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Adaptability responses to drought stress in the oak species *Quercus petraea* growing on dry sites

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Abstract: We studied sessile oak (*Quercus petraea)* growing on six dry sites to understand adaptability responses to drought stress. Pedunculate oak (*Quercus robur*) on a moderately dry site was tested in parallel. We analyzed accessions from mostly dry sites that were less sensitive to soil drought and found that the growth performance ranking was not the same before and after treatment. We used phenological plasticity approaches to study seed development and plant development before and after drought: the treatments included stem length, root length, and collar diameter, as well as dry above- and below-ground biomass performance. Additionally, after drought treatment, osmolytes and root surface were tested in *Q. petraea*. According to the analyses and results, the ranked sites did not maintain their ranking status, with *Q. petraea* exhibiting different rates of growth during each developmental stage from seed development until the end of the treatment of plant material. The smallest seeds came from the driest site, which may indicate more adaptability to drought stress. After drought treatment, large differences were found between the dry biomass performance, stem length, root length, and collar diameter of oaks grown on different sites. The osmolality of *Q. petraea* on most of the dry sites was higher under the reduced treatment than under the optimal treatment, but not significantly. After drought treatment, all accessions – and especially those from the driest site – showed large differences in growth performance between the treatments. The relationship between seed weight and seedling development before and after drought treatment differed according to the developmental stage.

Keywords: aboveground biomass; belowground biomass; phenotypical plasticity; *Quercus*; water availability

Global warming is considered to be a serious threat to 21st century forest ecosystems. Drought leads to water deficits in the soil and plant tissues, which in turn alters physiological processes and can have consequences for the growth, development and survival of plants (Lombardini 2006). More frequent and prolonged droughts will have strong impacts on tree growth and vigour, thus changing the stability and productivity of natural and managed forests (Leuzinger et al. 2005). The tree growth ability is affected by a reduction in water supply. It has been understood for many years that various forest species react differently to drought (Hamanashi, Campbell 2011).

Thus, for future forest management strategies, it will be important to consider individual tree species in terms of their ability to cope with water stress and the adaptability of the species based

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on phenotypical plasticity. While drought-sensitive species, such as European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and white fir (*Abies alba*), are at risk of habitat loss, more drought-tolerant species, such as oaks (*Quercus* spp.), may benefit from climate change through increased competitive strength (Mitchell Aide et al. 2001). Oaks are a major species group in Central Europe; in particular, *Q. robur* and *Q. petraea* occur widely across most of Europe, and range eastwards into central Russia, as far as the Urals (Jones 1959; Ducousso, Bordacs 2003; Eaton et al. 2016). These two species (*Q. robur* and *Q. petraea)* are highly valued in forestry and nature conservation because they provide high-quality timber, biodiversity and food resources for wildlife (McShea et al. 2007; Götmark 2013; Löf et al. 2016; Leuschener, Ellenberg 2017; Mölder et al. 2019).

The phenotypical characteristics of oaks allow them to maintain high water potentials during drought periods and thus avoid stress- and drought-related mortality. Oaks are commonly considered drought tolerant due to their development of deep taproot systems and xeromorphic leaf structures after changes in water availability (Vivin et al. 1993; Canadell et al. 1996; Nardini, Pitt 1999; Leuschner et al. 2001; Gallé et al. 2007; Pretzsch et al. 2013; Turcsán et al. 2016). Thomas and Gausling (2000) studied the effect of drought conditions on *Q. petraea* root growth, while Thomas et al. (2002), Bruschi (2010) and Kuster et al. (2013) used pot and container experiments to study *Q. petraea* and *Q. robur* for several purposes, including the analysis of drought stress tolerance. Conversely, the effect of regular flooding on these species has been investigated by Herzog and Krable (1999). Eaton et al. (2016) and Bogdan et al. (2017) found that *Q. robur* – a keystone forest tree of great socioeconomic importance that grows across most of Europe and under a wide range of climatic and soil conditions – tends to prefer mesic environments with moist and fertile soils. Leuschner and Ellenberg (2017) focused on the drought response of *F. sylvatica*, arguing that a shift in the root/shoot ratio of juvenile trees might depend on the intensity and duration of the drought stress. *F. sylvatica* has a high tolerance to drought, but a very low tolerance to shade (Van Hees 1997). The more drought-tolerant *Q. petraea* prefers to grow on light, well-drained, often rocky soils (hence the Latin name "*petraea*", meaning "of rocky places"). It generally occurs on slopes and hilltops and prefers more acidic soil conditions (Jones 1959; Zanetto et al. 1994; Roloff et al. 2010; Arend et al. 2011; Kuster et al. 2013; Praciak 2013; Savill 2013). These two species are both light-demanding trees, *Q. robur* more so than *Q. petraea* (Praciak 2013; Savill 2013).

Because the frequency of extreme drought events is increasing in Central Europe, accessions or provenances of trees on dry sites could become important sources for drought-resistant ecotypes (Wilmanns 1990; Czajkowski, Bolte 2006). Consequently, this study was focused on a growth experiment using autochthonous sessile oak *(Q. petraea)* seedlings from six dry sites [Forest Botanic Garden (FBG) 1 and 2, Waldfrieden, Tharandt, Schlottwitz and Pillnitz] distributed across Saxony (Germany) in which the responses of growth-related parameters to drought conditions were recorded. In parallel, seedlings of pedunculate oak from one moderately dry stand were tested. In this case, we only intended to check the responses to the treatment of *Q. robur*. In terms of our investigation, the following hypotheses were tested:

(*i*) seed size and seedling growth performance before the drought treatment (we defined these as control plants) are correlated;

(*ii*) seed size and seedling growth performance after drought treatment are correlated;

(*iii*) the ranking of plant growth performance is related to site conditions (focused on soil moisture);

(*iv*) the ranking of plant growth performance at different dry sites is the same before and after drought treatment.

MATERIAL AND METHODS

Plant resources and sites. In October 2013, a total of 7 000 acorns (1 000 acorns from each site) of *Q. petraea* and *Q. robur* were collected from seven different sites (Table 1) in Saxony (Germany). While the seven sites were close to each other, the site conditions were specific to each location, so that it could be assumed that the autochthonous plant material was well adapted to the specific soil and growth conditions of each location. The intention of the main focus was *Q. petraea* from six of the sites. We just tested *Quercus robur* from one site only in order to compare growth performance between the treatments.

Experimental design. All the acorns were numbered on their coats. Each was weighed before the

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Table 1. Description of the studied sites

No.	Site name	Species	Average annual precipitation (mm)	Nutrient level	Water status at location	Category of the drought
1	FBG 1	*Q. petraea*	700–900	fairly poor	dry	D0
2	Tharandt		700–900	moderately nutritious	moderately dry	D1
3	Schlottwitz		700–900	moderately nutritious		
4	Waldfrieden		700–900	moderately nutritious	extremely dry	D3
5	FBG 2		700–900	moderately nutritious		
6	Pillnitz		500–620	moderately nutritious		
7	Graupa	*Q. robur*	680–820	moderately nutritious	moderately dry	D1

FBG – Forest Botanical Garden

acorns were maintained in frost-free seed storage at 5 °C during the winter 2013–2014. Seed vitality was assessed in April 2014, at which point 98% of the acorns were found to have successfully survived the winter. The viable 7 000 acorns were sown in pots in April 2014.

The potting substrate consisted of 30% washed sand and 70% potting soil. From April 2014 until April 2015, all potted acorns were kept under optimal irrigation conditions at an average temperature of 18.6 °C and humidity of 58% (Staatsbetrieb Sachsenforst, Graupa Meteorological Station, 2014–2015). In April 2015, the vitality of the young plants was assessed, at which point 88% of the seedlings (6 160) were found to have survived and so were deemed usable for the experiment. Following this survival inventory, when changing the pots to prepare the plants for the experimental treatment, five plants representing each site were harvested due to time constraints. These variables (stem length, root length, collar diameter, biomass performance) were measured to obtain a general overview of plant development before the experiment. These 35 plants constituted the control group.

Then, 100 plants representing each site were randomly chosen to be transplanted into larger (2 L) pots. All these potted plants (700) were placed in a greenhouse and subjected to optimal irrigation conditions for another six weeks in order to acclimatise them to the environmental conditions of the intended experimental location.

The drought experiment was carried out from June 15 to September 15, 2015. The plants from each site were divided into two treatment groups (optimal irrigation and reduced irrigation) so that 50 plants were assigned to each treatment group. At the end of the experiment, in September 2015, 25 plants were harvested from each group, with the other half (350 plants in total) being kept for observation in 2016. The remaining 350 plants were irrigated fully until October 15, 2015 due to winter preparation. The soil water availability of 10–15% volumetric water content was maintained for the reduced-irrigation group during the experiment, while the 20–25% volumetric water content was provided to the optimally irrigated group. The water contents were measured using a TRIME-PICO 64/32 sensor (Micromodulertechnik GmbH, Germany). The water status of the soil was measured every day in order to accurately adjust the water regime. During the treatment period, the greenhouse temperature was maintained at an average of 21.8 °C and the air had an average humidity of 66.4% (Staatsbetrieb Sachsenforst, Graupa Meteorological Station, 2015).

The acorn/plant measurements included: (*i*) at preparation time – acorn weight and length; (*ii*) prior to treatment – stem and root length of the control plants from the six dry sites; and (*iii*) after treatment – stem length, root length, collar diameter, dry above- and belowground biomass, root surface area and osmolality.

At this point, the plants were transferred from the greenhouse to the laboratory to take the final measurements. Stem length, collar diameter and root length were measured to assess plant development in response to the applied drought stress.

To determine the aboveground parameters, the leaves were cut from the stems, and the fresh and dry weights of the leaves and stems were measured and estimated. We considered only the dry biomass of the above- and belowground portions

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of the plant. The roots of five plants from each treatment were randomly selected, and these were scanned and estimated using WinRHIZO Tron and XLRHIZO software (Version Pro, 2015). The osmolality of the pressed root sap was measured using a Type 5R Digital Micro-Osmometer (Hermann Roebling Messtechnik, Germany). In some cases, not enough sap could be pressed from the roots to obtain 100 μL necessary for the measurement. In these cases, dilutions were prepared using distilled water. The measurement and results were corrected according to the mixing ratio. Then, the dry weight of the investigated roots was determined. For this purpose, the root tissues were placed in Petri dishes and dried at 60 °C for 48 h in a drying oven (Binder FD 115, Binder GmbH, Germany) before weighing. Fine roots (< 2 mm in diameter) were selected, following McCormack et al. (2015). To determine the correlations between seed weight and stem length, root length, and above- and belowground dry biomass before the treatment, N = 30 control plants were used. To calculate the correlation between seed weight and stem length, root length, and above- and belowground dry biomass after the treatment, N = 150 plants (25 plants × 6 sites) from each treatment were used.

Statistical analysis. The statistical package IBM SPSS (Version 28, 2020) was used for the statistical analysis. Shapiro-Wilk and Kolmogorov tests were applied to test the normality and data distribution. One-way analysis of variance (ANOVA) was used to determine differences between control plant performance and treated plant development. We also used one-way ANOVA, followed by the Mann-Whitney U test, to determine differences in morphological and biomass performance. The significant level was considered to be $P < 0.05$ in each case. Pearson's correlation was performed between the parameters of plant development before and after the treatment.

RESULTS

Seed performance. Seed morphology analysis was used to evaluate the association between acorn size and the development of the resulting plant. It was also of interest to determine whether the plant groups maintained their developmental rankings before the drought treatment and after the drought treatment. Based on the ranking by acorn weight (i.e. mean fresh weight), ANOVA tests indicated that the *Q. petraea* acorns from the six dry sites formed four distinct statistical groups (A, AB, B, C). Group A had the heaviest seeds: FBG 2 (2.5 g), Waldfrieden (2.4 g) and Tharandt (2.3 g). The next was group AB including FBG 1 (2.1 g), followed by group B, including Schlottwitz (1.8 g). The smallest acorns were from group C: Pillnitz (1.4 g) (Figure 1). In comparison with *Q. petraea*, the *Q. robur* seeds were the heaviest at 4.7 g, but because this group served only for obtaining a general overview of plant development, it was not included in the ranking.

Seedling development (control plants). Based on stem length development, the *Q. petraea* seedlings formed four statistical groups. The tallest plants were 22.2 cm (mean stem length) from Tharandt (group A). The second was Waldfrieden, with a mean stem length of 15.8 cm (group B). The third group comprised FBG 2, Schlottwitz and Pillnitz (group BC), with FBG 1 forming the shortest group C, with a mean stem length of 7.9 cm (Figure 2).

Seedling development after treatment. In terms of the stem length, for most locations the optimally irrigated plants and those with reduced irrigation belonged to the same statistical group. Table 2 shows the impact of the drought and Figure 3A indicates the separate treatments for each group. The one exception was Schlottwitz, where the optimally treated group was AB, whereas the plants with reduced irrigation were in group B. Overall, the plants fell into four main statistical groups (A, B, AB

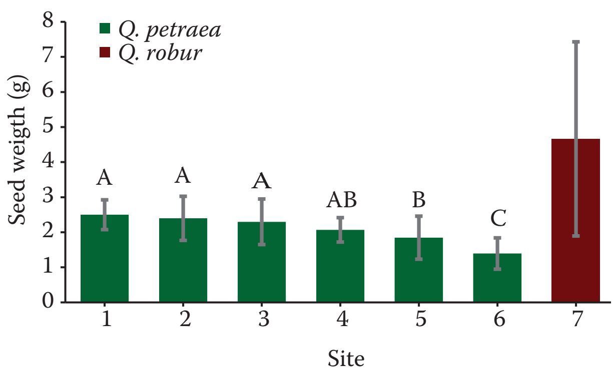

Figure 1. Growth ranking by acorn weight for *Q. petraea* and *Q. robur* from seven different sites

1 – FBG 2; 2 – Waldfieden; 3 – Tharandt; 4 – FBG 1; 5 – Schlottwitz; 6 – Pillnitz; 7 – Graupa; FBG – Forest Botanical Garden
Letters indicate significant differences among the sample sites and similarities in the groups ($P < 0.05$) based on ANOVA

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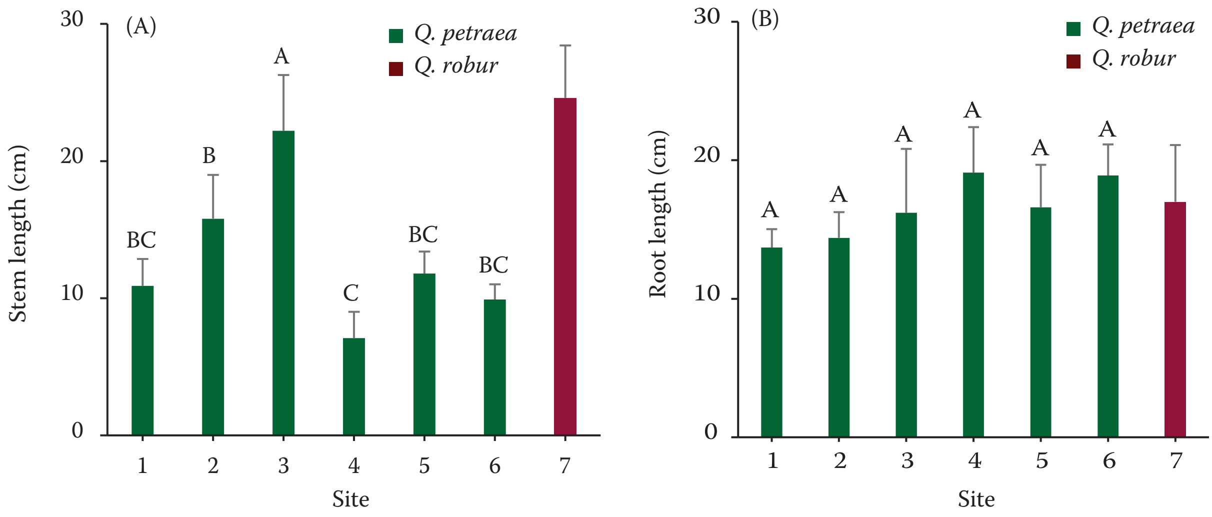

Figure 2. Growth ranking in the control plants of (A) stem lengths, and (B) root lengths

1 – FBG 2; 2 – Waldfieden; 3 – Tharandt; 4 – FBG 1; 5 – Schlottwitz; 6 – Pillnitz; 7 – Graupa; FBG – Forest Botanical Garden
Letters indicate significant differences among the sample sites and similarities in the groups ($P < 0.05$) based on ANOVA

and C) as shown in Figure 3A. The same letter indicates no difference in studied traits. So, group AB and group B are similar. Group A included Tharandt (optimal 26.12 cm, reduced 20.8 cm), with a difference of 20.36% ($P < 0.017$). Group AB included Waldfrieden (optimal 21.08 cm, reduced 17.56 cm), with a difference of 16.69% ($P < 0.037$), and Schlottwitz (optimal 21.16 cm, reduced 13.2 cm), with a large difference of 37.62% ($P < 0.001$). Group B included FBG 2 (optimal 16.24 cm, reduced 13.16 cm), with a growth reduction of 18.96%, which is significant ($P < 0.024$), and FBG 1 (optimal 14.84 cm, reduced 14.68 cm), with a difference of only 1.07% ($P < 0.861$). Group C included Pillnitz (optimal

Table 2. Seedling growth performance and comparison between treatments

No.	Site	Species	Treatment	Stem length			Root length			Collar diameter			Statistical group	
				mean (cm)	difference (%)	P	mean (cm)	difference (%)	P	mean (cm)	difference (%)	P	stem length	root length
1	FBG 2	*Q. petraea*	optimal	16.24	18.96	0.024	26.7	23.66	0.002	5.77	2.25	0.838	B	AB
			reduced	13.16			20.8			5.64			B	A
2	Waldfrieden		optimal	21.08	16.69	0.037	23.68	7.93	0.217	6.50	6.76	0.217	AB	AB
			reduced	17.96			21.8			6.06			AB	A
3	Tharandt		optimal	26.12	20.36	0.017	24.2	9.91	0.07	7.83	19.02	0.001	A	AB
			reduced	20.8			21.8			6.34			A	A
4	FBG 1		optimal	14.84	1.07	0.861	27.04	23.44	0.002	5.67	–	0.536	B	AB
			reduced	14.68			20.7			5.19			B	A
5	Schlottwitz		optimal	21.16	37.62	0.000	30.2	21.45	0.210	7.07	27.29	0.001	AB	A
			reduced	13.2			23.72			5.14			B	A
6	Pillnitz		optimal	16.2	25.68	0.006	28.68	41.77	0.000	5.12	18.75	0.001	B	A
			reduced	11.98			16.7			4.16			B	B
7	Graupa	*Q. robur*	optimal	45.72	17.32	0.05	36	37.66	0.000	10.09	27.75	0.001	–	–
			reduced	37.8			22.44			7.29			–	–

A, B – significant differences among the sample sites and similarities in the groups; FBG – Forest Botanical Garden

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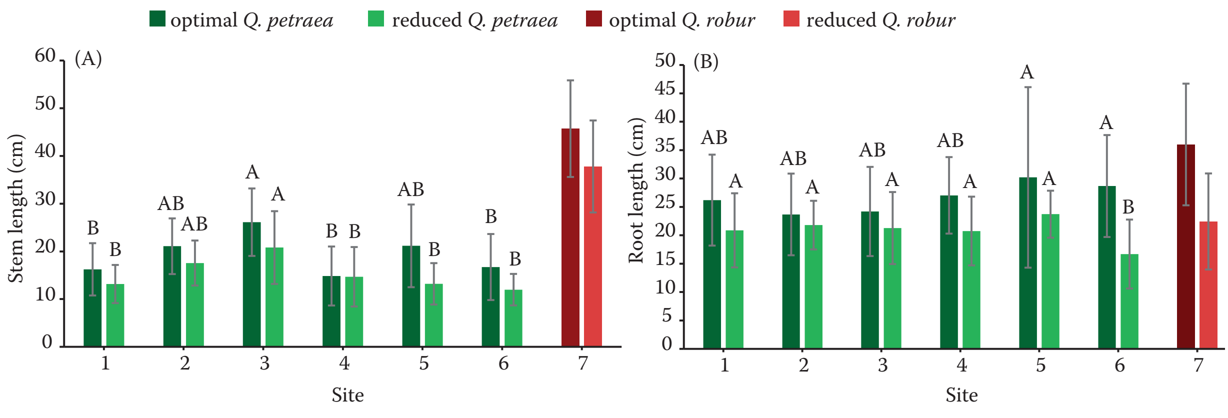

Figure 3. Growth ranking in treated plants of (A) stem length, and (B) root length

1 – FBG 2; 2 – Waldfieden; 3 – Tharandt; 4 – FBG 1; 5 – Schlottwitz; 6 – Pillnitz; 7 – Graupa; FBG – Forest Botanical Garden

Vertical bars indicate standard deviation from the mean value; letters indicate significant differences among the sample sites and similarities in the groups ($P < 0.05$) based on ANOVA

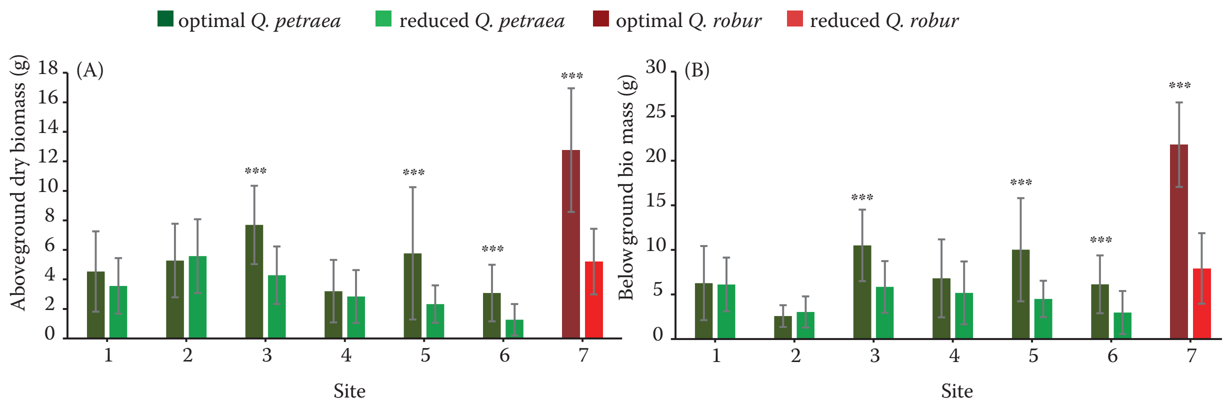

Figure 4. Dry biomass for *Q. petraea* and *Q. robur* (A) aboveground, and (B) belowground

***significant differences between treatments ($P < 0.05$) under the nonparametric Mann–Whitney U test; 1 – FBG 2; 2 – Waldfieden; 3 – Tharandt; 4 – FBG 1; 5 – Schlottwitz; 6 – Pillnitz; 7 – Graupa; FBG – Forest Botanical Garden

Vertical bars indicate standard deviation of the mean value

16.2 cm, reduced 11.98 cm), which is a difference of 25.68%. This growth reduction was significant at $P < 0.006$. For *Q. robur*, the average stem length with optimal irrigation was 45.72 cm and, with reduced irrigation it was 37.8 cm, which corresponded to a reduction of 17.32% ($P < 0.05$) (Table 2).

Root length formed three statistical groups (A, B, AB) with the different treatments. The plants with optimal treatment fell into group A (Schlottwitz and Pillnitz) and AB (FBG 2, Waldfrieden, Tharandt and FBG 1). For the reduced irrigation, only Pillnitz fell into group B, whereas the other five sites were in group A. The mean root length of *Q. robur* from group A was the longest overall (Figure 3B). When comparing the treatments against root length for *Q. petraea*, FBG 1, FBG 2 and Pillnitz showed highly significant differences, whereas Waldfrieden and Tharandt indicated differences, but they were not significant (Table 2).

The average collar diameters (Table 2) for both treatment groups of *Q. petraea* showed small differences for FBG 1, FBG 2 and Waldfrieden. The other three sites showed a hugely significant difference between the treatments (Tharandt – optimal 7.83 mm, reduced 6.34 mm, $P < 0.000$; Pillnitz – optimal 5.12 mm, reduced 4.16 mm, $P < 0.001$; and Schlottwitz – optimal 7.07 mm, reduced 5.14 mm, $P < 0.000$). Additionally, for *Q. robur* from

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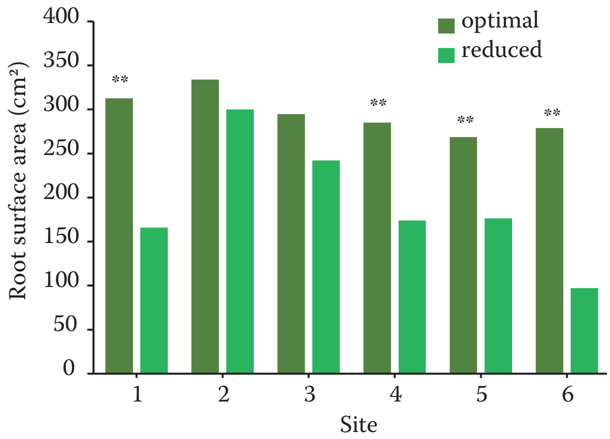

Figure 5. Root surface area in *Q. petraea* after treatment

**significant differences between treatments ($P < 0.05$) under the nonparametric Mann–Whitney U test; 1 – FBG 2; 2 – Waldfieden; 3 – Tharandt; 4 – FBG 1; 5 – Schlottwitz; 6 – Pillnitz; FBG – Forest Botanical Garden

Vertical bars indicate standard deviation

group A, the difference was significant at $P < 0.001$ (optimal 10.09 mm, reduced 7.29 mm).

Biomass. As expected, the biomass parameters for the optimal treatment were significantly higher for each site (Figure 4A, B) than those of the group with reduced treatment. In particular, Tharandt, Schlottwitz and Pillnitz showed highly significant differences in the above- and belowground dry biomass. The (mean) aboveground dry biomass for Pillnitz was 3.07 g for optimal irrigation, with the biomass from reduced irrigation being 58.95% lower (1.26 g, $P < 0.001$). There was a difference of 51.62% in the mean belowground biomass of Pillnitz between optimal and reduced irrigation conditions (optimal 6.14 g, reduced 2.97 g, $P < 0.001$). For Schlottwitz and Tharandt, there were reductions of 59.12% and 44.27%, respectively, with 55.18% for Schlottwitz and 44.38% for Tharandt when irrigation was reduced.

Root to shoot ratio. The root to shoot ratios were calculated as the dry weight of the belowground plant parts to the dry weight of the aboveground plant parts. This ratio was calculated for both species and treatments (Table 3).

The root to shoot ratios were 1.70 for the optimal treatment and 1.52 for the reduced treatment in *Q. robur*. For *Q. petraea*, the ratios were: FBG 2 – optimal 1.38, reduced 1.74; Waldfrieden – optimal 0.48, reduced 0.54; Tharandt – optimal 1.36, reduced 1.36; FBG 1 – optimal 2.12, reduced 1.82; and Schlottwitz – optimal 1.77, reduced 1.92. A higher root to shoot ratio was also observed for the reduced Pillnitz group (optimal 2.0, reduced 2.35). Regarding the ranking of the sites and the reduced irrigation treatment, the highest root to shoot ra-

Table 3. Details of the root: shoot ratio

Site	Treatment	Dry weight (g)		Root : shoot ratio	*P* value of root : shoot ratio
		aboveground	belowground		
FBG 2	optimal	4.5	6.27	1.38	0.028
	reduced	3.5	6.12	1.74	
Waldfrieden	optimal	5.28	2.57	0.48	0.668
	reduced	5.57	3.03	0.54	
Tharandt	optimal	7.68	10.5	1.36	0.433
	reduced	4.28	5.84	1.36	
FBG 1	optimal	3.206	6.80	2.12	0.539
	reduced	2.84	5.18	1.82	
Schlottwitz	optimal	5.7	10.2	1.77	0.355
	reduced	2.33	4.49	1.92	
Pillnitz	optimal	3.07	6.14	2.0	0.712
	reduced	1.26	2.94	2.30	
Graupa	optimal	12.76	21.80	1.70	0.009
	reduced	5.20	7.92	1.52	

FBG – Forest Botanical Garden

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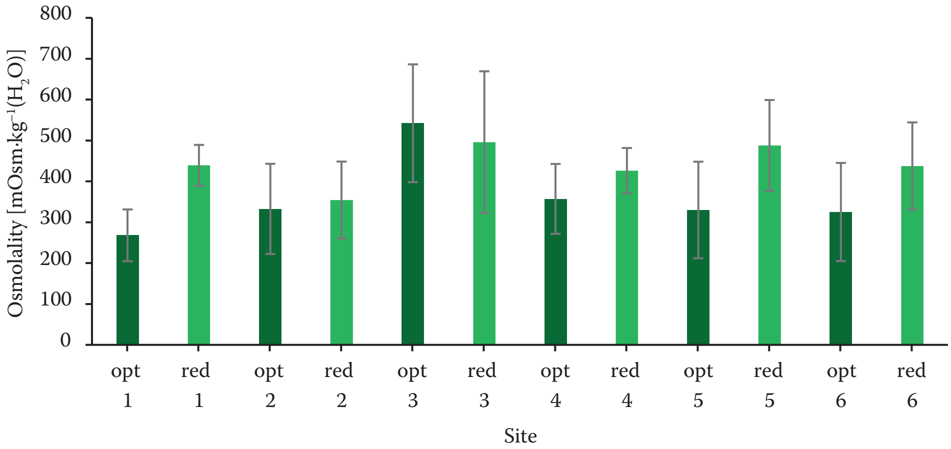

Figure 6. Osmolality in *Q. petraea*

Opt – optimal; red – reduced; 1 – FBG 2; 2 – Waldfieden; 3 – Tharandt; 4 – FBG 1; 5 – Schlottwitz; 6 – Pillnitz; FBG – Forest Botanical Garden

Error bars indicate standard deviation

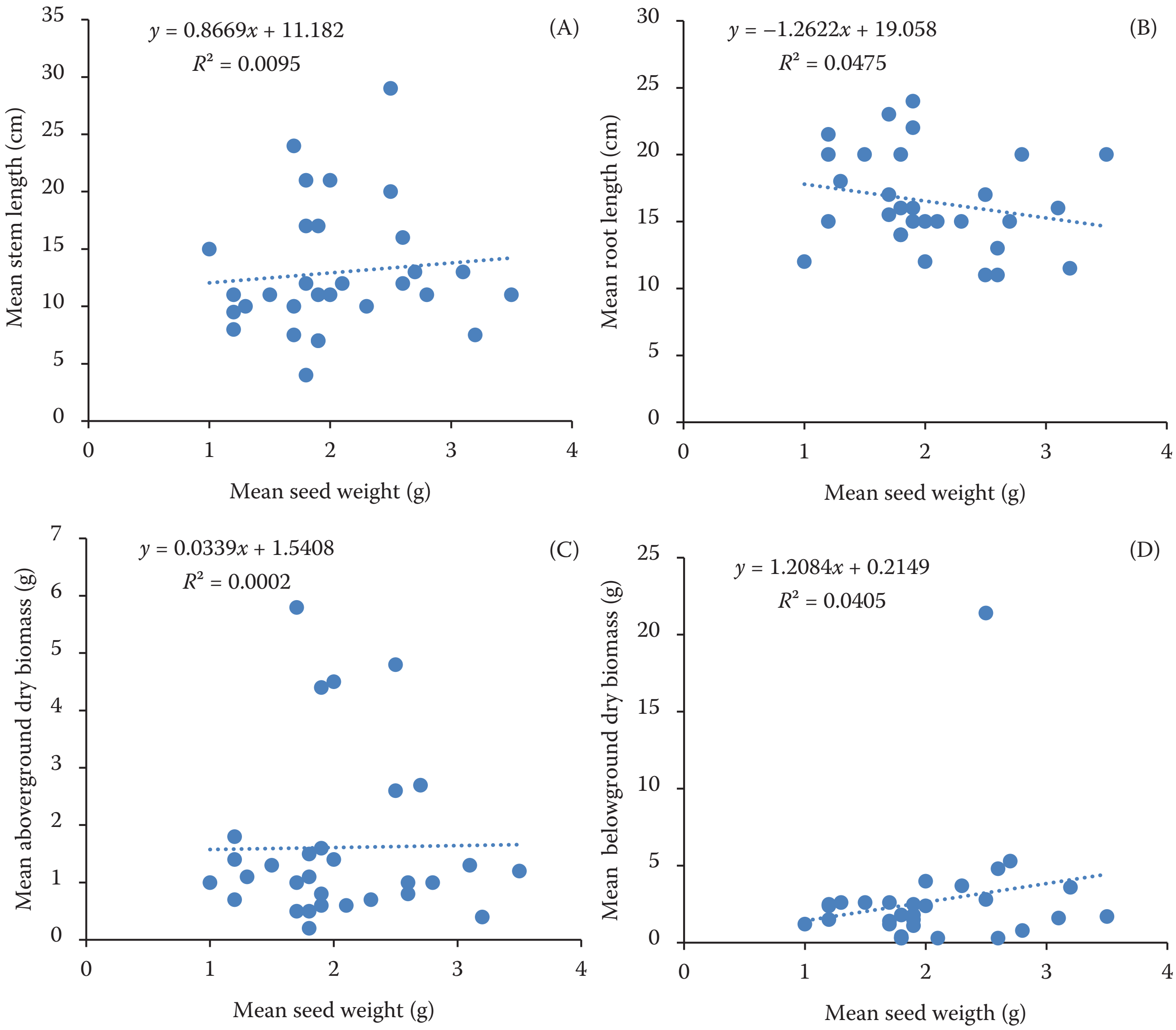

Figure 7. Relationship between *Q. petraea* mean seed weight before drought treatment ($N = 30$) and (A) mean stem length; (B) mean root length; (C) mean aboveground dry biomass; and (D) mean belowground dry biomass

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tio was recorded for Pillnitz, with the second being for Schlottwitz, the third for FBG 1, the fourth for FBG 2, the fifth for Waldfrieden and the last for Tharandt (Table 3).

Root surface area. Among the optimally treated variants on all the sites, Tharandt had the largest mean root surface area (356.92 cm^2), whereas the smallest fine root surface area was 283.72 cm^2 from Pillnitz. The largest mean root surface area for the reduced treatment was 238.11 cm^2 from Waldfrieden, whereas the smallest fine root surface area was 71.26 cm^2 from Pillnitz. A test was performed to compare the treatments. The optimally irrigated plants had larger root surface areas than the plants with reduced treatment on all sites. Based on the *t*-test, except for Waldfrieden and

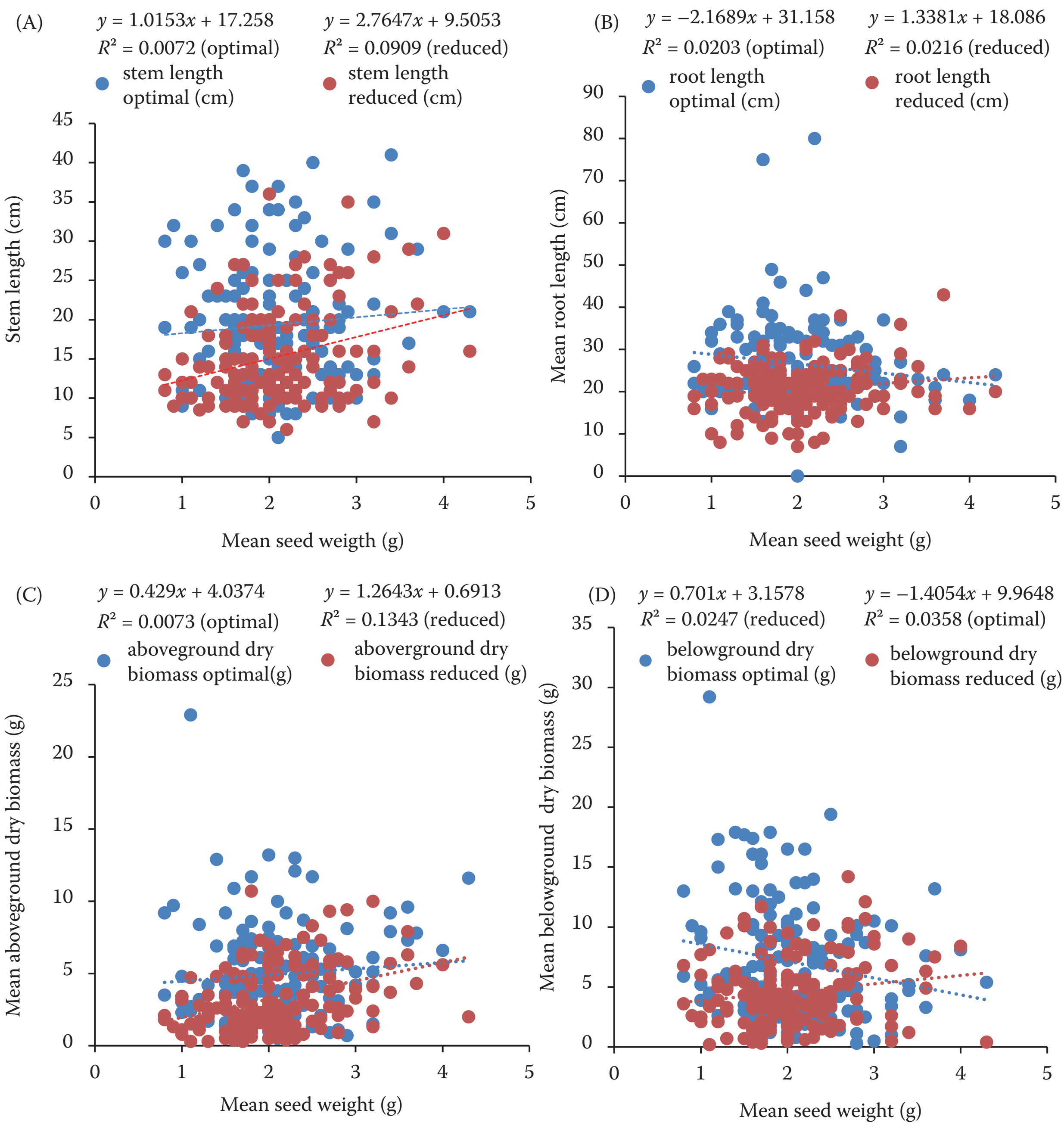

Figure 8. Relationship between mean *Q. petraea* seed weight after drought treatment (N = 150 optimal, 150 reduced) and (A) mean stem length, (B) mean root length, (C) mean aboveground dry biomass, and (D) mean belowground dry biomass

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Tharandt, the sites had significantly high differences, with FBG 2 at $P < 0.032$, FBG 1 at $P < 0.032$, Schlottwitz at $P < 0.008$ and Pillnitz at $P < 0.04$ (Figure 5).

Osmolality. Comparing the optimal treatments, Tharandt had highest osmolyte content [539.25 mOsm·kg^{-1}(H_2O)], with Schlottwitz next [417 mOsm·kg^{-1}(H_2O)], and then FBG 1 [347.55 mOsm·kg^{-1}(H_2O)], Waldfrieden [332.66 mOsm·kg^{-1} (H_2O)] and Pillnitz [325 mOsm·kg^{-1}(H_2O)] being relatively close to each other. FBG 2 had the lowest value [268 mOsm·kg^{-1}(H_2O)].

For the reduced treatment, Tharandt had the highest osmolyte concentration [450 mOsm·kg^{-1}(H_2O)], with four sites having relatively close values, as with the optimal treatment, and the lowest being Waldfrieden [354 mOsm·kg^{-1}(H_2O)]. From the comparison test between the optimal and reduced treatments, the osmolality values of the plants with reduced watering were higher than those of the optimally watered ones, with one exception – Tharandt (Figure 6).

Correlations between seed weight and seedling growth development before and after treatment. Stem and root length and above- and belowground dry biomass were selected to examine the relationship with seed weight. There was a weak positive relationship between belowground dry biomass and seed weight ($R^2 = 0.009$, $P < 0.93$, $r = 0.201$, $N = 30$) and a weak negative relationship between seed weight and root length ($R^2 = 0.04$, $P < 0.24$, $r = -0.21$, $N = 30$). There were no correlations between seed weight and stem length or aboveground dry biomass (Figure 7).

In terms of the correlation between seed weight and stem length, root length, and above- and belowground dry biomass after treatment (optimal and reduced), there were no relationships between the parameters in the optimal case. There was a moderate positive relationship between seed weight and stem length for the reduced irrigation treatment ($R^2 = 0.098$, $P < 0.001$, $r = 0.313$, $N = 150$), a moderate positive relationship ($R^2 = 0.188$, $P < 0.001$, $r = 0.43$, $N = 150$) between seed weight and aboveground dry biomass, and a weak positive relationship between seed weight and belowground dry biomass for *Q. petraea* after the treatment, but no relationship between seed weight and root length ($R^2 = 0.002$, $P < 0.06$, $r = 0.24$). Although the relationship is significant, its R^2 is really low (Figure 8).

DISCUSSION

Seedling growth and morphology can be affected by access to various resources and environmental conditions (Pérez-Ramos et al. 2010). The size of *Quercus* acorns is one of the major determinants of the early establishment of seedlings of this woody species, having a generally favourable effect on seedling survival and growth (Bonfil 1998; Quero et al. 2007; Borucki Castro et al. 2008). The development of an effective root system is especially important on dry sites, where the plants have access to fewer water resources in the soil.

In this study, seed weight and seedling aboveground dry biomass had a closer relationship than all other parameters both before and after drought treatment, although this relationship was weak. This finding supports the results of several studies that followed a similar approach.

Long and Jones (1996) investigated 1–2-year-old potted plants representing 14 oak species native to different soil moisture habitats in order to determine the seedling growth strategies and seed size effects. The authors found that acorn weight was generally unrelated to plant size and morphology within the respective species. Quero et al. (2008) looked into the effects of drought and shade on the seedlings of four *Quercus* species in Spain. The authors used potted seedlings for the drought treatment and found a strong effect of irradiance on the importance of seed mass as a driver of absolute growth, with the relationship between seedling biomass and seed mass being consistent between the two watering treatments. Pérez-Ramos et al. (2010) investigated the seedling growth and morphology of three oak species and variations in their seed mass, revealing a seedling age-dependent response. The authors found that seedling growth and total aboveground biomass were affected by light conditions and the seed mass. Bonfil (1998) documented an investigation on the effect of seed size and seedling growth on 2-year-old potted seedlings of two different oak species, finding the effect of the seed size to be significant in both species, with a positive correlation between seed mass and survival and growth.

Acorn mass represents the amount of reserves an embryo needs to begin its first life stages (Quero et al. 2007). Here, no relationships were found between the phenotypic parameters of the optimally irrigated plant group, whereas the plants under reduced irrigation showed sufficiently positive relation-

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ships between seed weight and stem length, and seed weight and aboveground dry biomass, with a weak positive relationship between seed weight and belowground dry biomass. The relationship between acorn size and seedling development was here found to differ between the pre- and post-drought treated plants.

In this study, the six different dry sites were ranked in terms of the seed size and seedling development both before and after drought treatment. The results indicate that the plants did not maintain these rankings in their different developmental stages – the heaviest seeds did not necessarily produce the tallest seedlings, the smallest seeds did not produce the smallest seedlings. The seedlings from the smallest seeds (at the driest site) exhibited a hugely significant difference in phenotypic traits and biomass performance after drought treatment. The seedlings from the largest seeds showed differences between the reduced and optimal treatments but they were not significant.

The drought stress imposed in this study was high enough to force the seedlings to express potentially adaptive traits without causing a mortality rate that would end the experiment. The findings of this study concerning growth (stem length, root length and collar diameter) are similar to those from other studies. Van Hees (1997), Oren and Pataki (2001), Zweifel et al. (2005) and Vander Mijnsbrugge et al. (2020) all indicated that the physiological response of trees to drought stress, in terms of transpiration and growth, depends on the water status of the soil. The morphological responses to water limitation observed in this study are in agreement with the findings of Abrams (1990), Fotelli et al. (2000) and Früchtenicht et al. (2018a, b, 2021).

In this study, the growth of the stem length, root length and collar diameter was significantly decreased by the reduced irrigation treatment, which is in agreement with previous studies (Koslowski 1982; Vivin et al. 1993; Collet, Guehl 1997; Thomas, Gausling 2000; Saxe et al. 2001; Ponton et al. 2002; Arend et al. 2011; Früchtenicht et al. 2018a). In terms of the root to shoot ratios based on the below- and aboveground dry biomass, all of the plants exposed to reduced irrigation had higher values than the optimally treated seedlings, except for those in Forest Botanic Garden 1. The root to shoot ratio of plants usually increases under the influence of drought because they reduce the leaf growth to increase their water-absorbing area, thereby decreasing their transpiration area, as confirmed in oaks by Dickson and Tomlinson (1996), Thomas and Gausling (2000), Arend et al. (2011) and Vander Mijnsbrugge et al. (2017, 2020). This is widely considered to be an adaptive mechanism by which the plant can restore the balance between absorption of soil water by the roots and water loss by the leaves (Arend et al. 2011).

The ability of sessile oaks to adapt their osmoregulation in response to drought was demonstrated by Abrams (1990), Collet and Guehl (1997) and Thomas and Gausling (2000). In the present study, the osmolality of the plants was determined by measuring the pressed root sap, with the difference in mean values providing information on the occurrence or extent of the osmoregulation processes. Except for the plants from Tharandt, all the others had higher osmolality under the reduced irrigation treatment than under the optimal treatment. This may indicate that pot studies underestimate the osmoregulatory capacity of plants. Also, Thomas and Gausling (2000) claimed that a slower onset of drought may induce greater osmoregulatory adaptation, and that oak seedlings under natural conditions likely respond more strongly than seedlings under controlled conditions with rapidly induced drought. In this study, it was also revealed that, at all locations, the plants under drought conditions developed the significantly smaller fine root surface area than the optimally watered plants. Our findings prove that the fine root surface area decreases in response to drought.

Drought stress in trees inevitably leads to a reduction in growth and to different patterns of resource allocation. Thomas and Gausling (2000) interpreted these signs as adaptations that reduced the transpiration surface area and increased the water supply to the plant. However, Epron and Dreyer (1990, 1993), working with 30-year-old plant material, could not demonstrate any differences in drought sensitivity between the two species Q. *petraea and Q. robur*, which both exhibited the same photosynthetic responses to summer drought. Here, it was found that the biomass performance decreased in both species under reduced water treatment, confirming the findings of Davidson et al. (1992), Leiva and Fernández-Alés (1998), Thomas and Gausling (2000), Rose et al. (2009), Arend et al. (2011) and Vander Mijnsbrugge et al. (2017). In this study, *Q. petraea* in around 50% of sites exhibited significant reductions in biomass under reduced water treatment.

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CONCLUSION

According to our findings, however, seedling development is not dependent on seed weight. The seedlings exhibited relatively tolerant responses to the drought. Oak species, especially *Quercus petraea,* could thus be good plant resources for silvicultural activities in areas affected by drought.

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