



Functional response of *Quercus robur* L. to taproot pruning: a 5-year case study

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Abstract

• **Key message** *Quercus robur* seedling mass was affected more by planting density than by taproot pruning. Root pruning enhanced stem biomass at the expense of roots in later growth stages. Alteration of biomass allocation due to nursery practices may result in greater susceptibility to injury and death of the seedlings under unfavorable environmental conditions.

• **Context** Plants adjust their growth and modulate the resource allocation in response to applied treatments and environmental conditions.

• **Aims** The aim was to examine how taproot pruning in seedlings grown at different densities affected long-term growth of *Quercus robur*.

• **Methods** Seedlings, sown as acorns at two planting densities, with or without pruned roots were harvested in the second, fourth, and fifth years of growth. The effect of root pruning on biomass allocation was determined by measuring leaf, stem, and root mass fractions; carbohydrate concentrations in the roots; and C/N ratios. Specific leaf area and root length were also determined to assess morphological adaptations to growth conditions.

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- **Results** Total seedling mass was affected more by planting density than by taproot pruning. After 4 years of growth, root mass fractions were lower and stem mass fractions were greater in seedlings planted at a higher density. Five-year old root-pruned seedlings also had a lower root mass fraction and higher stem mass fractions than unpruned seedlings. Specific root length was not affected by root pruning or planting density.
- **Conclusion** Decrease of relative root biomass with simultaneous increase of stem biomass may be a long-term consequence of taproot pruning of *Q. robur*, and the effects may manifest years after the seedling stage.

Keywords Oak · Forest nursery practice · Taproot pruning · Biomass allocation · Morphological traits

1 Introduction

Effective forest management relies on high-quality seedlings that have a balanced root/shoot ratio. Various management practices in forest nurseries reduce the time required to produce seedlings and theoretically improve the ability of seedlings to cope with adverse environmental conditions (Duryea 1984). Consequently, most studies assessing the quality of seedlings used in reforestation programs have focused on either aboveground development or biomass allocation during the time period in which seedlings are grown in nurseries (Wilson and Jacobs 2006). The long-term consequences of nursery practices after seedlings are used in plantings have been overlooked.

Taproots are often pruned in forest nurseries, which mainly affects the root system but also indirectly influences shoot growth. The main response of seedlings to root pruning is the development of a dense and extensive root system, a compensatory mechanism that allows seedlings to acquire sufficient water and nutrients (Bréda et al. 2006). The ability of a plant to compensate for lost roots, however, largely depends on plant species (Peter and Lehmann 2000; Tsakalidimi and Ganatsas 2006). Other factors, such as planting density, can also affect seedling root systems (Moreno and Cubera 2008), and therefore, may also modify the effect of root pruning on water and nutrient uptake (Dong et al. 2016; Dumroese et al. 2013; Poni et al. 1992). A high stand density can contribute to the tree decline in *Quercus* spp. and other tree species by increasing competition for nutrients. Competition is especially enhanced on low nutrient soils (Kabrick et al. 2008). Greater competition can affect the allocation of resources to aboveground and belowground organs of seedlings (Duryea 1984; Grossnickle 2012). An increase in root number and root absorptive area due to root pruning, together with high planting densities, may result in greater competition for nutrients. The effects of root pruning and high planting densities on seedling allometry in a nursery, and on nutrient acquisition traits, however, are not well understood. It is not known if these factors have a long-term effect on specific plant organs or on whole tree growth. Determining the impact of root pruning and planting density on root traits are of particular importance because of the essential role the root plays in resource acquisition (Bonan 2008).

Plant growth is typically impacted more negatively by belowground competition than by aboveground competition (Wilson 1988; Jagodziński and Oleksyn 2009). Importantly, changing root system architecture by root pruning can alter the root/shoot ratio as well as nutrient acquisition (Clemens et al. 1999). Shifts in biomass allocation between shoots and roots (quantitative adjustment) (Enquist and Niklas 2002; Poorter et al. 2012; Shipley and Meziane 2002) enable plants to survive in resource-limited environments. Other strategies also minimize the negative effect of resource limitation. Morphological and biochemical alterations of functional traits (qualitative adjustments), such as specific leaf area (SLA) and specific root length (SRL), may also enable a plant to adapt to resource limitations (Freschet et al. 2010; Hill et al. 2006; Kerkhoff et al. 2006; Ryser and Eek 2000). Changes in root length may reduce the overlapping of roots among different plants (Valverde-Barrantes et al. 2013). Such changes, along with biomass partitioning, theoretically minimize the constraints of limited aboveground or belowground resources (Valladares et al. 2007; Van Kleunen and Fischer 2005). Poorter and Ryser (2015) suggested that organ biomass in plants is less plastic than organ morphology with respect to environmental constraints. Indeed, qualitative adjustments in SLA when light is restricted have been found to be a more effective adaptation than changes in the leaf mass fraction (LMF) (Curt et al. 2005; Freschet et al. 2013; Poorter et al. 2012). Important questions, however, still remain about the effect of management practices on root specific traits and biomass partitioning (Andersen et al. 2000; Riedacker and Poda 1977). Changes in nutrient availability have been found to affect SRL (Ostonen et al. 2007), but to a lesser extent than its effect on changes in root biomass allocation, i.e., the root mass fraction (RMF) (Freschet et al. 2013). Thus, leaves and roots exhibit contrasting patterns of adjustment (Poorter and Ryser 2015). Root competition affects the morphology of fine roots much more than biomass allocation (Curt et al. 2005), and therefore represents a long-term impact of various nursery practices. While the effects of root pruning and abiotic stresses (Dong et al. 2016) and competition between roots (Kong et al. 2016) have been studied in various tree species, the integrated responses of whole plants to management practices remain largely unknown.

Pedunculate oak (*Quercus robur* L.) is an economically important tree species that is widely distributed in Europe (Köble and Seufert 2001), although the future range of this species may change distinctly within the next 50 years (Dyderski et al. 2017). Poor tree survival in oak plantations has been frequently linked to restricted access to soil nutrients and the poor quality of seedlings grown in forest nurseries (Retana et al. 1999; Tsakalidimi et al. 2005; Valdecantos et al. 2006). Although root pruning is known to impact shoot growth under in vitro conditions (Harmer and Walder 1994), the effects of nursery management practices on root plasticity remain poorly understood. The effect of plant density and root pruning, however, are known to affect root system architecture and growth of red oak (*Quercus rubra* L.) and walnut (*Juglans regia* L.) (Schultz and Thompson 1990). A prior study on the capacity of the *Q. robur* root system to utilize soil water suggests that changes in root architecture might also have important effects on tree growth under field conditions (Zadworny et al. 2014). Despite the importance of seedling planting density and root pruning for subsequent growth, little is known about how the interaction between these factors induces alterations in biomass allocation; and consequently affects the morphology of roots and shoots in *Q. robur* seedlings after 1 year of growth.

The objective of the present study was to determine if taproot pruning and planting density affected the growth of *Q. robur* seedlings by biomass allocation and characterizing both root and shoot morphological traits in 2-, 4-, and 5-year-old seedlings. We hypothesized that (1) in response to taproot pruning, oak seedlings will allocate more resources to roots than shoots; (2) taproot pruning will modify root traits in order to optimize the acquisition of resources; (3) taproot-pruned seedlings will exhibit smaller phenotypic adjustments in LMF than in SLA; (4) RMF (a quantitative factor) will change more than SRL (a qualitative factor) in taproot pruned seedlings; and (5) tree density will affect leaf and root morphological parameters (SLA and SRL, respectively) rather than those associated with biomass allocation (LMF and RMF).

2 Materials and methods

2.1 Plant material and experimental treatments

Acorns of *Q. robur* L. from a storehouse in Jarocin, Poland, were subjected to thermotherapy by placing in a water bath (41 °C) that contained MAXIM 025FS (which contains fludioxonil at a concentration of 25 g/l) at 2 g/kg for 2.5 h. Acorns whose mass differed considerably from the average mass for 1000 acorns were excluded from further use in order to decrease variability that may contribute to the experimental results. Approximately 33% of the acorns were rejected on the basis of a Gaussian seed mass distribution. A hole was drilled

in the coat of each acorn to encourage uniform germination (Giertych and Suszka 2011) before they were sown in 120 l plastic containers which were buried to two thirds of their height in experimental fields at the Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland (52° 14' 41" N, 17° 5' 57" E, 68 m a.s.l.) in spring. Climatic characteristics are described in Appendix S1. Each container was filled with soil collected from an oak forest stand in the Zwierzyniec experimental forest (Appendix S2 and S3). The layers of the forest soil profile were preserved but not the integrity of the soil structure. Adequate drainage was ensured by installing a 9 cm, 50- μ m mesh membrane filter in the bottom of each container. In each container, seedlings were thinned to a final number of four and eight seedlings at the end of the first year of growth. Following standard nursery procedures, the taproots and accompanying fine roots below a depth of 15 cm were pruned once in half of the containers in early spring in the second growing season (see photographs in Appendix S4). Containers within the same treatment group (planting density and pruning treatment) were organized in two blocks that were not protected from the environment throughout the experiment. Seedlings grown under open conditions were watered during dry periods. Weeds were removed by hand on a weekly basis and fungicides were applied to the seedlings during the growing season to limit fungal diseases. Seedlings were harvested in September at the end of the second, fourth, and fifth growing seasons. The container was removed from the ground and the walls of the container were carefully cut and removed to expose the root system (see Appendix S5). The root systems of the seedlings were then washed with water to remove the soil.

Between two and six randomly selected containers were removed in each of the harvest years to minimize the effects of container location on the results. A range between 8 and 32 seedlings were analyzed for each treatment and year.

2.2 Analysis of soils filling the containers

Six litter samples and six mineral soil samples from the 0–10 cm soil depth were collected from the same plot where the soil used in the experiments was collected. Mineral soil samples were sifted by hand to remove rocks and plant material. The samples were then air dried at room temperature, crushed and subsequently passed through a 1 mm sieve as described by Reich et al. (2005). Percent organic carbon (C) and N were determined by using the Tyurin and Kjeldahl volumetric methods, respectively. The pH of water and KCl suspensions of the litter and mineral soil samples were also measured. Hydrolytic acidity (Hh) and cation exchangeable bases (CEB) were determined using the Kappen method (Raczuk 2001). Cation exchange capacity (CEC) was estimated using the following equation: $CEC = CEB + Hh$. The extent of base saturation of the soil sorption complex was calculated as

follows: $\%VCEB = CEB/CEC \times 100$, and the degree of hydrogen saturation of the soil sorption complex was defined with $\%VHh = Hh/CEC \times 100$ (Ostrowska et al. 1991). Organic carbon of litter samples, composed of oak and elm leaves, was measured by loss on ignition. Soil type was classified in an excavation pit at the soil collection site to the depth > 1 m, according to World Reference Base (WRB). The soil type was classified as histosols (murshic) (Appendix S2 and S3).

2.3 Parameters related to biomass allocation

Each harvested plant was divided into leaves, stems, and roots. The taproots and fine roots (< 2 mm in diameter) were separated and the samples were dried at 65 °C for 3 days and then weighed. Dry mass of the samples was then used to determine leaf mass fraction (LMF; dry leaf mass/total dry mass ratio, in $g\ g^{-1}$), stem mass fraction (SMF; dry stem mass/total dry mass ratio, in $g\ g^{-1}$), root mass fraction (RMF; dry root mass/total dry mass ratio, in $g\ g^{-1}$), and the fine root mass fraction (fRMF; dry fine root mass/total dry mass ratio, in $g\ g^{-1}$).

2.4 Leaf, stem, and root traits

Five mature fully expanded leaves per plant were scanned at harvest using a Perfection 3200 PHOTO scanner (Epson, Nagano, Japan) and the images were analyzed using WinFOLIA image software (Regent Instruments, Quebec, Canada). Each individual leaf was then dried at 65 °C, weighed, and the SLA (the projected leaf area per unit of leaf dry biomass, in $m^2\ kg^{-1}$) was determined.

Randomly selected branches of the root system were collected from the uppermost layer of each root system (0–15 cm below the stem base). Subsamples of the roots were scanned using a Perfection 3200 PHOTO scanner (Epson), analyzed using WinRHIZO software (Regent Instruments), and then dried for 3 days at 65 °C to enable the determination of the SRL (the root length per unit dry mass, in $m\ g^{-1}$) (as described by Jagodzinski et al. 2016).

The efficiency of biomass investment for height gain was determined by calculating the specific stem length (SSL; stem total length per biomass unit, in $m\ g^{-1}$).

2.5 Root nutrient content

In order to obtain information on the storage of resources, the concentrations of starch and glucose and the C/N ratios were determined in the taproots and fine roots. Dried fragments of fine roots and taproots from the uppermost layer of each root system (0–15 cm below the stem base) were ground in an MM 200 mixer mill (Retsch, Haan, Germany) and then analyzed. The concentrations of C and N were determined using an ECS

4010 CHNSO elemental analyzer (Costech Instruments, Milan, Italy). The protocol described by Oleksyn et al. (2000) was used to estimate the concentration of non-structural carbohydrates, including total soluble sugars and starch. Dried roots were extracted with a 12:5:3 (by volume) methanol:chloroform:water mixture (Avantor Performance Materials, Gliwice, Poland). To measure the level of soluble carbohydrates in the extract, anthrone reagent (Sigma-Aldrich, St Louis, MO, USA) was added to the extract. The resulting mixture was placed in a water bath (100 °C) for 12 min, and the absorbance (625 nm) of the anthrone/extract mixture was measured within 30 min. The insoluble material was converted into glucose by adding amyloglucosidase (15 U/ml; Sigma-Aldrich) and incubating the mixture at 50 °C for 24 h. To determine the concentration of glucose, peroxidase–glucose oxidase–*o*-dianisidine dihydrochloride reagent (Sigma-Aldrich) was added to the mixture, incubated at 25 °C, and the absorbance at 450 nm was measured within 30 min. The concentrations of soluble sugar and starch (using glucose as a standard) were expressed as percentages of the dry mass.

2.6 Statistical analyses

Biomass allocations were estimated using LMF, SMF, RMF, and fRMF. This approach was used to limit statistical errors that are related to asymmetry when comparing small changes within relatively variable data and the loss of actual allocation patterns (Poorter and Sack 2012; Reich 2002). Measurements of parameters other than LMF, SMF, and RMF were \log_{10} transformed to ensure a normal distribution of the data and homogeneous variances. Given that the values of most of the measured parameters were dependent on the year of harvesting, changes in the effect of planting density and root pruning as the seedlings developed were determined using a two-way ANOVA of the data for each harvest year, using planting density and pruning as categorical variables. Differences between the average values for the parameters that were analyzed were assessed using a post-hoc Tukey's test (using a significance level of $p < 0.05$). Pearson's correlation coefficients were used to identify interrelated changes and to determine the strength of the interdependence of the studied traits.

The coefficient of variability, defined as the ratio of the standard deviation to the mean (Valladares et al. 2006), was estimated for each container and was included in the analyses to enable variation between the seedlings in each experimental treatment to be estimated. All of the statistical analyses were performed using Statistica 8.0 software (Dell, Round Rock, TX, USA).

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

3 Results

The biomass of the oak seedlings increased during the course of the experiment (Fig. 1a). Planting density influenced total seedling mass. Plants grown at the higher planting density accumulated less biomass after 4 years of growth than plants grown at the lower planting density. This difference, however, was not observed after 5 years of growth (Fig. 1a). Root pruning did not affect the accumulation of total biomass in the seedlings after 5 years of growth ($p = 0.829$).

Seedling age had a significant effect on LMF, SMF, RMF, and fRMF (see Table 1). Greater biomass accumulation occurred in leaves and roots at the end of the second season of growth than in stems. At the end of the fourth season of growth, however, SMF increased and LMF, RMF, and fRMF decreased (Fig. 1b–e). Planting density and root pruning did not affect LMF in any year of the experiment (Fig. 1b, Table 1). Relative stem biomass (SMF) was greater at the higher planting density after the fourth year than at the lower planting density. This occurred at the expense of the root system biomass (RMF) (Table 1, Fig. 1). In comparison to unpruned control seedlings, there is an increase of stem biomass and decreased RMF in the root-pruned seedlings (Fig. 1c, d). This pattern was also observed after the fifth growth season in root-pruned seedlings grown at the lower planting density (Fig. 1d). Growth of the root system occurred concurrently with leaf development during the experiment (Table 2). Increase of stem biomass, however, occurred primarily at the expense of the root system and, to a much lesser extent, at the expense of the leaves ($r = -0.92$ for the stem and root system and $r = -0.29$ for the stem and leaves). The C/N ratio in the taproots was lower in seedlings grown at the higher planting density than those grown at the lower planting density. The C/N ratio in the fine roots, however, exhibited the opposite trend (Appendix S6).

Leaf traits (SLA) and root traits (SRL) exhibited less differences than biomass allocations (Figs. 1 and 2). This pattern, however, was not consistent throughout the experiment. SLA was greater in seedlings grown at the higher than at the lower planting density (Fig. 2a), but decreased with seedling age (Fig. 2a, Table 1). In contrast, SRL was not affected by either root pruning or planting density (Fig. 2c, Table 1). As expected, LMF was negatively correlated with SLA but RMF and fRMF was not correlated with SRL (Table 2).

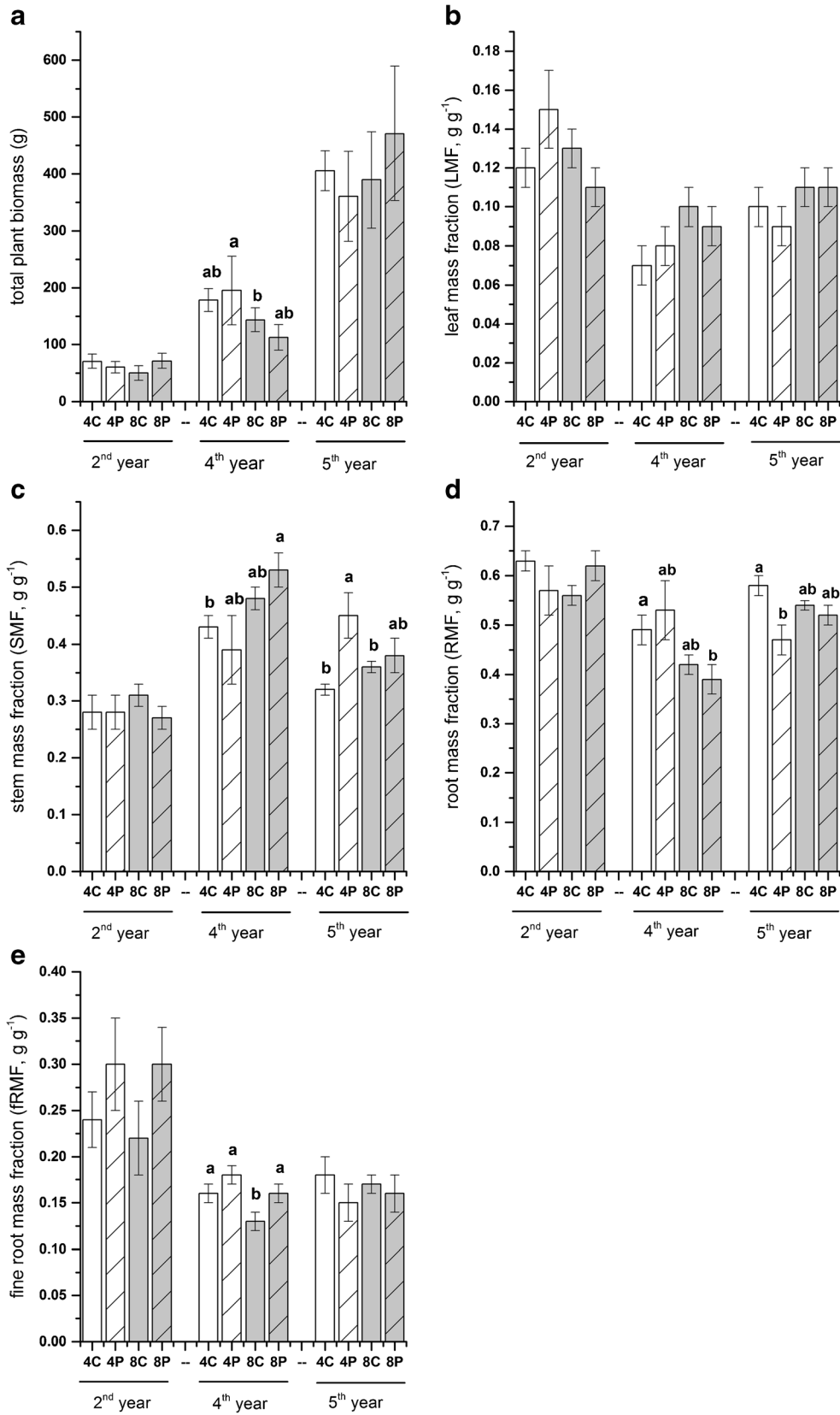
When considering the extent of variability in relation to the mean of the population, SSL had the highest coefficient of variation, while RMF was the least variable after the second growth season (Table 3). SRL varied the most in taproot-pruned seedlings grown at the lower planting density. SRL varied more than fRMF after the fourth growth season. At the end of the experiment (i.e., after the fifth growth season),

all of the measured traits exhibited similar levels of variability in all three experimental treatments (pruned seedling planted at high and low density and unpruned seedlings planted at the lower density). Within unpruned seedlings at the higher planting density, SRL was the most variable and RMF was the lowest.

4 Discussion

Plants alter their allocation of biomass to leaves or roots in order to reduce the effects of limited external resources (Enquist and Niklas 2002; Poorter et al. 2012; Shipley and Meziane 2002). Our initial hypothesis was that taproot pruning would increase root biomass in order to balance the acquisition of resources; however, the opposite trend was observed in the current study. Taproot pruning induced a gain in stem mass, and a lower relative root biomass. Considering the results of previous studies (Freschet et al. 2013; Poorter et al. 2012), the limited changes that were observed in SRL (which is related to resource acquisition) suggest that root morphology did not adjust to compensate for the decrease in the ability of the pruned root system to acquire nutrients. This was contrary to our expectations. The lack of a shift in biomass allocation or morphological adjustments, despite the decreased ability to acquire resources, may indicate that the limitation of nutrients was not strong enough to trigger a reaction. The higher increase in the aboveground parts of the plants, in comparison to the belowground root system, could have negative consequences for trees stability to wind storm when growing in more fertile forest stands, i.e., more frequent uprooting of taproot-pruned trees.

It is possible that the observed higher relative biomass of leaves and roots in 2-year-old seedlings, relative to older seedlings, may have been related to a phenomenon described by McConnaughay and Coleman (1999). These authors found that the biomass allocation strongly depends on plant ontogeny. We expected that greater biomass would be allocated to roots after root pruning in order to optimize the acquisition of aboveground and belowground resources. Instead, we found that root pruning decreased the relative root biomass, after the fifth season of growth, but not earlier. Given that total seedling mass at the end of the experiment was unaffected by the examined management practices, the higher relative biomass in stems in taproot-pruned seedlings than in the unpruned seedlings could reflect a strong selective growth characteristic in oak trees. In fact, well-developed stems are an attribute of the forest niche occupied by oak trees. Preferential increase of stem biomass at the expense of roots may also be advantageous when managing forests, especially since the fine root fraction remained unchanged across all of the experimental treatments. However, in our experiment, seedlings showed a temporal dynamics in the relative allocation of biomass. We



assumed that after 4 years of growth, increased stem mass fraction associated with higher stem elongation at the expense

of relative root mass allow shade intolerance oak seedling to compete for light, as competition for light strongly regulates

◀ **Fig. 1** Changes in the allocation of biomass by year, seedling planting density, and taproot pruning status. **a** Total plant biomass. **b** Leaf mass fraction (*LMF*). **c** Stem mass fraction (*SMF*). **d** Root mass fraction (*RMF*). **e** Fine root mass fraction (*fRMF*). One-way ANOVA results were obtained for values within an experimental year, then Tukey's test was performed: **a** Total plant mass (second year $F=1.00$, $p=0.397$; fourth year $F=3.60$, $p=0.016$; fifth year $F=0.98$, $p=0.625$); **b** LMF (second year $F=1.68$, $p=0.178$; fourth year $F=0.97$, $p=0.406$; fifth year $F=2.63$, $p=0.61$); **c** SMF (second year $F=0.48$, $p=0.690$; fourth year $F=3.97$, $p=0.010$; fifth year $F=5.98$, $p=0.001$); **d** RMF (second year $F=1.06$, $p=0.369$; fourth year $F=4.81$, $p=0.003$; fifth year $F=5.70$, $p=0.002$); **e** fRMF (second year $F=1.10$, $p=0.351$; fourth year $F=6.40$, $p=0.001$; fifth year $F=1.09$, $p=0.361$). Values marked with different letters are significantly different at $p < 0.05$ (Tukey's test). Treatments were matched as follows: seedling density per container (four or eight) and pruning status (C = control and P = seedlings with pruned taproots). Number of analyzed seedlings; 2012— $4C=24$, $4P=24$, $8C=24$, $8P=16$; 2014— $4C=24$, $4P=8$, $8C=32$, $8P=32$; 2015— $4C=12$, $4P=8$, $8C=16$, $8P=16$

light gathering, water and nutrient economy, and available for the growth carbon reserves (Gil-Pelegrín et al. 2018). Thus, stem elongation supports the production of carbohydrate reserves for the subsequent development of organs that limit the growth of, e.g., roots. The positive effect of taproot pruning on seedling growth might be particularly noticeable in fertile habitats where shallow root systems have optimal access to water and nutrients. The preferred increase of the stem biomass at the expense of the root system, however, was more pronounced at the lower density planting. At the higher density plantings, however, nutrient competition reduced this positive effect to some extent, which is most likely attributed to the effect of fine root biomass on plant productivity. Higher allocation of biomass to roots is considered to be a good predictor of successful stand development (Wu et al. 2004). The growth of different plant organs is limited equally by resources (Bloom et al. 1985) and the balance between root and stem growth depends on the availability of aboveground vs. belowground resources (Shiple and Meziane 2002, but see Reynolds and D'Antonio 1996). *Q. robur*, however, produces a deep root system that reaches into low levels of groundwater (Boratyński and Bugała 2000). Indeed, taproots make oak tree growth less dependent on surface soil layers that tend to dry out, and limit overexploitation of the resources present in a narrow soil profile (Cavender-Bares and Bazzaz 2000; Pierret et al. 2016). The inability of a tree species, such as *Q. robur*, to regenerate a pruned taproot (Ogijevskij and Popova 1954) may be essential for the optimal acquisition of nutrients and water [see Maeght et al. 2013 and literature cited therein]. Despite the response that occurred in our experimental system, a similar pattern of biomass partitioning might not occur under drought conditions or in less fertile soil, thus limiting the interpretation or extrapolation of the present findings.

No relationship was found between SLA and leaf biomass in our study. Indeed, leaf morphological adjustments rather than biomass partitioning (i.e., changes in SLA rather than LMF) could be caused by a plant responding to differences in light availability (Curt et al. 2005; Freschet et al. 2013; Freschet et al. 2015; Poorter et al. 2012). In agreement with this, SLA was higher when plants competed for light (i.e., at the high planting density) but LMF remained stable. Such adjustments might enable a plant to function properly by ensuring proper level of photosynthesis. Poorter et al. (2012) suggested that even marginal amounts of leaves, stem, and roots support plant growth. Moreover, exhibited by SSL higher than other parameters variation has important implications on a way oaks respond to higher density. A higher stem length per unit of stem biomass (i.e., a higher SSL) reflects accelerated stem elongation, which occurs to avoid shading by other plants in a low-light environment (Sasaki and Mori 1981). This alteration in SSL, therefore, may balance the aboveground acquisition of resources. When considering belowground relationships, quantitative adjustments in biomass allocation to roots have been found to be more important than qualitative adjustments (i.e., in SRL) in trees under nutrient stress (Freschet et al. 2015). This is in contrast to what has been reported for leaves (Poorter et al. 2012). Given that root biomass did not change to compensate for the lost taproot, however, we expected that generating roots with a high root length per unit biomass invested could be a strategy used to increase root absorptive surface in *Q. robur*. Limitations in nutrient availability should lead also to the domination of conservative root traits including low SRL (Freschet et al. 2010). SRL, which has been used as a surrogate of absorptive strategies, as a linear relationship is often expected between high SRL and enhance nutrient uptake, however, was similar in all of the treatments in our study. This apparent contradiction could have been a result of SRL being more variable than RMF among seedlings within the same group. Thus, we did not observe any pattern of root adjustment in our study. In fact, this was what was observed in all of the experimental treatments after the second and fourth growth seasons. Most likely, another explanation for the observed result comes from indirect competitive interactions involving other association that affect the way in which root traits are formed. Since *Q. robur* is an ectomycorrhizal species, it is plausible that colonization by different species of fungi, a parameter that was not monitored in our study, might also affect SRL (Ostonen et al. 2009; Sun et al. 2010). Since the association with ectomycorrhizal fungi occurs generally dependently of the trees density (Peay et al. 2011), mycorrhizal symbionts variability must translate into high SRL variation. Phenotypic plasticity (qualitative adjustment), however, is an adaptive response to environmental change (Freschet et al. 2013). Therefore, the additive or synergistic effects of taproot pruning and higher planting densities could make *Q. robur* seedlings more prone to unpredictable

Table 1 Results of ANOVAs for the morphological and biochemical/physiological traits measured in three harvesting years (* for the SLA, only 2 years, 2014 and 2015, were considered) using the harvesting year, root pruning status, and planting density as the factors. *F* and *p* values are included, and nonsignificant interactions are excluded

Trait	Value	Year (df=2)	Root pruning (df=1)	Seedling density (df=1)	Year × root pruning (df=2)	Year × seedling density (df=2)	Root pruning × seedling density (df=1)	Year × root pruning × seedling density (df=2)
SLA*	<i>F</i>	8.16		3.94				
	<i>p</i>	0.005		0.049				
SSL	<i>F</i>	60.73						
	<i>p</i>	0.000						
SRL	<i>F</i>	83.88						
	<i>p</i>	0.000						
LMF	<i>F</i>	11.05						
	<i>p</i>	0.000						
SMF	<i>F</i>	35.52				3.46		
	<i>p</i>	0.000				0.033		
RMF	<i>F</i>	18.73		4.17		3.22		
	<i>p</i>	0.000		0.042		0.041		
fRMF	<i>F</i>	13.72						
	<i>p</i>	0.000						
C/N of fine roots	<i>F</i>	86.42					9.28	9.49
	<i>p</i>	0.000					0.003	0.000
C/N of taproot	<i>F</i>	26.72			4.13	9.89		
	<i>p</i>	0.000			0.018	0.000		
Starch in fine roots	<i>F</i>	232.24				3.09	10.19	10.72
	<i>p</i>	0.000				0.049	0.002	0.000
Starch in tap root	<i>F</i>	9.20						
	<i>p</i>	0.000						
TNC in fine roots	<i>F</i>	59.82					6.40	4.22
	<i>p</i>	0.000					0.013	0.017
TNC in tap root	<i>F</i>	8.17						
	<i>p</i>	0.000						

SLA specific leaf area, SSL specific stem length, SRL specific root length, LMF leaf mass fraction, SMF stem mass fraction, RMF root mass fraction, fRMF fine root mass fraction, TNC total non-structural carbohydrates

Table 2 Pair-wise relationships between biomass and resource acquisition traits. Pearson's correlation coefficients (*r*) and the levels of significance (*p*) are given

	LMF	SMF	RMF	fRMF	SLA	SSL
SMF	<i>r</i> = -0.29 <i>p</i> = 0.005					
RMF	<i>r</i> = -0.11 <i>p</i> = 0.294	<i>r</i> = -0.92 <i>p</i> = 0.001				
fRMF	<i>r</i> = 0.25 <i>p</i> = 0.018	<i>r</i> = -0.38 <i>p</i> = 0.001	<i>r</i> = 0.29 <i>p</i> = 0.006			
SLA	<i>r</i> = -0.28 <i>p</i> = 0.008	<i>r</i> = -0.07 <i>p</i> = 0.511	<i>r</i> = 0.19 <i>p</i> = 0.075	<i>r</i> = -0.23 <i>p</i> = 0.027		
SSL	<i>r</i> = -0.19 <i>p</i> = 0.070	<i>r</i> = -0.19 <i>p</i> = 0.080	<i>r</i> = 0.27 <i>p</i> = 0.010	<i>r</i> = -0.02 <i>p</i> = 0.864	<i>r</i> = 0.37 <i>p</i> = 0.001	
SRL	<i>r</i> = -0.07 <i>p</i> = 0.515	<i>r</i> = 0.09 <i>p</i> = 0.419	<i>r</i> = -0.06 <i>p</i> = 0.570	<i>r</i> = -0.15 <i>p</i> = 0.152	<i>r</i> = 0.09 <i>p</i> = 0.386	<i>r</i> = -0.07 <i>p</i> = 0.367

LMF leaf mass fraction, SMF stem mass fraction, RMF root mass fraction, fRMF fine root mass fraction, SLA specific leaf area, SSL specific stem length, SRL specific root length

Significance level *p* < 0.05 is matched as italics

environmental changes than seedlings of other species (Dyderski et al. 2017).

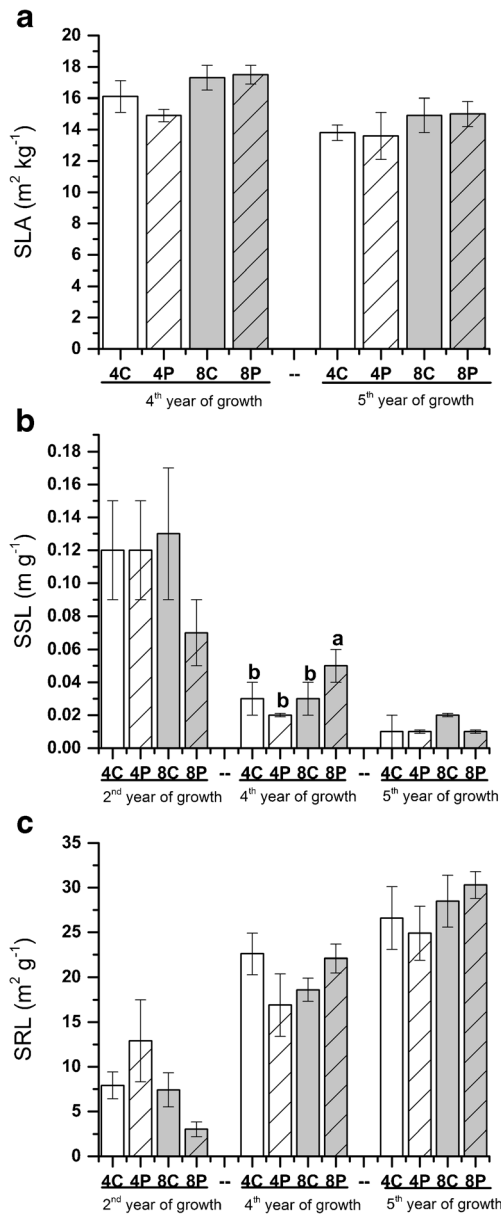


Fig. 2 Changes of morphological traits along year, seedling planting density, and taproot pruning status. **a** Specific leaf area (SLA). **b** Specific stem length (SSL). **c** Specific root length (SRL). One-way ANOVA results were obtained for values within an experimental year, then Tukey’s test was performed: **a** SLA (fourth year $F=1.30$, $p=0.280$; fifth year $F=0.44$, $p=0.720$); **b** SSL (second year $F=0.34$, $p=0.792$; fourth year $F=4.12$, $p=0.009$; fifth year $F=0.45$, $p=0.716$); **c** SRL (second year $F=1.36$, $p=0.265$; fourth year $F=1.23$, $p=0.304$; fifth year $F=0.51$, $p=0.674$). Treatments were matched as follows: seedling density per container (four or eight) and pruning status (C = control and P = seedlings with pruned taproots). Number of analyzed seedlings; 2012—4C=24, 4P=24, 8C=24, 8P=16; 2014—4C=24, 4P=8, 8C=32, 8P=32; 2015—4C=12, 4P=8, 8C=16, 8P=16

Table 3 Coefficient of variation in the traits studied by year, seedling planting density, and root pruning status. Values marked with the same lowercase letter are not different at $p < 0.05$ within columns, and values marked with the same uppercase letter are not different at $p < 0.05$ within rows within each experimental year. Seedling planting density per container (four or eight) is shown in row two and pruning status (C = control and P = seedlings with pruned taproots) is shown in row three

	2012 (year of pruning)				2014 (3 years after pruning)				2015 (4 years after pruning)										
	4		8		4		8		4		8								
	C	P	C	P	C	P	C	P	C	P	C	P							
SLA	101 a	102 ab	80 a	80 a	100 a	100 a	6	21 bc	18 d	18 d	15	24	25 abc	18	0.45	0.724			
SSL	66 a, B	132 a, A	66 a, B	66 a, B	57 ab, B	57 ab, B	30	64 a	83 a	83 a	0.402	0.376	33	47	67 a	46	0.66	0.599	
SRL	26 ab	34 bc	18 bc	18 bc	37 bc	37 bc	41	33 abc	39 bc	39 bc	0.270	0.270	32 A	36 A	40 ab, A	13 B	4.01	0.046	
LMF	35 ab	38 bc	20 bc	20 bc	32 bc	32 bc	31	19 abc	27 cd	27 cd	0.049	0.049	17	28	19 abc	16	0.47	0.711	
RMF	13 b	36 c	15 c	15 c	19 c	19 c	21	25 abc	42 bc	42 bc	0.084	0.084	15	21	12 bc	16	0.81	0.522	
fRMF	53 ab	83 abc	56 ab	56 ab	41 bc	41 bc	13	15 c	8 e	8 e	0.100	0.100	10	15	9 c	10	1.32	0.328	
F	5.22	5.77	12.46	12.46	16.02	16.02	4.75	4.56	48.41	48.41	0.188	0.188	27	35	20 bc	27	0.28	0.839	
P	0.004	0.003	0.004	0.004	0.002	0.002	0.001	0.004	0.001	0.001	0.056	0.766	0.001	0.056	0.766	0.001	0.091		

SLA specific leaf area, SSL specific stem length, SRL specific root length, LMF leaf mass fraction, SMF stem mass fraction, RMF root mass fraction, fRMF fine root mass fraction
Significance level $p < 0.05$ is matched as italics

5 Conclusions

Changes in the availability of resources, either aboveground or belowground, affect the equilibrium of biomass accumulation in roots and shoots, as well as organ morphology. Root pruning of oak seedlings increases stem biomass instead of an expected increase in root biomass. The presented results indicate that root pruning may benefit the production of oak timber and appears to be an advantageous for forestry practice. However, well-developed aboveground parts of *Q. robur*, with a simultaneous production of a more profuse system of shallow fine roots in response to taproot pruning root, may reduce the support and stability of mature trees, as has been shown in other tree species (Stofko and Kodrik 2008). This potential impact in oak needs to be further clarified. Given that maximum root depth is often established during the seedling stage (Hoffman and Lyr 1967), management practices which alter the structure of a root system may have irreversible, long-term effects on plant growth. In the present study, water was not limited and lack of fertilization may only result in a gradual limitation in nutrients. Thus, these abiotic factors may not have been strong enough in our study to impact the response of oak tree seedlings to root pruning. Whether or not our results also apply to tree stands with water and stronger nutrient limitations remain to be examined. This is especially important to consider since the demands of aerial portions of a plant for nutrients and water will not be met by a reduced root system. Given that anticipated changes in climate, particularly in water availability, will have striking effects on the environmental conditions to which plants are exposed (Dyderski et al. 2017), additional research should focus on determining whether or not root pruning exacerbates water and nutrient stress.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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