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Original article

Morphological and physiological responses of oak seedlings (*Quercus petraea* and *Q. robur*) to moderate drought

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Abstract – To study their responses to a moderate drought, seedlings of sessile (*Quercus petraea* [Matt.] Liebl.) and pedunculate oak (*Q. robur* L.) were grown in outdoor lysimeters that allowed unrestricted root growth. They were subjected to a moderate drought from mid-June to the end of August. The stomatal conductance remained almost unaffected by drought. In the drought-stressed seedlings, the relative foliar water deficits were significantly higher, and the predawn leaf water potentials were significantly lower than in the control plants. The decrease in osmotic pressures at maximum turgor and at the point of turgor loss in the drought-stressed plants indicated osmotic adjustment. The ratio of leaf to fine-root biomass was significantly diminished in the drought-stressed seedlings. In combination with previous observations, the results indicate that, in the Central-European oak species, a shift in biomass compartmentation is the predominant process in acclimation to drought since it also occurs under severe drought stress in contrast to osmotic adjustment, which was only found under conditions of a moderate drought.

***Quercus* / drought / leaf-root biomass ratio / osmotic adjustment / pressure-volume analysis**

Résumé – Réponses morphologiques et physiologiques de semis de chêne *(Quercus petraea* et *Q. robur)* face à une sécheresse modérée. Afin d'étudier leur réaction face à une sécheresse modérée, des plantules de chêne sessile (*Quercus petraea* [Matt.] Liebl.) et de chêne pédonculé (*Q. robur* L.) ont été cultivées à l'extérieur, dans une cuve lysimétrique permettant un développement illimité des racines. Le régime de sécheresse modérée leur a été appliqué de mi-juin jusqu'à fin août. La conductance foliaire stomatique n'a guère été affectée par la sécheresse. Le degré du déficit hydrique foliaire relatif des plantules stressées par la sécheresse avait augmenté de façon significative alors que le potentiel hydrique foliaire mesuré avant l'aube fut plus bas que celui des plantules témoins. La diminution des pressions osmotiques en pleine turgescence et au point zéro turgor des plantules stressées indiquerait un ajustement osmotique. Les plantules stressées ont montré un ratio de la biomasse foliaire par rapport à la biomasse des racines fines qui avait baissé de manière significative. Les résultats complètent ainsi des études antérieures indiquant que pour les chênes européens le changement de la compartimentation de la biomasse serait le processus prédominant dans l'acclimatation à la sécheresse. En effet, ce phénomène surgit également lors d'une sécheresse excessive tandis que l'ajustement osmotique n'a été constaté que lors d'une sécheresse modérée.

***Quercus* / ajustement osmotique / analyse pression-volume / rapport des biomasses feuilles-racines / sécheresse**

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1. INTRODUCTION

Besides beech (*Fagus sylvatica* L.), pedunculate (*Quercus robur* L.) and sessile oak (*Q. petraea* [Matt.] Liebl.) are the most common deciduous forest tree species in Central Europe. Within this region, under natural conditions, they have a lower competitive power than beech at sites with a moderate to optimum supply of water and nutrients. Therefore, they tend to gain dominance over beech mainly at sites with more extreme soil moisture conditions [8]. Although, compared to the sessile oak, the pedunculate oak was found to have a larger water requirement [17] and to be more sensitive to drought stress [4, 27], this species also occurs at sites with low water supply, e.g. on nutrient-poor sandy soils (*Betulo-Quercetum roboris;* [29]), or on plateaus and exposed slopes of well-drained limestone hills (xerothermic mixed oak forests; cf. [13]). At those sites, drought tolerance is a prerequisite for the establishment of seedlings.

Morpho-anatomical and physiological mechanisms of drought tolerance are known. Morpho-anatomical mechanisms involve alterations in leaf area, cell wall elasticity, or biomass compartmentation between shoot and roots [15]. Physiological mechanisms include an effective stomatal control of water loss and osmotic adjustment, i.e. a change in osmotic pressure larger than the passive change resulting from the loss of cell water [11]. In *Q. petraea*, severe drought resulted in an increased production of fine-root biomass, and in a decrease in the following: the biomass of leaves and stems, the biomass ratio of leaves to fine roots, and the number of buds. In *Q. pubescens*, with regard to biomass parameters, only the average mass of the individual buds was significantly lowered by drought; but, in this species, indications were found for an increase in tissue elasticity as an acclimation to drought [24]. However, in neither of the two species was osmotic adjustment found as a response to severe drought [24], nor was it detected in most of the drought-resistant shrubs, including *Q. pubescens*, that were investigated at drought-prone sites in Austria and the Mediterranean region [11]. In contrast, indications for osmotic adjustment as a means of acclimation to drought was provided by a study carried out in a mixed stand of *F. sylvatica, Q. petraea* and *Q. pyrenaica* in central Spain [3].

Osmotic adjustment may occur during ontogeny, and not only in response to drought [2]. Therefore, the assumption of osmotic adjustment needs to be corroborated by comparisons between drought-stressed and adequately watered plants, which are in a comparable developmental stage. In a recent study conducted on seedlings of sessile oak, osmotic adjustment was less pronounced after a rapid onset of drought than in the case of a slower rate of soil dehydration. This indicates that the degree of the stress affects the performance of osmotic adjustment [5]. However, in that particular study, the osmotic pressure at maximum turgor (Π_o) was measured in sap which had been pressed out of the leaf tissue. Due to dilution of the cell sap by apoplasmic water, this method generally leads to an overestimation of Π_o (i.e., less negative values [20]). Seedlings of the pedunculate oak were shown to osmotically adjust their leaf water potential when subjected to consecutive drying cycles [19]. However, these plants were grown under greenhouse conditions, and in containers with restricted rooting volume as was also the case in other studies [9, 28]. Therefore, we conducted a study on pedunculate and sessile oak seedlings whose roots were allowed to grow without restriction outside the greenhouse under controlled conditions. The objectives of the investigation were to examine whether (1) osmotic adjustment would develop under a moderate drought, and (2) morphological alterations as responses to a moderate drought would be similar to those caused by severe stress. The results are discussed against the background of findings from a previous investigation on the effects of a severe drought on oak seedlings [24].

2. MATERIALS AND METHODS

2.1. Plant material and cultivation

For the experiments, selected reproduction material originating from the north German heathland and hill country (sessile oak (*Quercus petraea* [Matt.] Liebl.); derived from the Forest Seed Centre in Oerrel, Lower Saxony), or originating from the hilly and mountainous country of southern Germany (pedunculate oak (*Quercus robur* L.); obtained from a tree nursery) was used. In February 1998, the acorns were sawn into germination dishes filled with quartz sand and cultivated in a greenhouse with a temperature of 15 °C and a photosynthetic photon flux density (*PPFD*; Osram HQJE, 400 W) of 135 to 210 μmol m^{-2} s^{-1} (day; 6.00 – 20.00 h), 10 °C (night), and a relative humidity of 50 to 85%. In mid-May, when the shoots were approximately 10 – 15 cm tall, the seedlings were planted into four lysimeters situated in the Botanical Garden. These were 5 m long, 1.2 m wide and 1 – 2 m deep, and were filled with calcareous sand (pH(H_2O) approx. 7). In each lysimeter, 60 seedlings (30 sessile and 30 pedunculate oaks) were arranged in four rows at a distance of approximately 25 cm from the adjacent plants or from the side of the lysimeter to prevent shading effects. The oaks were thoroughly watered, and the water level in the lysimeters was adjusted to 40 cm below the soil surface. During the first two weeks after planting, the seedlings were protected from intensive solar radiation by shading.

The drought experiment started in mid-June. In two of the four lysimeters (the drought lysimeters), the water level was lowered to 80 cm below the soil surface. A complete drainage was avoided to allow the plants to use the higher water contents of deeper soil layers by progressive root growth. By lowering the water table, the volumetric water content (*SWC;* measured by TDR; type 6050X1, Trase System I, Soil Moisture Equipment Co., Santa Barbara, CA, USA) of the uppermost 15 cm of the soil decreased from 19% to 7% within 10 days. In this soil layer, it was kept at 7% by controlled superficial watering until the end of the experiment. After finishing the experiment, *SWC* was 10% in 35 – 50 cm of soil depth, and almost 15% in 50 – 65 cm of soil depth in the drought lysimeters. In the uppermost 15 cm of the remaining two lysimeters (the control lysimeters), the *SWC* was adjusted to 15 – 20% during that time (*figure 1*). The soil moisture relations were uniform in both lysimeters of a given treatment. All lysimeters were protected from uncontrolled watering by an automatically operated roof which was moved over the plants in the event of precipitation. However, to document the weather conditions during the experimental period, the daily precipitation is shown together with the daily maximum air temperature in *figure 1*. June, July and August were drier than the long-term average. May was warmer, and July and August were cooler, than normal. However, warm, dry periods occurred during the second half of July and the first half of August (*figure 1*).

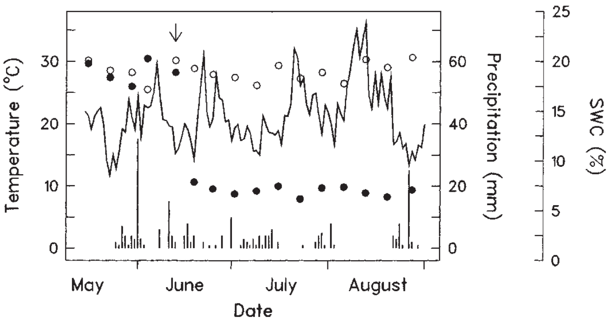

Figure 1. Daily maximum air temperature (solid line), daily amounts of precipitation (vertical bars), and volumetric water contents (SWC; circles) of the uppermost 15 cm of soil during the experimental period. Means of SWC are presented for the control (open circles) and drought lysimeters (solid circles). The arrow indicates the start of the drought treatment. The climate data are derived from Deutscher Wetterdienst ([6], meteorological station of Göttingen).

To supply the plants with nutrients, 10 l of nutrient solution were added to each lysimeter once at the end of May and again at the end of July. The solution contained 4 mM NH_4NO_3 and the following concentrations of macro- and micronutrients, which had been proven to be appropriate for the growth of oak seedlings in previous investigations: K, 6.0 mM; Mg, 2.1 mM; Ca, 0.9 mM; P, 0.5 mM; S, 7.3 mM; Fe, 0.14 mM; B, 13.5 µM; Mn, 7.5 µM; Zn, 6.0 µM; Mo, 3.6 µM.

2.2. Water relations and biomass

At the beginning of the drought and on three consecutive dates at the end of July and in August, the stomatal conductance of the leaves (*g*, mmol H_2O m^{-2} s^{-1}), predawn leaf water potential (Ψ_P), parameters derived from pressure-volume curves (*pV* curves), relative water deficits of the leaves (*RWD*), biomass of leaves and fine roots (diameter ≤ 2 mm), leaf mass per unit area (*LMA*) and rooting depths were determined. The seedlings selected from the control and the drought lysimeters were similar with respect to their developmental stage. On sunny days between 12.00 and 14.00 h (*PPFD* > 1 mmol m^{-2} s^{-1}), *g* was measured in each three leaves from three seedlings per species and lysimeter with a steady-state porometer (LI-1600, LI-COR, Lincoln, NE, USA). In the upper shoot sections of three seedlings per species and treatment, Ψ_P was determined with the aid of a pressure chamber [22]. In those seedlings, *RWD* was also obtained from one combined sample per plant, consisting of ten leaf discs, by weighing before and after 3 h of rehydration, and after drying at 105 °C [23, 25]. In three seedlings per species and treatment, *pV* curves were established with shoots, which had been rehydrated overnight, by the expression of xylem sap at several pressure steps that were applied within a pressure chamber [20]. From the plots of the cumulative amount of expressed xylem sap (*x*-axis) against the inverse value of the applied pressure (*y*-axis), the following parameters were calculated [20]: Π_o (MPa), osmotic pressure at maximum turgor; Π_P (MPa), osmotic pressure (or leaf water potential, respectively) at the turgor loss point; $\Delta\Pi$ (MPa), difference between Π_o and Π_P; RWC_P, relative water content of the leaf tissue at the turgor loss point; RWC_{sym}, relative water content of the saturated symplast; ε_{max} (MPa), maximum bulk modulus of tissue elasticity. RWC_{sym} was computed as the ratio of the *x*-axis intercept (which is considered to be the total amount of symplasmic water [20]) to the total water content of the tissue (which is the difference between the fresh mass after rehydration and the dry mass). ε_{max} was calculated from the slope of the linear portion of the plot of turgor

(P) against RWC (relative water content of the tissue) according to

$$\varepsilon_{max} = dP/dRWC * (RWC_{mean} - RWC_{apo});$$

where RWC_{mean} = average RWC of the considered portion of the plot, and RWC_{apo} = relative water content of the apoplasm (cf. [14]).

The rooting depths of the seedlings that had been used for *pV* analyses were assessed. Leaf and root biomass of those seedlings were determined after drying for 24 h at 105 °C. In three plants per species and treatment, the leaf area of three freshly harvested leaves was measured with a leaf-area meter (LI-305 CA/4 and LI-3000, LI-COR). After drying at 105 °C and weighing, LMA (g_{DM} m^{-2}) was calculated. During the entire experiment, the plants were monitored for the development of a second flush. At the end of September, the number of buds was counted on nine seedlings per species and treatment.

2.3. Chemical analyses

In mid-September, three to five leaves per seedling were harvested from 13 pedunculate and 16 sessile oaks per treatment. After drying at 105 °C and pulverizing, one combined sample per plant was made. Two replicates per sample, each comprising 0.5 – 1 mg, were analyzed for N (to determine the nutrient status) and for δ^{13}C, i.e. the deviation of the ^{13}C fraction of the leaf from a standard (to obtain a measure of the long-term water-use efficiency [10]), with an isotope mass spectrometer (Delta^{plus}, Finnigan, Bremen, Germany) coupled to a C-N-analyzer (NA 1500, Carlo Erba, Rodano/Milan, Italy). The standards were acetanilide (for N) and Peedee Belemnite (for C).

2.4. Statistics

In the presentation of the results, the means and standard errors are given. Within the species, the differences between control and drought-stressed seedlings on a given date were tested with the Mann-Whitney Ranked Sum Test (U test). The significance of the correlation coefficients resulting from linear regressions was tested using the distribution of t values. Differences between treatments in the fraction of plants that had generated a second shoot were tested with the χ^2 test. The significance level was 5% ($P < 0.05$) in each case.

3. RESULTS

On the sampling dates, no significant differences were found between the fine root biomass of drought-stressed and control seedlings of the two species. In contrast, after the onset of drought, the leaf biomass of the stressed seedlings was slightly lower than in the control ones. In two instances (early August, pedunculate oak; mid-August, sessile oak), the differences were significant *(table I)*. Those alterations resulted in significantly decreased ratios of leaves to fine roots on a dry-mass basis in the drought-stressed plants (*figure 2d*). The *LMA* exhibited a slight tendency to increase from June to late August, but none of the species exhibited significant differences between treatments (*table I*). In the drought-stressed seedlings, a smaller fraction of plants developed a second flush, and the number of buds decreased slightly, compared to the control plants. However, the differences between treatments were insignificant (*table II*). As a consequence of root growth, the rooting depths increased from early June to the end of August (*table I*). Within the species, differences between treatments were not detected. Within a given treatment, the oak species did not exhibit distinct differences with regard to the determined growth parameters (leaf and root biomass, *LMA*, rooting depth, generation of a second flush, number of buds; *tables I, II*).

At the end of July and in mid-August, Ψ_P in the drought-stressed seedlings of both species was significantly lower than in the control plants (*figure 2a*). Accordingly, leaf *RWD* was higher in those seedlings, except for the pedunculate oak in late July (*figure 2b*). Due to the relatively large variations of the mean values, the stomatal conductance g of the drought-stressed oaks was not significantly lower than that of the control plants, except for the sessile oak in late June (*figure 2c*). Nevertheless, g of the droughted seedlings remained below the controls during the entire drought treatment. In early and mid-August, $\prod_o$ and $\prod_P$ in the drought-stressed seedlings of both species were significantly lower than in the control plants (*figures 3a, c*). At the end of August, however, no significant differences in water relation parameters between treatments were found *(figures 2, 3)*. At that time, the roots of the drought-stressed seedlings had reached soil layers with a water content of at least 10% (cf. 2.1 and *table I*). In none of the species did $\Delta\Pi$ significantly differ between treatments (data not shown).

After the onset of drought, RWC_P was significantly higher (early August), and RWC_{sym} was lower (mid-August) in the stressed pedunculate oaks (*figure 3b*). In the sessile oak, no significant differences occurred between treatments (*figure 3d*). From the RWC_P values, the relative water deficit at the turgor loss point (RWD_P) can be calculated ($RWD_P = 1 - RWC_P$). In August, on a per cent basis, these values generally were lower than the respective foliar *RWD* values (cf. *figures 2b, 3b, 3d*). This would mean that, in August, the foliar water content was

Table I. Leaf and fine-root biomass, leaf mass per unit area (*LMA*), and rooting depth of seedlings of *Quercus robur* and *Q. petraea*, which were adequately supplied with water (“Control”) or subjected to a moderate drought ($n = 3$). *, significant difference within the species on a given date.

Date and parameter	*Quercus robur*		*Quercus petraea*	
	Control	Drought	Control	Drought
Leaf biomass (g_{DM})				
June 12	0.61 ± 0.05	0.57 ± 0.05	0.59 ± 0.10	0.51 ± 0.09
August 8	0.76 ± 0.05	0.60 ± 0.02*	0.72 ± 0.09	0.62 ± 0.04
August 20	0.71 ± 0.05	0.66 ± 0.03	0.80 ± 0.03	0.52 ± 0.04*
August 30	0.86 ± 0.14	0.65 ± 0.07	0.95 ± 0.22	0.55 ± 0.07
LMA (g_{DM} m^{-2})				
June 12	62 ± 1	61 ± 3	58 ± 2	59 ± 1
August 8	61 ± 1	63 ± 2	61 ± 1	60 ± 2
August 20	61 ± 1	61 ± 2	62 ± 1	64 ± 2
August 30	63 ± 2	65 ± 2	61 ± 2	62 ± 2
Fine-root biomass (g_{DM})				
June 12	0.39 ± 0.04	0.42 ± 0.04	0.37 ± 0.06	0.43 ± 0.08
August 8	0.51 ± 0.03	0.52 ± 0.04	0.56 ± 0.05	0.52 ± 0.07
August 20	0.62 ± 0.06	0.52 ± 0.03	0.52 ± 0.04	0.55 ± 0.01
August 30	0.60 ± 0.05	0.63 ± 0.11	0.56 ± 0.06	0.66 ± 0.13
Rooting depth (cm)				
June 12	15 ± 2	18 ± 2	16 ± 2	17 ± 2
August 8	34 ± 3	32 ± 5	34 ± 5	37 ± 3
August 20	39 ± 3	43 ± 3	44 ± 2	41 ± 3
August 30	46 ± 5	43 ± 6	50 ± 6	45 ± 3

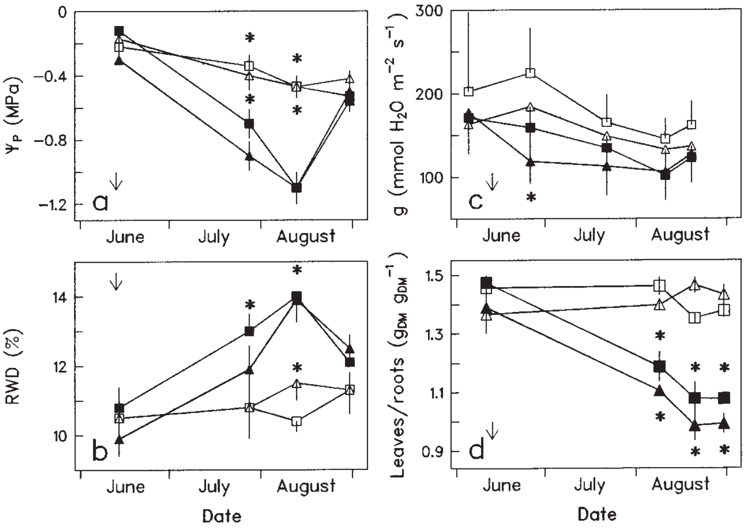

Figure 2. Water and biomass relations in seedlings of *Quercus petraea* (triangles) and *Q. robur* (squares) which were adequately supplied with water (open symbols) or subjected to a moderate drought (solid symbols). a) Predawn leaf water potential (Ψ_P). b) Relative water deficit of the leaves (*RWD*). c) Stomatal conductance (*g*). d) Biomass ratio of leaves to fine roots. The arrow indicates the onset of the drought. *, significant difference between treatments within the species on a given date.

Table II. Portion of plants with a second flush ($n = 60$), number of buds per plant ($n = 9$), and the deviation of the foliar ^{13}C fraction from a standard ($\delta^{13}C$; $n = 13$ in *Q. robur*, $n = 16$ in *Q. petraea*) in seedlings of *Quercus robur* and *Q. petraea*, which were adequately supplied with water ("Control") or subjected to a moderate drought.

Parameter	*Quercus robur*		*Quercus petraea*	
	Control	Drought	Control	Drought
Portion of plants with a second flush (%)	18.3	13.3	23.3	18.3
Number of buds per plant	10.3 ± 0.6	9.3 ± 0.8	11.2 ± 0.9	9.4 ± 1.0
$\delta^{13}C$ (‰)	–28.46 ± 0.28	–28.42 ± 0.24	–28.33 ± 0.20	–28.16 ± 0.17

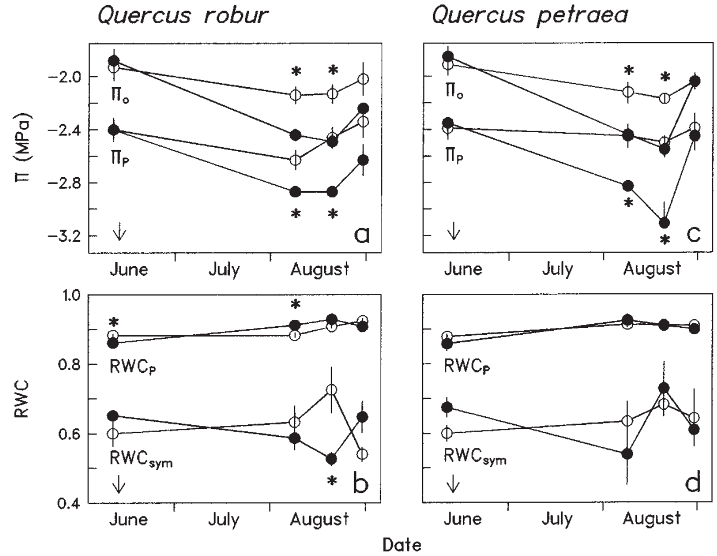

Figure 3. Water relation parameters of adequately watered (open circles) and drought-stressed (solid circles) seedlings of *Quercus robur* and *Q. petraea* as derived from pressure-volume analyses. a) and c) Osmotic pressure (Π) at maximum turgor (Π_o) and at the turgor-loss point (Π_P). b) and d) Relative water content (*RWC*) of the leaf tissue at the turgor-loss point (RWC_P), and of the symplasm at water saturation (RWC_{sym}). The arrow indicates the onset of the drought. *, significant difference between treatments within the species on a given date.

below the threshold of turgor loss. This is rather improbable. Probably, the discrepancy between the foliar *RWD* and the RWD_P values results from the differences in the methodical approach. The rehydration procedure of the leaf discs may have resulted in an oversaturation due to an infiltration of intercellular space at the margin of the discs, although such an infiltration was not detected by visual inspection. An oversaturation of the tissue results in an underestimation of the relative water content and, thus, in an overestimation of *RWD*. Therefore, the results of the different methods are not immediately compatible. However, the foliar *RWD* data can be used for a rough assessment of effects exerted by the drought treatment.

The mean values of ε_{max} were between 13 and 23 MPa in the sessile oak, and between 13 and 20 MPa in the pedunculate oak, and did not exhibit a distinct tendency to decrease or increase with time (data not shown). In only few instances (sessile oak, early June and late August; pedunculate oak, early August) was the ε_{max} of the drought-stressed seedlings significantly higher than in the control plants.

In *figure 4*, the osmotic pressure of the seedlings computed from the *pV* curves is plotted against the respective Ψ_P values that were measured at maximum four days after the determination of Π. In the drought-stressed

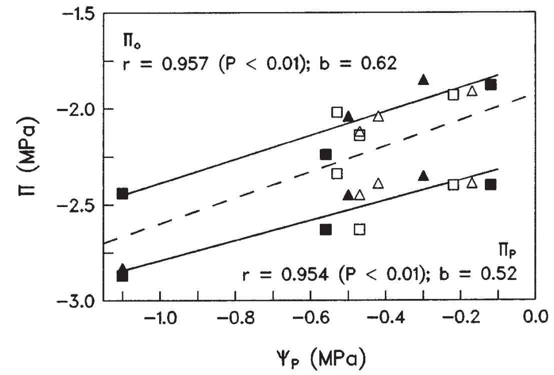

Figure 4. Osmotic pressure (Π) at maximum turgor (Π_o; above the broken line) and at the point of turgor loss (Π_P; below the broken line) plotted against the predawn leaf water potential (Ψ_P). The data are derived from seedlings of *Quercus petraea* (triangles) and *Q. robur* (squares) which were adequately supplied with water (open symbols) or subjected to a moderate drought (solid symbols). The correlation coefficients (*r*) and the slopes (*b*) were computed from combined data of both species' drought-stressed seedlings.

seedlings, Π_o as well as Π_P decreased with decreasing Ψ_P. The slope *b* indicates the degree of osmotic adjustment (cf. [5]). Calculated from the combined data of both species' drought-stressed seedlings, osmotic adjustment was 0.62 MPa(Π) $(\text{MPa}(\Psi))^{-1}$ with regard to Π_o, and 0.52 MPa(Π) $(\text{MPa}(\Psi))^{-1}$ with regard to Π_P.

The mean $\delta^{13}C$ ratios did not reveal significant differences between species or treatments (*table II*). The mean foliar N concentrations were 20 – 22 mg g_{DM}^{-1}, and significant differences did not occur between treatments. They were within the "normal range" given for seedlings of the investigated species [26].

4. DISCUSSION

The drought applied during the experiment was sufficiently intense to reduce Ψ_P and to increase *RWD*. However, *g* was only weakly affected as were growth and biomass of the separate plant compartments. In contrast, young sessile oaks, which had been subjected to a severe drought, reacted with a significant decrease not only in *g*, but also in the biomass of leaves and shoot axes, in the number of buds, and in the fraction of plants which produced a second flush [24]. Thus, in accordance with the intention of the experiment, the drought applied in the present study can be assessed as moderate. Other morpho-anatomical features that could provide acclimation to drought stress are an increase in *LMA*, and in tissue elasticity, detectable by a decrease in ε_{max}. Drought imposed during leaf ontogeny may result in an alteration in *LMA*. An elevation in *LMA* is sometimes associated with increased water-use efficiency [1]. Normally, in mid-June, when the drought treatment of the present study was started, oak leaves are fully expanded, but the leaf thickness generally increases until late summer. This was observed, at least in tendency, in the present study (*table I*) and was also found, to an even more pronounced extent, in previous investigations. Thus, an alteration in *LMA* had to be taken into account as a possible morpho-anatomical response to drought. A higher tissue elasticity allows the plant to maintain turgor at lower leaf water potentials [15]. However, *LMA* and ε_{max} were neither decreased by a moderate drought (this investigation) nor, in the case of sessile oak, by severe drought stress [24]. Nor was a uniform response of ε_{max} to drought stress found in North American oak species [1]. The long-term water-use efficiency of pedunculate and sessile oaks also remained unchanged by a moderate drought as was indicated by the lack of significant differences in the $\delta^{13}C$ ratios between treatments (*table II*). The same result was obtained after young *Quercus petraea* were subjected to severe drought stress; whereas in drought-stressed *Q. pubescens*, long-term water-use efficiency was even decreased, as was obvious through lower $\delta^{13}C$ ratios [24].

The decrease of Π in the drought-stressed seedlings (*figures 3a, c*) can be interpreted as osmotic adjustment in the sense of Hinckley et al. (1980) [11]. This is justified since the *RWC* of the drought-stressed seedlings as determined by *pV* analysis did not decrease in most instances of the reduction in Π (*figures 3b, d*). An exception is the significant reduction in the RWC_{sym} of drought-stressed pedunculate oak seedlings in mid-August (*figure 3b*). In this case, a calculation of the expected change in Π_o based on the reduction in RWC_{sym} showed that the decrease in symplasmic water content at saturation can account for the decrease in osmotic pressure.

The change in Π_o with respect to the change in Ψ_P (0.62 MPa MPa^{-1}; *figure 4*) was larger than in the sessile oak seedlings investigated in an earlier study (0.32 – 0.45 MPa MPa^{-1}; [5]). This probably is due to the different method of the determination of Π_o, which was not derived from *pV* analysis, but measured in sap pressed out of the leaves. In this process, the solute concentration of the cytoplasm is diluted by apoplasmic water [e.g. 20]. Since the volume of apoplasmic water within the tissue is regarded to be constant over the entire range of positive turgor (e.g. [20]), its fraction in total leaf water must increase with decreasing leaf water content and, thus, decreasing Ψ. Therefore, the overestimation of Π_o (due to measuring less negative values) increases with decreasing Ψ, resulting in a smaller value of the slope when Π_o is plotted against Ψ.

The degree of osmotic adjustment – calculated as the difference between the osmotic pressure of control and drought-stressed seedlings – was similar in both species and was, on average, 0.30 – 0.38 MPa for Π_o, and 0.24 – 0.61 MPa for Π_P. These values are very similar to those obtained from mesic to xeric North American oak species (0.25 – 0.60 MPa in *Quercus alba, Q. macrocarpa* and *Q. stellata* [21]), and fit into the usual range of the degree of osmotic adjustment, which is generally less than 1.0 MPa [15]. In North American oaks, osmotic adjustment is greater in species in the more arid regions [1]; whereas it seems to be marginal or even lacking in the less drought-resistant *Q. rubra* [1, 12]. Within the range of its occurrence, osmotic adjustment can provide an effective physiological means of dehydration tolerance by maintaining turgor. This allows the continuation of root extension, leaf expansion and photosynthesis [18]. Accordingly, in the present study, leaf conductance remained largely unaffected. Generally, osmotic adjustment persists only for a few days after the cessation of the drought stress [16]. In our investigation, osmotic adjustment ceased at the end of August, when Π of the drought-stressed seedlings raised to the level of the control plants (*figures 3a, c*). The increase in Π was accompanied by an increase in Ψ_P and a decrease in *RWD* (*figures 2a, b*), indicating a recovery from drought. This was obviously due to the uninterrupted growth of the drought-stressed plants' roots which had, at the end of August, extended to 40 – 50 cm of soil depth, where *SWC* was as high as 10 – 15%.

Although the biomass of leaves and fine roots only was moderately influenced, the dry matter-related ratio of leaves to roots was significantly diminished in the drought-stressed seedlings. In addition to other morphological responses, a significant decrease in the leaf-root ratio also was found in young sessile oaks subjected to a severe drought stress, due to an even larger impact of drought on leaf and fine root biomass; whereas physiological reactions such as osmotic adjustment were lacking [24]. Thus, in the Central-European oak species, morphological reactions seem to gain importance with increasing degree of the drought stress – at the expense of physiological responses. This can be explained by the demand of carbon for performing the acclimation to the stress. In oaks, the increase in the concentration of solutes needed for osmotic adjustment obviously is achieved by a shift in carbohydrate formation from starch and sucrose to soluble glucose and fructose [9]. With increasing drought stress, the carbon gain is lowered by the reduction in *g*. Carbon is then preferentially channelled into the formation of roots. In the genus *Quercus*, a deep root system helps to avoid dehydration and to tolerate a decreased water supply [7]. Root growth is sustained at the expense of shoot growth and physiological acclimation of the leaves. The observation that osmotic adjustment in the leaves of drought-stressed pedunculate oaks only occurs at increased, but not at ambient CO_2 concentrations [28], is in accordance with the hypothesized mechanism.

In conclusion, alterations in biomass compartmentation, resulting in a decreased leaf/fine-root ratio, seem to be the most important processes of acclimation to drought stress in both Central-European oak species. At the leaf level, osmotic adjustment occurs as a physiological acclimation process to achieve dehydration tolerance. However, it only occurs under a moderate drought, but not under severe drought stress.

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