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Reaction of oak seedlings (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.) to water limitation

Reaktion von Eichensämlingen (*Quercus robur* L. und *Quercus petraea* (Matt.) Liebl.) auf Wasserlimitierung

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Schlüsselbegriffe: Wurzelhalsdurchmesser, Trockenstress, Gewächshaus, Eiche, Phänotyp, Wurzel- und Sprosswachstum, Allometrie

Abstract

Due to the expected increase in severe growing-season droughts in Central Europe, understanding how major forest timber tree species react to drought will become more important in future forest management. Young trees are particularly affected by dry periods during the growing season, as the root system is not well established and thus limited access to groundwater during early developmental stages. Here we tested the drought tolerance of *Quercus robur* and *Quercus petraea* seedlings by optimal and limited irrigation treatments. We measured root and stem length growth, biomass accumulation, root-shoot biomass ratio, and collar diameter development, to assess the plants performance. Our results indicate that both species immediately reacted to water limitation by reducing above- and belowground biomass production. *Q. petraea* reacted to drought by increasing the root-shoot ratio, whereas *Q. robur* more or less maintained this ratio across both treatments. The reaction exhibited by *Q. petraea* may be an adaptation to drier environmental conditions.

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Zusammenfassung

Wegen der zu erwartenden Zunahme von Trockenperioden während der Vegetationsperiode wird es in Mitteleuropa für die zukünftige Forstwirtschaft immer wichtiger werden zu verstehen, wie wichtige Waldbaumarten auf Trockenheit reagieren. Junge Bäume sind während der Vegetationsperiode besonders von Trockenperioden betroffen, da das Wurzelsystem noch nicht gut etabliert ist und damit die Pflanzen in diesem frühen Entwicklungsstadium nur begrenzten Zugang zu Grundwasser haben. Die Sämlinge von zwei Eichenarten, *Quercus robur* und *Quercus petraea*, wurden einer optimalen und einer reduzierten Bewässerungsbehandlung unterzogen. Wir haben das Wurzel- und Sprosslängenwachstum, die Biomasseakkumulation, das Verhältnis von Wurzel- zu Sprossbiomasse und die Entwicklung des Wurzelhalsdurchmessers gemessen, um die Pflanzenreaktion zu beurteilen. Unsere Ergebnisse zeigen, dass beide Arten unmittelbar auf die Wasserlimitierung reagieren, indem sie die ober- und unterirdische Biomasseproduktion reduzieren. *Q. petraea* reagiert auf Trockenheit mit einer Erhöhung des Wurzel-Spross-Verhältnisses, während *Q. robur* dieses Verhältnis in beiden Behandlungsvarianten nahezu beibehält. Die von *Q. petraea* gezeigte Reaktion kann als Anpassung an trockenere Umweltbedingungen interpretiert werden.

1 Introduction

Oak species belong to the genus *Quercus* within the family *Fagaceae*. The genus *Quercus* is native to the northern hemisphere and its range extends from temperate to tropical latitudes throughout America, Asia, Europe, and North Africa. In Germany, *Quercus robur* L. (pedunculate oak) and *Quercus petraea* (Matt.) Liebl (sessile oak) belong to the major deciduous tree species. Like *Fagus sylvatica* L, oaks are keystone tree species of complex forest ecosystems, which range from the lowlands to the sub-mountainous and even the mountainous regions. Oaks are extremely long-lived species and are exposed to more heterogeneous environments over time than any other predominant tree species (Herzog *et al.* 1993).

About 500,000 ha (7%) of the forest area in Europe is covered by oak stands (Szczepkowski *et al.* 2007). Among European white oaks, *Q. robur* and *Q. petraea* have the widest geographic distribution and cover most of the continent with the exception of northern Scandinavia (Zanetto *et al.* 1994; Thomas and Gausling 2000). Over the years, the taxonomic status of the two study species has been repeatedly discussed and assessed (Pretzsch *et al.* 2013) and several genetic markers have been developed to distinguish between those two species (Bordács and Burg 1997; Muir *et al.* 2000; Gömöry *et al.* 2001; Bakker *et al.* 2002; Reutimann *et al.* 2020). Furthermore, hybridization between white oak species is common. Still *Q. petraea* and *Q. robur* have been characterized as two distinct species, although the boundary between them is not clearly defined, and botanists continue to debate their taxonomic classification (Herzog 1996; Bacilieri *et al.* 1994; Hertel and Degen 2000; Roloff *et al.* 2008). Both species provide habitat and food for animals, and supply resources for the wood industry and forest enterprises, particularly by providing highly valuable timber (Annighöfer *et al.* 2015). Oaks, especially *Q. robur* and *Q. petraea*, are highly adaptable tree species (Bobiec *et al.* 2018). Both species have a broad ecological amplitude, grow in a variety of continental climates and can tolerate environmental conditions such as heat, drought (Thomas and Gausling 2000; Thomas *et al.* 2002; Bruschi 2010; Kuster *et al.* 2013) and *Q. robur* is able to resist flooding (Herzog and Krabel 1999). With the intensified debate of climate change several authors like *e.g.* Aide *et al.* (2000), Ohlemühler *et al.* (2006), Geßler *et al.* (2007) and Arend *et al.* (2011), who have highlighted how the drought tolerance of various tree species may contribute to future silviculture strategies in Europe. *Q. robur* has a high drought tolerance but a low shade tolerance (van Hees 1997), it grows well in fresh soils with periodic availability of groundwater (Bogdan *et al.* 2017), whereas *Q. petraea* tolerates poor and dry soil, it grows in dry conditions (Zanetto *et al.* 1994; Kuster *et al.* 2013). Nevertheless, Trudić *et al.* (2021) also reported for Serbia that due to climate change both species are under pressure since 1950.

The results found out by Vander Mijnsbrugge *et al.* (2017) suggest that the composition of oak species and their hybrids in natural oak forests could be altered after prolonged periods of precipitation deficit. In accordance with the results from Vander Mijnsbrugge *et al.* (2020), oaks exposed to drought adapt their growth and xylem structure to improve drought resistance. The growth of young *Q. robur* is more competitive, with faster juvenile growth than that of *Q. petraea*. Thus, it is possible that *Q. robur* seedlings may suffer more from intensified droughts than *Q. petraea* seedlings.

There are several authors *e.g.* Broadmeadow and Jackson (2000), Thomas and Gausling (2000), Brèteau-Amores (2018), who reported that *Q. petraea* seedlings are more tolerant to drought stress and show different growth reactions compared to *Q. robur* seedlings. Jensen and Hansen (2008) highlighted geographical variations in growth, phenological traits, survival and genetic components of adaptive traits. They tested the two species in long-term regional field trials by measuring root collar diameter, bud development (flushing) and leaf color change. Bruschi (2010) investigated the phenotypic plasticity of 5-year-old *Q. petraea* seedlings from different geographical areas grown in a common garden experiment under two different water regimes. Turcsán *et al.* (2016) investigated the immediate effects of a short drought in early summer on potted 1-year-old *Q. petraea* seedlings from three different regions. The above-mentioned studies focused on the morphological and phenotypical reactions of *Q. petraea* and *Q. robur* to drought stress but they did not observe the long-term growth development from seed maintenance until the end of the experimental period. The approach of Vander Mijnsbrugge *et al.* (2017, 2020) presents results of a drought treatment by investigating morphology and wood anatomical traits of *Quercus* seedlings over a longer observation period. However, the study does not focus on above- and belowground development of the plants.

The present approach should help to understand the growth strategy of *Quercus* seedlings to adapt to drought periods and thus to deliver information, which can be used for forest regeneration concepts dealing with the challenges of climate change.

2 Materials and methods

The criteria for mother stand selection were autochthonous stands categorized as "dry stand" (Staatsbetrieb Sachsenforst, pers. communication). Seeds from fifteen randomly chosen mother trees were collected per stand. In October 2012, 1000 acorns each of *Q. petraea* and *Q. robur* were gathered. We collected acorns of *Q. petraea* from Tharandt, Germany (50º981'675" N, 13º576'199" E, 373 m above sea level), and the acorns of Q. robur from Graupa, Germany (51º001'530" N, 13º554'410" E, 218 m above sea level). To reduce potential bias due to environmental effects on the seed material, all the seeds and young plants were treated in the same way. They were maintained at 5 °C in frost-free seed storage during the winter of 2012–2013. In April 2013, the seeds were sown in pots filled with 60% potting soil (pH = 5.7, Na = 0.2 mg 1^{-1}, K = 2.2–2.5 mg 1^{-1}, Ca = 25.2–27.8 mg 1^{-1}, Mg = 2.5–2.7 mg 1^{-1}, Mn = 0.1 mg 1^{-1}) and 40% washed sand. Pot volume was approximately 63 cm^3. During the summer of 2013 (from April to September), we cultivated the potted seeds in a greenhouse under optimal irrigation (20–25 % volumetric water content) conditions at an average temperature of 18 °C. In July, we transferred the germinated seedlings to 2-liter pots. Due to harsh and fluctuating frost conditions while overwintering in the field, we lost more than 95% of the plant material. During the subsequent cultivation and overwintering period (2013–2014) 78 (30 *Q. petraea*, 48 *Q. robur*) of the original 2000 seeds were viable and could be used for the experiment in 2014.

2.1 Experimental design

In April 2014, we transferred the 1-year-old seedlings into 4-liter polypropylene pots, filled with 30% washed sand and 70% potting soil. Then we placed the plants in the greenhouse under optimal irrigation conditions for six weeks in order to acclimate them to the environmental conditions of the experiment location. When starting the experiment (plant age = 13.5 months), plants appeared healthy and no plants died before the end of the treatment. Overall, the plants in the treatment groups differed in their growth between time points for all parameters, when compared to the control group. The experiment was carried out from June 15 to September 15, 2014. 78 plants were grouped into two treatments, one of which received optimal irrigation and one of which received reduced irrigation. We exposed 15 *Q. petraea* and 24 *Q. robur* seedlings to each treatment in the greenhouse. In the drought treatment, soil water availability was gradually decreased to 10–15% volumetric water content for the reduced irrigation condition, where 20–25% volumetric water content is considered optimal conditions. We measured the soil moisture daily using a TRIME-PICO 64/32 sensor (Micromodultechnik GmbH, Ettlingen, Germany), and adjusted the watering regimes accordingly. During the acclimatation time, the average temperature was 21.6 °C and air humidity was 76.0%. During the experimental period, the average temperature was 22.6 °C and air humidity was 81.7%.

We measured plant height, root length, and collar diameter at several time points (Table 1) and estimated increment growth of plant height, root length, stem length, and collar diameter, which were based on measurements taken at the beginning and end of the experiment. The dry biomasses of above- and belowground plant parts were determined at the end of the experiment. We estimated stem length and root length growth rates based on the measured parameters. For the final measurements, we selected twenty-one *Q. robur* and 12 *Q. petraea* from each treatment group for harvesting. The remaining number of plants was insufficient for statistical analysis; but three plants of each species from each treatment group were maintained in 2015 for future observation of survival and phenotype.

We divided the growth observation period into five different time points from month 3 to month 16.5 (Table 1).

Table 1: Overview of measurement occcasions and measured tree properties. Month 3 and 12: before the treatment began; month 13.5: start of the treatment (Ms = starting measurement); month 13.5 to 16.5: treatment duration (Mf = final measurement).

Tabelle 1: Übersicht der Messzeitpunkte und gemessenen Eigenschaften. Monat 3 and 12: Phase vor dem Versuchsbeginn; Monat 13.5: Versuchsbeginn (Ms = Start der Messungen); Monat 13.5 bis 16.5: Versuchsphase (Mf = finale Messung).

Age (months)	3	12	13.5 (Ms)	15.5	16.5 (Mf)
	July 2013 potted in 2l	April 2014, potted in 4l	June 2014	August 2014	September 2014
Plant height (cm)	Yes	Yes	No	No	Yes
Root length (cm)	Yes	Yes	No	No	Yes
Collar diameter (mm)	Yes	Yes	Yes	Yes	Yes

2.2 Measured tree properties

As it was not feasible to measure root development during the experimentation period, we measured root length and plant height while we potted the plants in April, before the acclimation period. Stem length and collar diameter were measured immediately before and after the experiment, enabling us to determine the mean incremental growth of stem length and collar diameter (at day 92), and plant height and root length (at day 143).

To determine biomass, the plants were divided into above- and belowground parts. We washed the belowground parts and their fresh weight was measured; stems and roots were dried at 65 °C for three days before their dry weight was measured. To determine the aboveground parameters, we cut the leaves off from the stems, and determined fresh and dry weights for leaves and stems. However, we considered only the dry above- and belowground biomass of the plants.

We calculated the increment of growth (IG) for each variable as an absolute difference in measurement value in the end and the beginning of the experiment.

IG_{92} = (Mf – Ms), for stem length and collar diameter.

IG_{143} = (Mf – Ms), for plant height and root length.

2.3 Statistical analysis

We performed descriptive statistics (Shapiro-Wilk and Kolmogorov tests) to test for normality and data distribution and we analyzed the treatment effects and interactions among treatments and species by using analysis of variance (ANOVA; general linear model procedure). We used a Mann-Whitney U test to look at differences between the treatment for the increment of the growth and biomass. The significance level was $p < 0.05$ in each case (* Is $p < 0.05$, ** is $p < 0.01$, *** is $p < 0.001$, **** is $p < 0.0001$). The graphs were produced using MINITAB 17. We used the statistical package IBM SPSS 27 (IBM Deutschland GmbH, Ehningen, Germany) for the statistical analysis.

3 Results

3.1 Plant growth

The mean plant height of *Q. robur* in the optimal treatment was 34.1 cm from month 3-12, and 75.6 cm from month 12-16.5; for *Q. robur* in the reduced treatment, the mean height increase was 28.1 cm from month 3-12 and 50.7 cm from month 12-16.5 (Figure 1). At the end of the experiment, the average plant height of *Q. robur* plants in the optimal treatment was significantly higher than that of those in the reduced treatment (157.9 cm and 125.5 cm, respectively; $p < 0.001$). The mean plant height of *Q. petraea* in the optimal treatment increased by 13.8 cm from month 3-12 and by 45.2 cm from month 12-16.5. In the reduced treatment, mean plant height increased by 13.7 cm from months 3-12 and by 23.2 cm from month 12-16.5 (Figure 1). This indicates that the treatment effect was highly significant (mean plant height of the optimal group was 90.6 cm, the reduced group was 64.5 cm; $p < 0.004$). When comparing the two species, there is a clear difference at each time point ($p < 0.001$); even before the drought treatment, *Q. robur* grew in height more quickly than *Q. petraea*.

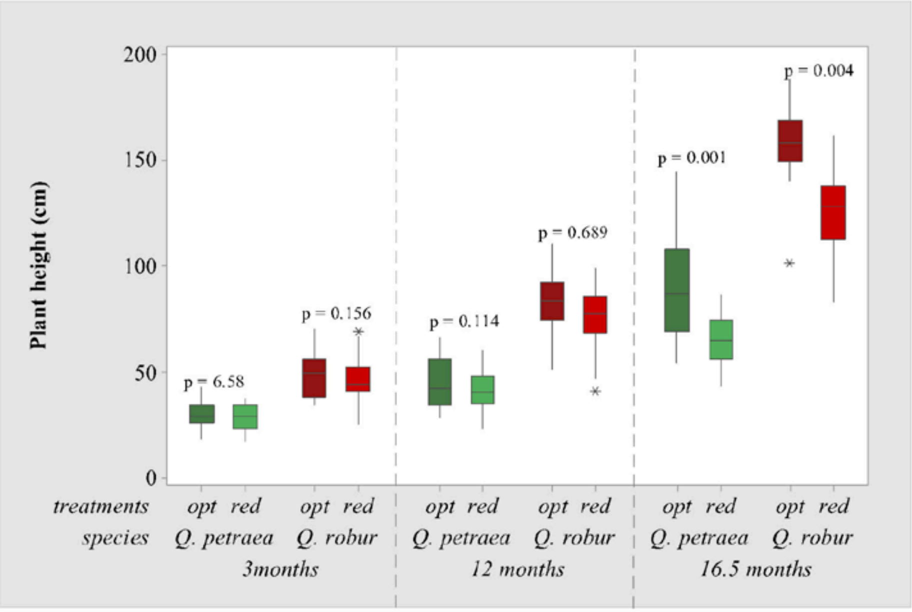


Figure 1: Plant height development of Q. robur (red) and Q. petraea (green) – optimal and reduced treatments. Whiskers indicate minimum and maximum values; the box shows the first quartile, the median and the third quartile of the data. The p-values indicate differences between the treatments (significance level p < 0.05). Stars symbolize outliers. The separation into treatment groups took place before the experiment in month 3.

Abbildung 1: Pflanzenhöhenentwicklung von *Q. robur* (rot) und *Q. petraea* (grün) – optimale und reduzierte Bewässerung. Antennen zeigen das Minimum und das Maximum der Werte an; die Boxen symbolisieren das untere, den Median und das obere Quartil der Daten. p-Werte kennzeichnen Unterschiede zwischen den Behandlungen (Signifikanzniveau $p < 0.05$). Sternchen symbolisieren Ausreißer. Die Einteilung in Behandlungsgruppen erfolgte vor dem Experiment in Monat 3.

The mean root length of *Q. robur* did not show significant differences between treatment groups until month 12. From month 12-16.5, the average root length increased by 35 cm for the optimal treatment and by 24.1 cm for the reduced treatment. At month 16.5, the average root lengths of *Q. robur* were 58.1 cm for the optimal treatment and 46 cm for the reduced treatment (Figure 2). For *Q. petraea*, the increase in mean root length for the optimal group was 5.67 cm from month 3-12 and 23.7 cm from month 12-16.5. In the reduced irrigated group, *Q. petraea* increased in mean root length by 6.7 cm from month 3-12 and 11.4 cm from month 12-16.5. The treatment effect on root growth was significant at month 16.5 ($p < 0.0001$). The root length growth of *Q. robur* was greater than that of *Q. petraea* at all three time points (month 3, 12, and 16.5; $p < 0.0001$ for each time point).

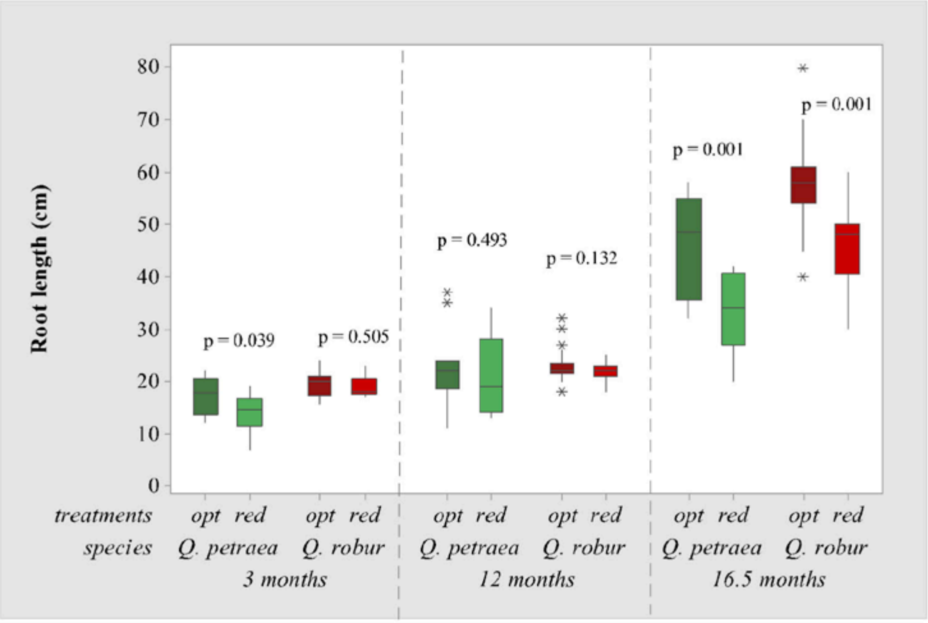


Figure 2: Root length development for Q. robur (red) and Q. petraea (green) – optimal and reduced treatments. Whiskers indicate minimum and maximum values; the box shows the first quartile, the median and the third quartile of the data. The p-values indicate differences between the treatments (significance level $p < 0.05$). Stars symbolize outliers. The separation into treatment groups took place before the experiment in month 3.

Abbildung 2: Wurzellängenentwicklung für *Q. robur* (rot) und *Q. petraea* (grün) – optimale und reduzierte Bewässerung. Antennen zeigen das Minimum und das Maximum der Werte an; die Boxen symbolisieren das untere, den Median und das obere Quartil der Daten. p-Werte kennzeichnen Unterschiede zwischen den Behandlungen (Signifikanzniveau $p < 0.05$). Sternchen symbolisieren Ausreißer. Die Einteilung in Behandlungsgruppen erfolgte vor dem Experiment in Monat 3.

The mean collar diameter for both treatment groups and species (Figure 3) increased more slowly than plant height and root length. The average collar diameter of *Q. robur* increased slightly until months 13.5; from month 13.5-15.5, it increased by 3.00 mm in the well-watered group and by 1.2 mm in the reduced watered group. From month 15.5-16.5, the average collar diameter for *Q. robur* increased by 1.0 mm in the optimal treatment and by 0.1 mm in the reduced treatment. There was a significant difference in collar diameter growth in *Q. robur* between treatment groups starting at month 15.5 ($p < 0.001$). For *Q. petraea*, the average collar diameter increased by 0.3 mm from month 3-12 for the optimal condition and 0.2 mm for the reduced watering condition. Mean collar diameter for *Q. petraea* increased by 0.6 mm from month 12-13.5 for the optimal treatment and by 0.2 mm for the reduced one. During the period between month 13.5-15.5 *Q. petraea* increased in mean collar diameter by 1.6 mm for the optimal and by 0.8 mm for the reduced treatment. The mean collar diameter of *Q. petraea* increased by 0.2 mm from month 15.5-16.5 for the optimal treatment and by 0.05 mm for the reduced treatment. There was a significant treatment effect starting at month 15.5 (*Q. robur*: $p < 0.001$; *Q. petraea*: $p < 0.027$) and at month 16.5 (*Q. robur*: $p < 0.001$; *Q. petraea*: $p < 0.033$). The growth data for each time point shows significant differences between the species ($p < 0.0001$).

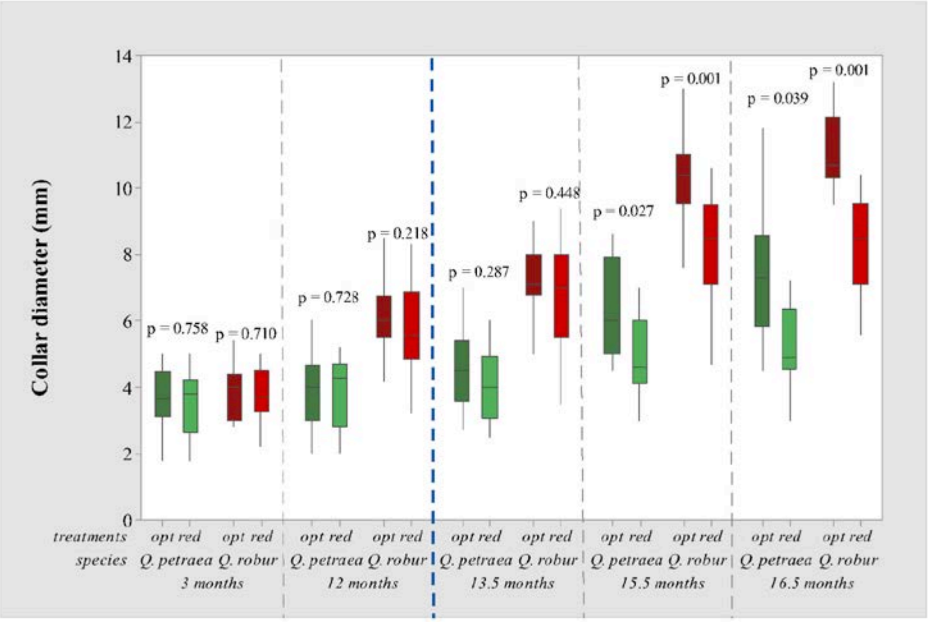


Figure 3: Collar diameter for Q. robur (red) and Q. petraea (green) – optimal and reduced treatments. The dashed blue line indicates the experimental starting time. Whiskers indicate minimum and maximum values; the box shows the first quartile, the median and the third quartile of the data. The p-values indicate differences between the treatments (significance level p < 0.05). The separation into treatment groups took place before the experiment in month 3.

Abbildung 3: Wurzelhalsdurchmesser von *Q. robur* und *Q. petraea* (optimale und reduzierte Bewässerung). Die unterbrochene blaue Linie kennzeichnet den Startzeitpunkt des Experiments. Antennen zeigen das Minimum und das Maximum der Werte an; die Boxen symbolisieren das untere, den Median und das obere Quartil der Daten. p-Werte kennzeichnen Unterschiede zwischen den Behandlungen (Signifikanzniveau $p < 0.05$). Die Einteilung in Behandlungsgruppen erfolgte vor dem Experiment in Monat 3.

3.2 Increment of growth

The increment of growth is calculated as the difference between the growth at the beginning of the time measurement period and the end of the experimental time measurement period (see Table 1).

The specific growth performances of plant height, stem length, collar diameter and root length during the drought stress treatment, over a period of 143 or 92 days (depending on the parameters that are explained in the methods section), are described below and depicted in Figure 4.

For *Q. robur*, the average growth increments (IG) for plant height were 75.6 cm for the optimal treatment and 50.7 cm for the reduced irrigated group. The mean difference between the treatments was 24.7 cm, which is statistically significant (p < 0.001). The average IG heights of *Q. petraea* were 45.2 cm for the optimal treatment and 23.2 cm for the reduced treatment. The mean difference between the groups was 22.0 cm (p < 0.008, Figure 5a). For *Q. robur*, we observed that the average IG stem length was 22.5 cm for the optimal treated group and 9.4 cm for the reduced one. The mean difference between the treatment groups was 11.8 cm (p < 0.006). A similar trend was observed for *Q. petraea*. The average IG stem length was 15.0 cm for the optimal group and 4.4 cm for the reduced watered group, but due to large variation in the data (Figure 4c), the difference was not significant (p < 0.198). For *Q. robur*, the average IG root length was 35 cm for the optimal group and 24.1 cm for the less-watered group. *Q. robur* plants in the optimal treatment had a greater mean root length than those in the reduced treatment (p < 0.001). *Q. petraea* plants in the optimal treatment had an IG root length approximately 11 cm smaller, and plants in the reduced treatment had an IG root length of 23.7 cm. This difference was highly significant (p < 0.005, Figure 4b). For both species, the difference between the average IG collar diameter of the treatment groups was highly significant (p < 0.001, *Q. robur* optimal/reduced: 4.0 mm/1.4 mm; *Q. petraea*: 2.8 mm/0.6 mm, p < 0.002; Figure 4d).

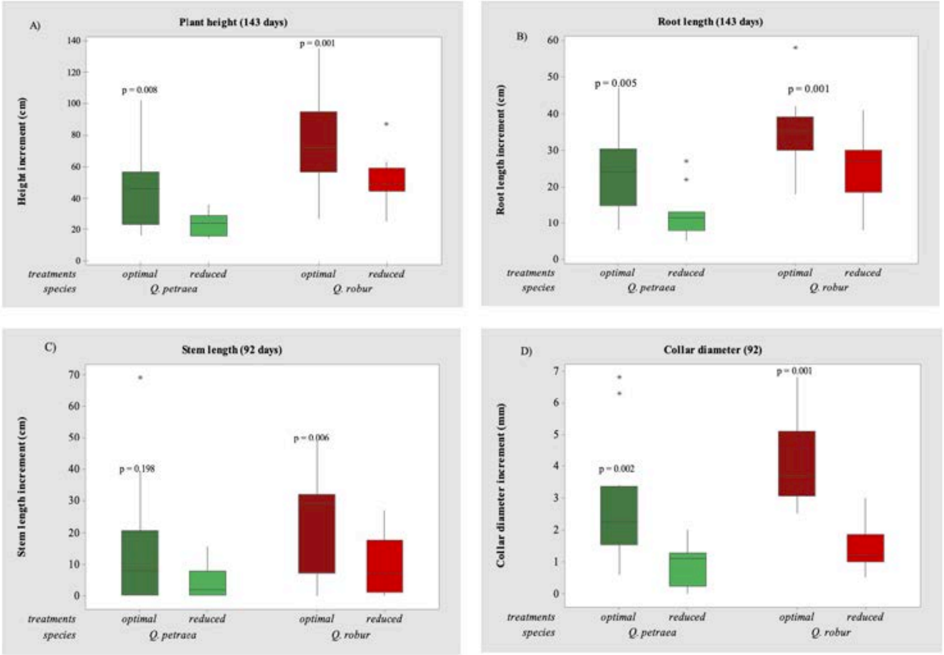


Figure 4: Increments of Q. robur (red) and Q. petraea (green). A plant height increment over 143 days); B root length increment over 143 days; C stem length increment over 92 days; D collar diameter increment over 92 days. Whiskers indicate minimum and maximum values; the box shows the first quartile, the median and the third quartile of the data. The p-values indicate the differences between the treatments for both species. Optimal and reduced irrigation treatments differed significantly according to the Mann-Whitney U test ($p < 0.05$).

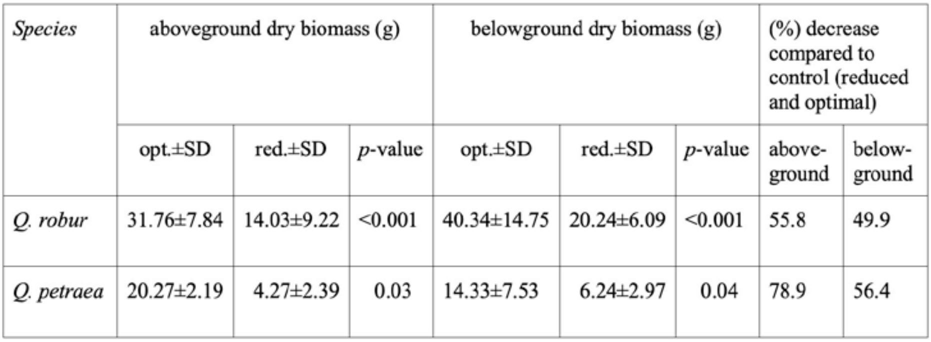
Abbildung 4: Zuwachsmessungen für *Q. robur* (rot) und *Q. petraea* (grün); A Höhenzuwachs über 143 Tage; B Zuwachs der Wurzellänge (143 Tage); C Zuwachs der Sprosslänge (92 Tage); D Zunahme des Wurzelhalsdurchmessers (92 Tage). Antennen zeigen das Minimum und das Maximum der Werte an; die Boxen symbolisieren das untere, den Median und das obere Quartil der Daten. Optimale und reduzierte Bewässerungsgruppen unterscheiden sich signifikant nach dem Mann-Whitney-U-Test ($p < 0.05$). P- Werte kennzeichnen Unterschiede zwischen den Behandlungsvarianten für beide Arten.

3.3 Biomass

As expected, the biomass of the optimal treatment group was significantly higher than that of the reduced treatment group ($p < 0.0001$), and *Q. petraea* had a lower biomass than *Q. robur* in both treatments (Table 2). First, we will compare data for aboveground dry biomass. For *Q. robur*, comparison of the treatment groups shows that the optimal treatment was 31.7 g and it was 14.0 g for the reduced treatment (55.8% lower, $p < 0.000$; Table 2). For *Q. petraea*, we measured 20.2 g for the optimal treatment and 4.2 g for the reduced treatment (78.9 % lower $p < 0.001$). Secondly, when comparing the above- and below-ground data for the dry biomass from the reduced treatment group, we observed that the aboveground plant parts decreased in biomass by 55.8 % in *Q. robur* and 78.9 % in *Q. petraea*; for belowground dry biomass decreased by 49.9 % in *Q. robur* and 56.4 % in *Q. petraea* (Table 2).

Table 2: Dry above- and belowground biomass for optimal (opt) and reduced (red) irrigated plants. We show mean plus-minus standard deviation (SD).

Tabelle 2: Ober- und unterirdische Trockenbiomasse der optimal (opt) und reduziert (red) bewässerten Pflanzen. Gezeigt werden Mittelwerte plus-minus Standardabweichung (SD).



Species	aboveground dry biomass (g)			belowground dry biomass (g)			(%) decrease compared to control (reduced and optimal)	
	opt.±SD	red.±SD	*p*-value	opt.±SD	red.±SD	*p*-value	above-ground	below-ground
Q. robur	31.76±7.84	14.03±9.22	<0.001	40.34±14.75	20.24±6.09	<0.001	55.8	49.9
Q. petraea	20.27±2.19	4.27±2.39	0.03	14.33±7.53	6.24±2.97	0.04	78.9	56.4

3.4 Growth rate

In order to evaluate the immediate reaction of the plants to the treatments, we calculated the daily growth rate over a treatment period of 92 days for stem length and 143 days for root length. The mean growth rate for stem length of *Q. robur* was 2.4 mm/day in the optimal treatment, and 1.0 mm/day for the reduced treatment - less than half that of the optimal treatment (Table 3). For *Q. petraea* the reduction in the stem length growth rate was even more obvious; the average rate for the optimal treatment was 0.16 mm/day, while that of the reduced treatment was only 0.04 mm/day. The mean root growth rate of *Q. robur* was 2.4 mm/day for the optimal treatment and decreased by 31.4% for the reduced treatment. In *Q. petraea*, the growth rate decreased by 47.5% (Table 3).

Table 3: Calculated daily growth rates of stem and root length for optimal (opt) and reduced (red) irrigated plants. We show mean plus-minus standard deviation (SD).

Tabelle 3: Berechnete tägliche Wachstumsrate des Sprosses und der Wurzeln der optimal (opt) und reduziert (red) bewässerten Pflanzen. Gezeigt werden Mittelwerte plus-minus Standardabweichung (SD).

Species	stem length (mm/day)		root length (mm/day)	
	opt.±SD	red.±SD	opt.±SD	red.±SD
Q. robur	2.46±1.59	1.02±0.94	2.44±0.53	1.68±0.56
Q. petraea	1.63±1.22	0.48±0.21	1.66±0.78	0.87±0.43

3.5 Root-shoot ratio

In our study we calculated the root-shoot ratio as the ratio of the dry weight of belowground plant parts to the dry weight of aboveground plant parts. This ratio was calculated for both species and for each treatment. For the optimal treatment, the root-shoot ratios were 1.27 for *Q. robur* and 0.70 for *Q. petraea*. For the reduced treatment, the root-shoot ratios were 1.44 for Q. robur and 1.46 for *Q. petraea*.

4 Discussion

In contrast to comparable studies (*e.g.* Fotelli *et al.* 2000, Turcsán *et al.* 2017), in which young plant material of oak species was examined for adaptation processes to drought, we treated plant material from *Q. petraea* and *Q. robur* in the same way from the time point of seed collection until the end of the drought experiment. This approach should show possible differences in the growth performance of the 1-year old seedlings, and the results should help to understand the "growth strategy" of young *Quercus* plants exposed to dry periods during an early ontogenetic stage.

For both oak species, biomass production diminished shortly after soil water content was reduced. The total fresh plant weight was reduced by approximately 60% for *Q. robur* and by approximately 74% for *Q. petraea*, which confirms the results of Davidson *et al.* (1992), Leiva and Fernández-Alés (1998) and Rose *et al.* (2009). However, when the data for below- and aboveground biomass are considered separately, it becomes clear that under drought conditions, *Q. petraea* shifted biomass production to the favor of root development, while *Q. robur* maintained nearly the same ratio of above- and belowground biomass under optimal and reduced irrigation conditions. The species maintains a balance between above- and belowground biomass during the 3-month experimental duration. These results may be contrasted with those of other investigations of root-shoot ratios under drought conditions. Studies on oak or beech seedlings *e.g.* by Fotelli *et al.* (2000), Rose *et al.* (2009), Leiva and Fernández-Alés (1998), Davidson *et al.* (1992), Madsen and Löf (2005) and Meier and Leuscher (2008) showed that shoot biomass was less affected by drought than root biomass. The experiments of Meier and Leuschner (2008) showed a more or less unchanged root-shoot ratio under drought conditions. Our results confirm the hypothesis of Rose *et al.* (2009), who concluded that species or genotypes with a higher root-shoot ratio in drought have advantages in drier conditions. Reducing the production of above-ground biomass, and promoting root growth is a drought response mechanism that was often investigated in oak species (Thomas and Gausling 2000; Arend *et al.* 2011). Vander Mijnsbrugge *et al.* (2020) characterized oaks exposed to drought as being able to adapt their growth and xylem structure to improve drought resistance. Young *Q. robur* trees appear to be more competition oriented, with faster yearly growth than *Q. petraea*, which seems to have invested more in precautious growth rates, perhaps being more prepared for stressful conditions. According to Vander Mijnsbrugge *et al.* (2017; 2020), it is possible that *Q. robur* seedlings may suffer more from intensified droughts than *Q. petraea* seedlings. It seems that during the early ontogenetic stages of plant development, this strategy of soil water exploitation is an important part of the phenotypic plasticity of trees. *Q. petraea* shows a higher root-shoot ratio under drought conditions, which fits to the observation that the species is known to be better adapted to drier environments than *Q. robur*. Leiva and Fernández-Alés (1998) found that genotype exhitbiting drought traits likely lose less water during the growth period than seedlings exhibiting the opposite traits. Since we found that *Q. robur* root tissue contains about 6–10% more water than that of *Q. petraea* under the same treatment conditions, we conclude that the two species follow different adaptation strategies from the beginning of plant development. We posit that the water demand of *Q. petraea* may be inherently lower than that of *Q. robur*. Epron and Dreyer (1990; 1993), working with 30-year-old plant material, could not demonstrate differences in drought sensitivity between the two species. They exhibited the same photosynthetic responses to summer drought. However, their studies observed a higher intrinsic water-use efficiency in *Q. petraea*, which they interpreted as an indication of the competitive advantage of this species in drier soils. The exploitation of soil water by investing in root length growth (Krabel *et al.* 2015; Larcher 2015) does not seem to be the strategy employed for adaptation to drier conditions, as our results show that root length growth decreased significantly under drought conditions. In his review focusing on the drought response of European beech, Leuschner (2020) argued that a shift in the root-shoot ratio for juvenile trees might depend on the intensity and duration of drought stress. In our study, the experimental conditions were the same for both species, so this argument can be excluded from the interpretation of the present findings. Our results indicate that the two species react differently to drought stress. At earlier growth stages, the root length increase of *Q. robur* is greater than that of *Q. petraea* when soil water is limited, which allows for the conclusion that *Q. petraea* invests in the development of more roots, rather than longer roots. Krabel *et al.* (2015) also achieved results that show different strategies of dealing with water availability, *e.g.* more instead of longer roots, with different poplar genotypes cultivated in containers and exposed to mild drought conditions. We followed the growth performance over a period of 92 days for stem length and collar diameter and a period of 143 days for plant height and root length. By measuring the plants before and after the treatment, we were able to calculate the daily growth rate of the stem and roots during these periods. Interestingly, the reduction in daily growth rates of *Q. petraea* under drier conditions was more significant than that of *Q. robur*. This was particularly true for *Q. petraea's* stem growth rate, which decreased by approximately 72% in comparison to *Q. robur*. The effect of the treatment on daily root growth rate was less pronounced than that of stem growth rate for both species. The approach focused on young plant material and the reaction during a drought period, similar to the situation, which can be observed during summertime in Central Europe. A study that will focus on a more severe but shorter drought period might be interesting to deal with. As such, an approach will increase the mortality of the seedlings; it would be of interest to characterize the genotypic structure of a population before and after a drought treatment in order to receive hints for the composition of the best adapted genotypes within a population.

Since studies have described recovery after watering drought-stressed plants (Turcsán *et al.* 2016), we subjected a small group of plants from both treatments to regular irrigation for one more vegetation period (data are not presented here). Although there were still differences between the treatment groups for growth and biomass parameters, they were not significant due to the small sample size. Our results may be interpreted as a slight recovery; however, it likely takes more than one vegetation period after a drought event for significant growth restoration to occur.

5 Conclusions

We conclude that during an early developmental stage the two studied *Quercus* species, *Q. petraea* and *Q. robur*, follow different growth strategies to cope with limited soil water content. Being aware that our results are only of limited significance due to the small sample size and the narrow timeframe in which the plants were tested, we conclude that *Q. robur* oak maintains growth performance as long as possible and *Q. petraea* oak adapts its growth by differentiating between root and shoot biomass.

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