboveground woody mass was lower than root tissue density in all three species.

Leaf traits

Specific leaf area (SLA) of *Q. petraea*, *F. sylvatica*, and *C. betulus* decreased with increasing TSF, with the strongest decrease observed in the radiation range 1–20% TSF for *Q. petraea* and *F. sylvatica*. The SLA of *Q. petraea* was significantly lower than that of *F. sylvatica* and *C. betulus* over

almost the entire radiation range, averaging 171 cm² g⁻¹ compared to 213 and 187 cm² g⁻¹, respectively (Fig. 5a).

Whereas total leaf area of *C. betulus* increased continuously with increasing TSF, in *Q. petraea* and *F. sylvatica*, it increased mainly within the radiation ranges of 1–20% and 50–70% TSF (Fig. 5b). Owing to high variability, differences in total leaf area between species were not statistically significant. It tended to be higher in *F. sylvatica* than in *Q. petraea* and was substantially higher in *C. betulus* compared to *Q. petraea* in the radiation range of 30–60% TSF. However, total leaf area of the three tree species converged again above 60% TSF (Fig. 5b).

Relationship between biomass allocation patterns and height growth

In addition to total biomass, the aboveground woody mass fraction, HD ratio, and oven-dry density of aboveground woody mass were significantly correlated with total height when analysing *Q. petraea*, *F. sylvatica*, and *C. betulus* in global models. Total height increased significantly with increasing aboveground woody mass fraction and HD ratio, with the HD ratio having a slightly stronger influence on total height. In contrast, total height decreased with increasing aboveground woody mass density. However, the influence of oven-dry density of aboveground woody mass on total height was significantly weaker than that of aboveground woody mass fraction and HD ratio (Table 1).

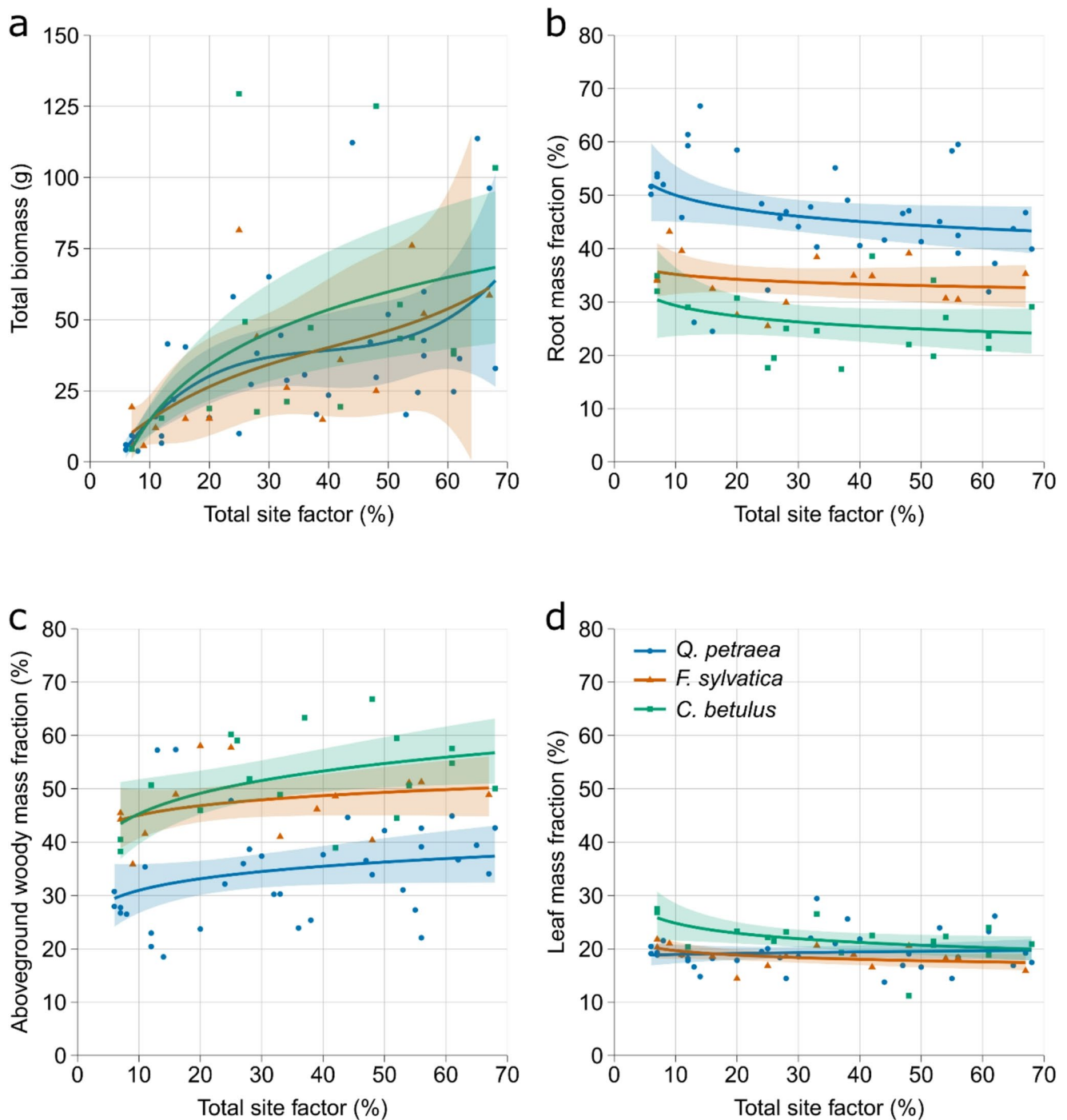


Fig. 3 Model predictions for **a** total biomass, **b** root mass fraction, **c** aboveground woody mass fraction and **d** leaf mass fraction of *Q. petraea* ($N=37$), *F. sylvatica* ($N=15$) and *C. betulus* ($N=17$) in rela-

tion to total site factor (TSF). Solid lines represent model fits and shaded areas indicate the 95% confidence intervals

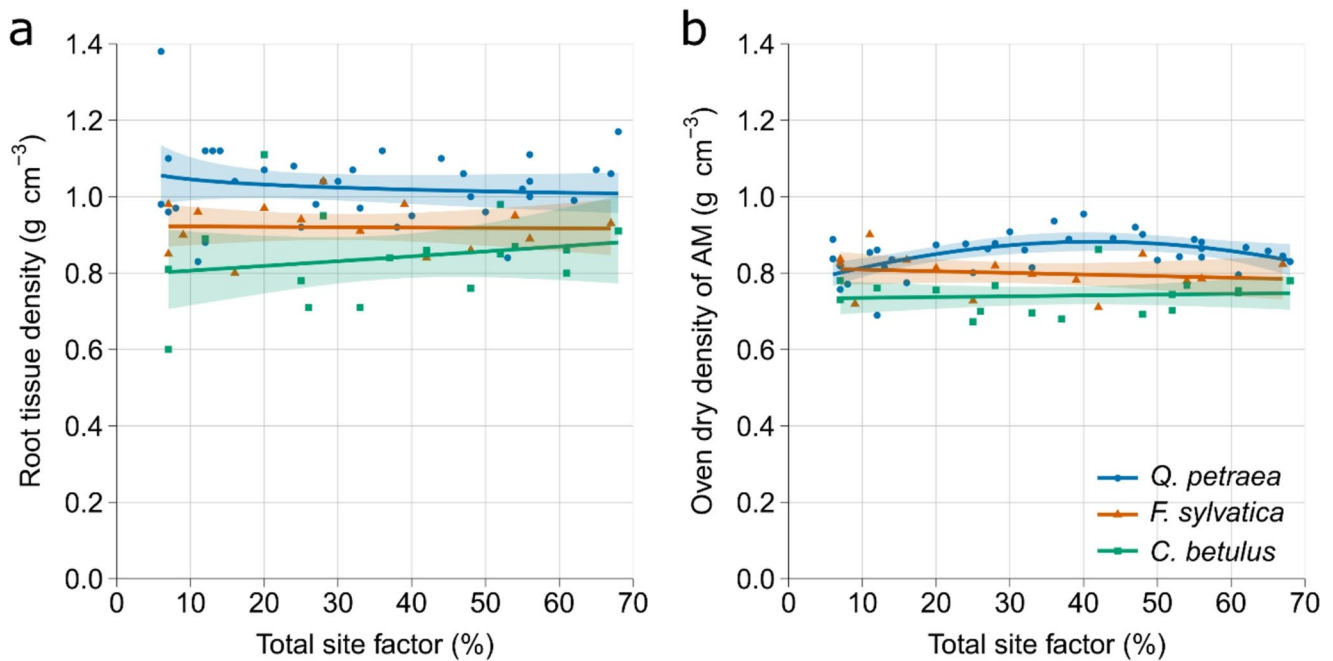


Fig. 4 Model predictions for **a** root tissue density and **b** oven dry density of aboveground woody mass (AM) of *Q. petraea* ($N=37$), *F. sylvatica* ($N=15$) and *C. betulus* ($N=17$) in relation to total site factor

(TSF). Solid lines represent model fits and shaded areas indicate the 95% confidence intervals

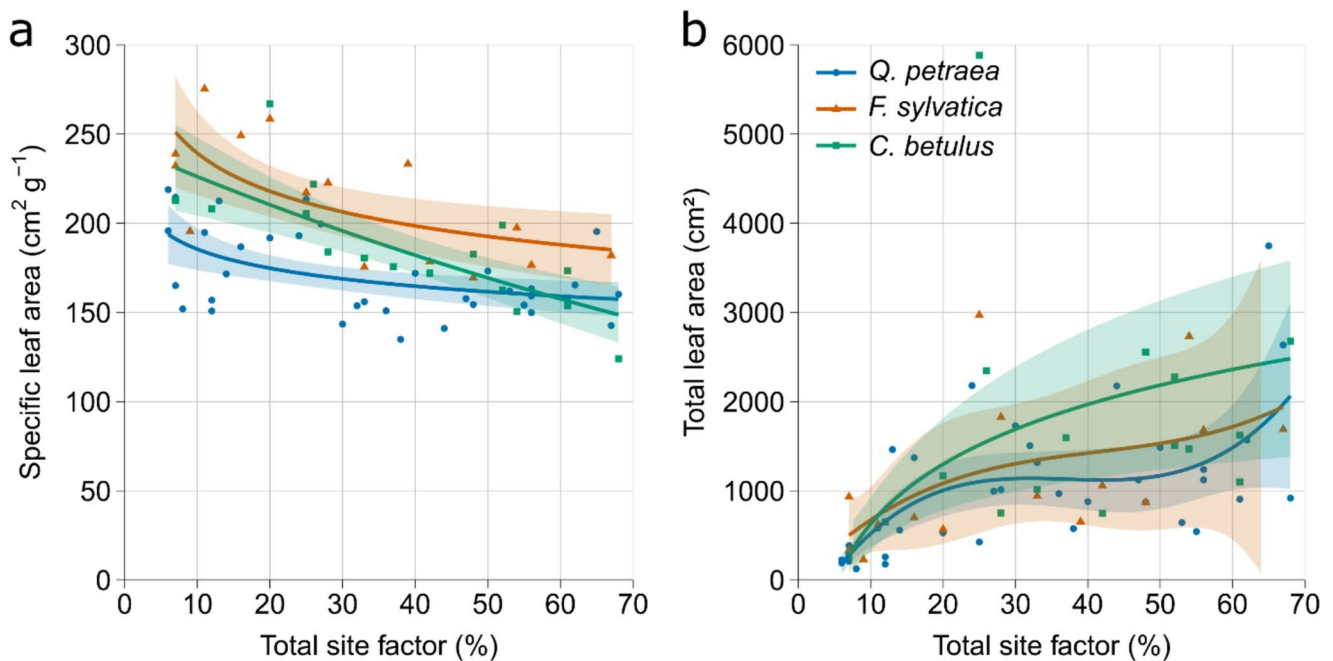


Fig. 5 Model predictions for **a** specific leaf area and **b** total leaf area of *Q. petraea* ($N=37$), *F. sylvatica* ($N=15$) and *C. betulus* ($N=17$) in relation to total site factor (TSF). Solid lines represent model fits and shaded areas indicate the 95% confidence intervals

Table 1 Parameter estimates and statistics of generalised linear models for average total height (TH) of all analysed four-year-old *Q. petraea* (N=37), *F. sylvatica* (N=15) and *C. betulus* (N=17) seedlings. In addition to total biomass, which was included in all three models, explanatory variables included (1) aboveground woody mass fraction (AMF), (2) height-to-root collar diameter ratio (HD ratio) and (3) oven-dry density of aboveground woody mass (AM)

Model	β	SE	t value	p value
TH=f(total biomass, AMF)				
Intercept	4.1584	0.0219	189.33	<0.0001
ln(total biomass)	0.2999	0.0246	12.17	<0.0001
ln(AMF)	0.3028	0.0246	12.28	<0.0001
TH=f(total biomass, HD ratio)				
Intercept	4.1446	0.0086	480.26	<0.0001
ln(total biomass)	0.3759	0.0088	42.53	<0.0001
ln(HD ratio)	0.3250	0.0088	36.77	<0.0001
TH=f(total biomass, density of AM)				
Intercept	4.1754	0.0307	135.861	<0.0001
ln(total biomass)	0.4224	0.0309	13.64	<0.0001
ln(density of AM)	-0.1934	0.0309	-6.246	<0.0001

Ln represents a natural logarithm transformation. Explanatory variables were standardised to compare their effect on total height between models

Discussion

At moderate light intensities, growth of juvenile oaks is inferior compared to competing vegetation

The species-specific patterns of total biomass, annual shoot length, total height, and root collar diameter were positively related to the TSF. Although these general patterns could be expected, our study unravelled a quite interesting specific pattern in *Q. petraea* and *F. sylvatica*: in these two species total biomass as well as height and diameter growth did not substantially increase between 20 and 50% TSF, which is an important finding regarding silvicultural management. This is consistent with light-related growth patterns of *Q. petraea* (Ligot et al. 2013; Van Couwenberghe et al. 2013; Modrow et al. 2020, 2025a) and *F. sylvatica* (Petriřan et al. 2009; Ligot et al. 2013; Van Couwenberghe et al. 2013; Modrow et al. 2025a) reported in other studies. It can be explained with limited leaf morphological acclimation in response to changing light conditions in *Q. petraea* and *F. sylvatica* within this radiation range (Modrow et al. 2025a). In contrast to *Q. petraea* and *F. sylvatica*, *C. betulus* exhibited an increase in growth patterns over almost the entire observed radiation range (cf. Kuehne et al. 2014), in particular also including the range of 20–50% TSF. When considering only the relationship between tree species and ground vegetation, the latter had a positive effect on seedling growth. This effect is not ecologically plausible, but rather reflects its strong correlation with light availability.

As observed in other studies, height growth in *Q. petraea* was inferior to *F. sylvatica* (e.g., Ligot et al. 2013; Van

Couwenberghe et al. 2013; Tinya et al. 2020) and especially *C. betulus* (e.g., Tobisch 2010; Tinya et al. 2020; Govedar et al. 2021). Height differences between *Q. petraea* and *F. sylvatica* hardly changed with radiation (cf. Modrow et al. 2025a), suggesting that competition between these species was relatively independent of light at this developmental stage. In contrast, *C. betulus* showed pronounced height superiority over *Q. petraea* at 30–60% TSF due to the different growth patterns, in line with our first hypothesis that competition intensity between these species is highly dependent on radiation. The increasing height difference between *Q. petraea* and *C. betulus* in this radiation range is also consistent with the results of other studies (Tobisch 2010; Modrow et al. 2025a). The apparent convergence of annual shoot length and total height of *Q. petraea* and *C. betulus* above 60% TSF has already been reported (Modrow et al. 2025a). Additionally, in the study by Modrow et al. (2025a), *Q. petraea* showed comparable total heights to *C. betulus* above 60% and to *F. sylvatica* along the entire radiation gradient from 1 to 70% TSF. This may be attributable to the drier and warmer climate and clay-dominated soils at the study site, conditions that favour *Q. petraea* over *F. sylvatica* (Ellenberg and Leuschner 2010).

As hypothesised, competition intensity between seedlings of *Q. petraea* and ground vegetation was highly dependent on radiation. Height and cover of ground vegetation increased with increasing radiation intensity, as observed in other studies (e.g., Gálhidy et al. 2006; Tobisch 2010; Kelemen et al. 2012; Kollár 2017; Modrow et al. 2025a). In this study, the height of natural regeneration of *Q. petraea* in the initial establishment phase was related to the height of ground vegetation along a radiation gradient. From a TSF > 40%, the height of the 4-year-old *Q. petraea* was lower than that of ground vegetation, indicating a strong negative influence. This negative effect is likely to increase with increasing radiation, as the negative difference between the height of *Q. petraea* and ground vegetation as well as the cover of ground vegetation increases, which can reduce seedling density and thus regeneration success (Harmer and Morgan 2007; Kuehne et al. 2020).

Biomass allocation to roots limits above-ground growth of juvenile Oaks

While total biomass of the 4-year-old seedlings of *Q. petraea*, *F. sylvatica* and *C. betulus* did not differ significantly, there were significant differences in biomass allocation. As hypothesised, *Q. petraea* had a significantly lower aboveground woody mass fraction and, correspondingly, a higher root mass fraction than *F. sylvatica* and *C. betulus*. The allocation patterns found in this study correspond with those reported for *Q. petraea* (Humphrey and Swaine

1997; Rodríguez-Calcerrada et al. 2008; Vernay et al. 2016), *F. sylvatica* (Welander and Ottosson 1998; Pastorella and Paletto 2014; Bebre et al. 2022) and *C. betulus* (Kawaletz et al. 2014; Kuehne et al. 2014; Konôpka et al. 2023) in previous studies. An increase in aboveground woody mass fraction with simultaneous decrease in root mass fraction with increasing radiation has also been observed in other studies of *Q. petraea* (Humphrey and Swaine 1997; Rodríguez-Calcerrada et al. 2008). However, this is the first study that directly compared biomass allocation of the three tree species in seedlings of the same age at the same site. This is important because biomass allocation is influenced by age and environmental factors such as water and nutrient availability (e.g. Poorter et al. 2012; Le Goff and Ottorini 2022). For example, in *F. sylvatica*, the root mass fraction decreases with increasing age, while the aboveground woody mass fraction increases (Pastorella and Paletto 2014; Le Goff and Ottorini 2022). Under limited water and nutrient availability, woody species on average allocate more biomass to their root system than under high resource availability (Poorter and Nagel 2000; Poorter et al. 2012).

Our study shows a significant influence of aboveground woody mass fraction on height differences among *Q. petraea*, *F. sylvatica* and *C. betulus*. However, this effect may change with increasing seedling age as well as under varying site conditions. It is possible that seedlings of *Q. petraea*, *F. sylvatica*, and *C. betulus* respond to limited water and nutrient availability with shifts in biomass allocation of differing magnitude. This may also explain why height differences among *Q. petraea*, *F. sylvatica*, and *C. betulus* vary across studies, and thus across sites (e.g. Modrow et al. 2025a). To date, however, no study has directly compared the biomass allocation of these species across different sites.

While annual shoot length and total height differed significantly between species, root collar diameters were similar across species, resulting in a significantly higher ratio of height to root collar diameter (HD ratio) in *F. sylvatica* and *C. betulus* compared to *Q. petraea*, in line with our second hypothesis. The higher HD ratio of *C. betulus* compared to *Q. petraea* is in accordance with other studies (Govedar et al. 2021). Interestingly, the HD ratios were almost constant or even slightly increasing (in *C. betulus*) across the light gradient. This indicates that the factors which influence the slenderness of juvenile trees were operating at similar strength across the observed radiation gradient. Diameter growth responds often more strongly to light availability than height growth, and decreasing competition increases diameter more than height (Annighöfer et al. 2022). Hence, results of our study suggest that increasing competition among seedlings and ground vegetation counterbalances

the influences of increasing light availability above seedlings. The importance of the HD ratio for competitiveness becomes evident when comparing *F. sylvatica* and *C. betulus*. Although both species had a similar aboveground woody mass fraction, *C. betulus* showed a significantly greater total height, reflecting the higher HD ratio.

The different biomass allocation between plant compartments and the different HD ratios are likely the most important reasons for the inferior height growth of *Q. petraea* compared to *F. sylvatica* and *C. betulus*.

Biomass density of *Q. petraea* is higher than that of the other tree species

As hypothesised, the wood density of *Q. petraea* was significantly higher than that of *F. sylvatica* and *C. betulus*. The differences in wood density of aboveground biomass between the species are largely consistent with the results of other studies on older trees (e.g. Komán and Fehér 2015; Petráš et al. 2020). The higher density of aboveground and belowground wood in *Q. petraea* is thus another factor that reduces its competitiveness in terms of height growth and space occupation when compared to the two companion species. Part of the density differences between the species may also be attributed to variation in non-structural carbohydrates (NSC; comprising starch and soluble sugars), as indicated by previous studies reporting higher NSC content in roots and aboveground woody mass of *Q. petraea* than in *F. sylvatica* during autumn (Barbaroux et al. 2003). Other studies found a significantly higher proportion of NSC in annual rings of *Q. petraea* compared to *F. sylvatica*, which can be attributed in particular to a higher starch content (Barbaroux and Bréda 2002; Michelot et al. 2012). In this study, a negative correlation was found between the wood density of aboveground mass and total height of *Q. petraea*, *F. sylvatica* and *C. betulus*. We assume that a possible influence of wood density on height differences between *Q. petraea*, *F. sylvatica*, and *C. betulus* is actually smaller than predicted by the model, because part of the wood density differences between species may be explained by variation in NSC content at the time of seedling harvest. However, NSC was not measured in this study.

Root tissue density and wood density of aboveground mass hardly varied with radiation in all three species. The wood density of aboveground mass in all three species tended to be higher than the average values found in the literature for *Q. petraea* (e.g., Guilley et al. 1999; Vavřík and Gryc 2012; Komán and Fehér 2015), *F. sylvatica* (e.g., Komán and Fehér 2015; Gryc et al. 2018; Petráš et al. 2020) and *C. betulus* (e.g., Pásztor et al. 2014; Kiaei et al. 2019;

Petráš et al. 2020). For a direct comparison of our results with published data, there is a lack of published studies in which the density of aboveground woody mass of seedlings of *Q. petraea*, *F. sylvatica* and *C. betulus* was determined. One explanation for the higher wood density could be that the wood density tends to decrease with increasing tree age, as observed in other studies for *Q. petraea* (Guilley et al. 1999; Vavrčík and Gryc 2012; Komán and Fehér 2015) and *F. sylvatica* (Komán and Fehér 2015; Gryc et al. 2018). The wood density of growth rings near the pith in older *Q. petraea* (Guilley et al. 1999; Vavrčík and Gryc 2012) and *F. sylvatica* (Gryc et al. 2018) observed in these studies was more comparable to the values of the present study. Another explanation for the comparatively high density of the aboveground woody mass is that branches, which were considered in this study when determining density, have a higher density than stem wood (Petrea et al. 2024). The proportion of branches in the aboveground woody mass decreases with increasing diameter and age and can be higher than the proportion of stem wood in very young trees with a DBH of less than 4 cm (Le Goff and Ottorini 2022; Petrea et al. 2024). An increased proportion of NSC at the time of seedling harvesting in August could also be responsible for the comparatively high density. In other studies, the highest NSC contents in organs of *Q. petraea* and *F. sylvatica* were found between the end of August and October (Barbaroux and Bréda 2002; Barbaroux et al. 2003; Gilson et al. 2014). For example, Barbaroux et al. (2003) found an average NSC content of about 7% and 4%, respectively, in approximately 40-year-old *Q. petraea* and *F. sylvatica* trees in October. The NSC content was highest in oak and beech twigs (12% and 10%, respectively) and in coarse oak and beech roots (16% and 13%, respectively).

A higher root tissue density compared to the wood density in the stem was also observed in other studies in Douglas fir (*Pseudotsuga menziesii* var. *menziesii*) (Peterson et al. 2007) as well as in tropical tree species (Christensen-Dalsgaard et al. 2007; Amoah et al. 2012). This increased root density may be due to a higher NSC content in the roots compared to the aboveground woody mass (Barbaroux et al. 2003).

Total leaf area is lower in *Q. petraea* than in companion species

Under similar light conditions, *Q. petraea* had a smaller total leaf area than *F. sylvatica* and *C. betulus*, as was hypothesised. Yet, the differences between *Q. petraea* and *F. sylvatica* were smaller than between *Q. petraea* and *C. betulus*. A lower total leaf area of *Q. robur* seedlings, a close

relative of *Q. petraea*, compared to *C. betulus* seedlings at TSF < 40% was already observed in another study (Kuehne et al. 2014). The differences in total leaf area can be largely attributed to differences in specific leaf area (SLA), which was significantly lower in *Q. petraea* than in *F. sylvatica* and *C. betulus* (see also Modrow et al. 2025a). The shade-tolerant *F. sylvatica* and *C. betulus* are thus able to compensate, at least partially, the lower photosynthetic capacity of leaves compared to *Q. petraea* (Modrow et al. 2025a) by a larger total leaf area.

Conclusions and silvicultural implications

In this study, the influence of different biomass allocation patterns on height growth and thus on competitive relationships among *Q. petraea*, *F. sylvatica* and *C. betulus* in the initial establishment phase of natural regeneration was investigated for the first time. In addition, we identified radiation levels at which *Q. petraea* seedlings can be overgrown by ground vegetation and thus potentially negatively influenced. However, the results should be viewed in light of certain limitations. The study focused on a subset of general growth traits and did not consider factors such as NSC and potential root–microbial interactions, which may influence competition. Data were collected at a single point in time, and thus interannual variation was not captured. Furthermore, we studied only four-year-old seedlings and could thus not capture changes in biomass allocation and competitive relationships with age. Therefore, the relevance of our findings is largely restricted to the initial establishment phase.

The significantly lower allocation of biomass to aboveground woody tissues, the lower height-to-diameter ratio at the root collar and the higher biomass density in *Q. petraea* compared to *F. sylvatica* and *C. betulus* explain why *Q. petraea* is inferior in height growth compared to the other two species on most sites, regardless of radiation conditions. Apparently, *Q. petraea* invests significantly more in stability and stress tolerance to biotic and abiotic factors than *F. sylvatica* and *C. betulus*. The larger total leaf area of *F. sylvatica* and *C. betulus* compared to *Q. petraea* also explains why the higher photosynthetic performance of *Q. petraea* leaves found in other studies (cf. Modrow et al. 2025a), especially under high radiation conditions, does not lead to a superior height growth compared to *F. sylvatica* and *C. betulus*.

Based on the observed growth patterns of *Q. petraea* and the height differences between *Q. petraea*, *F. sylvatica* and *C. betulus* as well as between *Q. petraea* and ground

vegetation, it is recommended to adjust radiation levels above the regeneration layer near 20% TSF during the initial establishment phase. Under these light conditions, growth of *Q. petraea* is significantly higher than under lower radiation. At the same time, the height inferiority of *Q. petraea* compared to companion species, in particular *C. betulus*, is lower than at higher radiation. The growth of the ground vegetation is strongly inhibited so that *Q. petraea* seedlings are not quickly overgrown. Maintaining radiation levels near 20% TSF during the initial establishment phase thus also reduced risks for oak regeneration and provides more management flexibility in terms of timing interventions in support of oak seedlings. In the subsequent growth phase, when *Q. petraea* seedlings have reached a height of about 0.8 m and are tall enough to no longer be overgrown by ground vegetation, a further increase in radiance to over 60% TSF is recommended to maintain the competitiveness of *Q. petraea* against *F. sylvatica* and *C. betulus* (Modrow et al. 2025a).

Based on the structure of the stand to be regenerated, in particular the proportion and spatial distribution of mature oaks, different silvicultural regeneration methods were recommended to facilitate optimal radiation conditions during the different successional development phases of *Q. petraea* natural regeneration (see Modrow et al. 2025b).

Appendix

See Table 2.

Table 2 Parameter estimates and statistics of generalised linear models for average total height, annual shoot length and root collar diameter of four-year-old *Q. petraea* ($N=37$), *F. sylvatica* ($N=15$) and *C. betulus* ($N=17$) seedlings growing under varying solar radiation levels quantified using total site factor (TSF, %)

Model	β	SE	p -value
<i>Annual shoot length</i>			
Intercept	1.3632	0.3439	<0.0001
<i>Q. petraea</i> :ln(TSF)	0.4349	0.1038	<0.0001
<i>F. sylvatica</i> :ln(TSF)	0.5689	0.1136	<0.0001
<i>C. betulus</i> :ln(TSF)	0.7473	0.1057	<0.0001
<i>Total height</i>			
Intercept	2.8918	0.2183	<0.0001
<i>Q. petraea</i> :ln(TSF)	0.3461	0.0659	<0.0001
<i>F. sylvatica</i> :ln(TSF)	0.3916	0.0721	<0.0001
<i>C. betulus</i> :ln(TSF)	0.5098	0.0671	<0.0001
<i>Root collar diameter</i>			
Intercept	-1.2391	0.1478	<0.0001
<i>Q. petraea</i> :ln(TSF)	0.3751	0.0446	<0.0001
<i>F. sylvatica</i> :ln(TSF)	0.3595	0.0488	<0.0001
<i>C. betulus</i> :ln(TSF)	0.3652	0.0454	<0.0001

Ln represents a natural logarithm transformation

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Data availability Data will be made available on request.

Declarations

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