ORIGINAL PAPER

Acclimatation of three co-occurring tree species to water stress and their role as site indicators in mixed pine-oak forests in the Sierra Madre Oriental, Mexico

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Abstract Water availability and salt excess are limiting factors in Mexican mixed pine-oak forest. In order to characterise the acclimatation of native species to these stresses, leaf water (Ψ_w) and osmotic potentials (Ψ_s) of *Juniperus flaccida, Pinus pseudostrobus* and *Quercus canbyi* were measured under natural drought and non-drought conditions under two different aspects in the Sierra Madre Oriental. Factorial ANOVA revealed significant differences in Ψ_w and Ψ_s between two aspects, species and sampling dates. In general, all species showed high predawn and low midday values that declined progressively with increasing drought and soil–water loss. Seasonal and diurnal fluctuation of Ψ_w and Ψ_s were higher for *J. flaccida* and *Q. canbyi* than for *P. pseudostrobus*. Leaf Ψ_w and Ψ_s were mainly correlated with soil water content, while Ψ_s of *P. pseudostrobus* were hardly correlated with environmental variables. Thus, species have different strategies to withstand drought. *P. pseudostrobus* was identified as a species with isohydric water status regulation, while *J. flaccida* and *Q. canbyi* presented water potential patterns typical for anisohydric species. The type of water status regulation may be a critical factor for plant survival and mortality in the context of climate change. Nevertheless, for precise conclusions about the advantages and disadvantages of each type, further long-term investigations are required.

Communicated by A. Merino.

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Introduction

Mixed pine-oak forests are widely distributed in the higher altitudes of the Eastern Sierra Madre, including ecologically and economically important tree species such as *P. pseudostrobus* (Rzedowski 1986). These forests are exposed to extreme climatic conditions of high temperatures and low precipitation distributed irregularly through the year. Under field conditions, water stress or rather soil water availability is in general one of the major limiting factors in plant growth and affects most physiological processes in these ecosystems (Kozlowski et al. 1991; Kramer 1983; Kramer and Boyer 1995; Mitlöhner 1998; González et al. 2003). Moreover, water scarcity and high potential evaporation lead to salt excess in the vegetation's rhizospheres, another serious and significant environmental problem that plants have to face in arid and semi-arid environments (Szabolcs 1994; Mitloehner and Koepp 2007). So far, water scarcity, soil salinity as well as climate induced salinity can be considered natural processes, and the native vegetation is adapted to these environmental conditions (Mitloehner and Koepp 2007).

Even so, climatic change makes conditions for plant growth even more acute. The response of forests to these changes is uncertain and has the potential to greatly alter the distribution and productivity of tree species (Pastor and Post 1988; Kramer 1983; Tschaplinski et al. 1998; Rötzer et al. 2005; Ricker et al. 2007). Inappropriate land-use contributes further to the acceleration of forest degradation and deforestation in great parts of the mountain chain Sierra Madre Oriental due to anthropogenic pressures (Domínguez and Návar 2000; Cantú and González 2002; González Tagle et al. 2005). Especially inadequate irrigation and the clearing of deep-rooted native vegetation cause secondary salinisation in dryland areas worsening and/or impeding natural regeneration and reforestation (Szabolcs 1994; Munns 2002; Mitloehner and Koepp 2007). In Chiapas, southern Mexico, the thinning of the canopy in tropical highland forests by human activities increased solar radiation and exposed seedlings and juveniles to more extreme temperatures at the forest floor level, thus decreasing soil moisture availability (Ramírez-Marcial et al. 1996, 2001). The response of forest ecosystems to such climatic and anthropogenic stresses will depend in great part on the drought (Tschaplinski et al. 1998) and salt tolerance of the individual species (Mitloehner and Koepp 2007).

Hence, understanding water uptake patterns, the physiological response of species to water stress, salt excess and their tolerance scope under severe environmental stress is required to explain differences among species in survival and distribution. It also allows determining the relative suitability of species for ecological restoration of degraded lands (Jurado et al. 1998; Ramírez-Marcial et al. 2001; González et al. 2003; Gebrekirstos et al. 2006). Elsewhere, previous works on plant water relations and forest restoration (Gebre et al. 1998; Jurado et al. 1998; Vertovec et al. 2001; González et al. 2003; Gebrekirstos et al. 2006, Mitloehner and Koepp 2007) emphasised the need to investigate water relations of native species and their physiological responses to changes in resource availability. There are few studies in the field of forest ecology and tree ecophysiology from the Sierra Madre Oriental including leaf water and leaf osmotic potential measurement on native tree species.

Plant internal water potential is a consequence of the soil–plant atmospheric continuum and consists of the tension caused by the water pressure deficit of the atmosphere, regulative processes of leaves, general flow regulation resistances and the soil water potential (Philip 1966; Duhme and Richter 1977; Kozlowski et al. 1991; Kramer and Boyer 1995; Donovan et al. 2003). It is a dependable measure of plant and soil water status and quickly measured directly in the field, a great advantage especially for plant comparison (Slatyer 1967; Sala et al. 1981; Pallardy et al. 1991; Kramer and Boyer 1995; Mitlöhner 1998; Vertovec et al. 2001; Donovan et al. 2003). The water balance of a plant becomes negative when the uptake of water is insufficient to meet the requirements of transpiration (Sellin 1998) and plants begin to suffer water stress. Declining water potentials indicate water stress, which can be divided into static stress and dynamic stress. The first one is caused by low water availability in the soil, and the second one results from the resistance of water flow through the plant due to transpirational water loss from foliage, so plant water potentials decline (Tyree and Ewers 1991). The dynamic of leaf water potentials at a certain daytime (Ψ_{wmd}, in our case at midday) can be treated as the sum of predawn water potential (Ψ_{wpd}, base water potential) and diurnal depression from the base level (Ψ_d, depression potential): $\Psi_{wmd} = \Psi_{wpd} + \Psi_d$ (Hinckley and Ritchie 1973; Lassoie et al. 1983; Pothier et al. 1989; Sellin 1998). Ψ_{wpd}, measured before dawn, is determined by soil water availability and should express the static water stress; Ψ_d, in comparison, is influenced by atmospheric conditions and plant hydraulic capacity indicating the level of dynamic water stress (Sellin 1998).

Species can be partitioned into two categories across the continuum of stomatal regulation of water status, named isohydric and anisohydric regulation (Tardieu 1993; Tardieu and Simonneau 1998; McDowell et al. 2008). Isohydric plants maintain a relatively constant midday water potential (Ψ_{wmd}) regardless of drought conditions due to reduced stomatal conductance, while anisohydric species

allow midday values to decline as soil water potential decreases with drought (McDowell et al. 2008). Hence, anisohydric species maintain higher stomatal conductance for a given Ψ_{wmd} than isohydric plants, effectively allowing Ψ_{wmd} to decline with decreasing soil water availability (McDowell et al. 2008). By means of information about leaf water potentials, native tree species can be assigned to one of these two categories.

The osmotic potential (Ψ_s), in contrast, indicates the prime adaptation of plants towards spatially and periodically altered soil solute concentration and soil water deficit (Kramer and Boyer 1995; Mitloehner and Koepp 2007). Dehydration-tolerant species (according to the terminology of Kramer (1980)) reduced Ψ_s and/or accumulate solutes (osmotic adjustment; Morgan 1980) by incorporating ionic osmotica (i.e. NaCl among other salts from the soil) as well as by processing non-ionic osmotica (i.e. other plant-born organic compounds such as sucrose) into and within their cells (Mitloehner and Koepp 2007) reflecting plant adjustment to water shortage at the cell level. In this way, a plants' capacity to take up water from dry soils is enhanced and recovery after drought is facilitated (Gebre et al. 1998; Tschaplinski et al. 1998; Nguyen-Queyrens et al. 2002). Osmotic and pressure-driven water flow into plant roots occur simultaneously (Kramer and Boyer 1995). Furthermore, an osmotic (or concentration) gradient in the soil–plant continuum (Pressarakli 1991) and within the plant between its cells are a basic condition for plant life (Mitloehner and Koepp 2007).

Osmotic adjustment can be estimated by the difference between Ψ_s of well-hydrated and dehydrated plants at similar relative water content (Gebre et al. 1998). It is difficult to determine osmotic adjustment under ambient field conditions due to the need to sample well-hydrated and dehydrated plants during the same period. Therefore, studies of osmotic adjustment have been based rather on comparison of seasonal variation in Ψ_s due to difference in precipitation within a season or between seasons (Bahari et al. 1985; Abrams 1990; Gebre et al. 1998).

In general, a species' capacity of acclimatation to environmental site conditions is regarded as the basic requirement for a plants' 'suitability as an indicator' (Mitlöhner 1997). During the last two decades, the Mexican Government has made an effort to restore degraded forest areas, mainly using fast growing pines or introduced species. However, the conservation-oriented interest in native broad-leaved species is increasing lately, and information on their biology and silvics is urgently needed (Quintana-Ascencio et al. 2004).

Hence, the specific objectives of our study were to (1) compare three dominant tree species of mixed pine-oak forests in the Sierra Madre Oriental with respect to their acclimatation to water deficit and their salt tolerance scope; (2) compare the effect of two different sites on the water status of the species and (3) identify their strategies to withstand periods of drought.

Methods

Site description

This research was carried out at the Experimental Forest Research Station of the Faculty of Forest Science, Universidad Autónoma de Nuevo León (UANL) in the Sierra Madre Oriental (24°42'N; 99°51'W), located 15 km southeast of Iturbide in the state of Nuevo Leon, Mexico. The Experimental Forest Research Station extends over an area of about 1,035 ha and due to its protection status received 20 years ago, it provides good conditions for the study of undisturbed ecophysiological processes. Two sites in different pine-oak forests were selected for the study: (1) a major closed stand on a North-facing aspect (Plot-N) at 356° and with 26° inclination and (2) an open fragmented stand on a South-facing aspect (Plot-S) at 135° and with 21° inclination. Both sites are located from each other in a distance of about 200 m on the same mountain ridge at an elevation of approximate 1,600 m. The mean annual air temperature is 13.9°C and the average annual precipitation is 639 mm, which is concentrated from May to October. The dominant soils are rocky and comprise upper cretaceous lutite or siltstone (Cantú and González 2002). Some physical and chemical properties of the soil at profile depths of 0–10 and 20–30 cm are shown in Table 1. Remarkable is the higher electric conductivity (μScm^{-1}) at soil depth 0–10 cm compared to layer 20–30 cm and the slightly higher values at the northern in comparison to the southern aspect.

Sampling procedures and water potential measurement

In each sampling plot, five juvenile individuals (replications) of each tree species were randomly selected within a 500 m^2 circle from the understory for repetitive measurements of plant water potentials. The plant species were *Juniperus flaccida* Schltdl. (Cupressaceae), *P. pseudostrobus* Lindl. (Pinaceae) and *Q. canbyi* Trel. (Fagaceae). Sampling trees varied in mean diameter at breast height between 2.05 ± 0.33 and 3.07 ± 0.55 cm, and in mean height between 2.70 ± 0.32 and 3.85 ± 0.44 m, depending on the species. The leaf water potentials (Ψ_w, MPa) were determined twice a month from January until August 2006, and leaf osmotic potentials (Ψ_s, MPa) were measured once a month during the same period. Plant water potentials were measured with a Scholander pressure chamber (Model 3005, Soil Moisture Equipment Corp.,

Table 1 Some physical and chemical soil properties at the two study sites (North and South aspect)

Sampling site	Soil profile depths (cm)	Bulk density (Mg m^{-3})	Sand[a] %	Silt[b] %	Clay[c] %	pH	EC (µScm^{-1})	OM (%)
Plot-N	0–10	0.69	25.9	47.6	26.6	7.6	159.2	11.4
Plot-N	20–30	ND*	12.6	39.3	48.1	7.7	75.9	2.7
Plot-S	0–10	0.85	30.0	41.6	26.4	7.6	141.8	11.3
Plot-S	20–30	ND*	39.6	43.8	16.6	7.7	72.1	2.5

Each value is the mean of five replications

EC electric conductivity, *OM* organic material

* *ND* no data available

[a] Soil particle size: 0.063–2.0 mm

[b] Soil particle size: 0.002–0.063 mm

[c] Soil particle size: <0.002 mm

Santa Barbara, CA, USA) (Scholander et al. 1965) immediately after cutting the leaves or terminal twigs of each sample tree and monitored twice a day, at 6:00 h (Ψ_{wpd}) and 12:00 h (Ψ_{wmd}), which is a widely used method (Sellin 1996). For safety reasons, and per operating instructions, the lowest limit of the pressure chamber was −7.3 MPa.

For determination of the osmotic potential (Ψ_s, MPa), plant samples were taken with a hole puncher from leaves of *Q. canbyi*. In the case of *J. flaccida* and *P. pseudostrobus,* parts of photosynthetic twigs and pine needles were cut, respectively. Plant samples were collected at 6:00 h (Ψ_{spd}) and 12:00 h (Ψ_{smd}) and immediately saved in small tubes and shock-frozen in liquid nitrogen to conserve them for later laboratorial analysis. Once in the laboratory, the osmotic potential of leaf tissues was assessed with a thermocouple psychrometer using three Wescor C-52 sample chambers and an HR 33T microvoltmeter (Wescor Inc., Logan, UT) calibrated at 25°C and standardised with 50 µl of known NaCl molal solutions (Wilson et al. 1979).

Environmental data

Simultaneously, meteorological data of air temperature (°C) and relative humidity (%) was registered in each plot on an hourly basis by using a thermo-hygrometer (HOBO® Pro Series Weatherproof Data Loggers, Forestry Suppliers, USA) that was located between the sampling trees directly in the sampling site 1.5 m above ground in the understory. Likewise, daily precipitation (mm) was obtained from self-emptying rain gauges (Onset® Data Logging Rain Gauge, Forestry Suppliers, USA) installed 1.5 m above ground at an open place close to each plot. Vapour pressure deficit (VPD) was calculated on the basis of air temperature and relative air humidity (RH). On each sampling date, soil cores at different depths of 0–10, 20–30, 40–50, and 60–70 cm (five replications each) were collected using a soil sampling tube (Soil Moisture Equipment Corp.) for

determining the gravimetric soil water content beneath the tree canopy in each plot. The soil water content was finally determined and expressed in per cent by weight (%).

Statistical analysis

The desire was to test the null hypothesis of no effect of tree species, site and sampling date on the water potentials (leaf Ψ_w and leaf Ψ_s each at predawn and midday) of common species in pine-oak forests in the Sierra Madre Oriental.

Differences between the two aspects (N and S), the tree species and the sampling dates (January to August 2006) were examined with three-way analyses of variance (three-way ANOVA), while aspect and species were considered as between-subject factors and sampling date (sd) as within-subject factor (Zar 1999). The three-way ANOVA was conducted for predawn and midday data separately. Assumption of normality and homogeneity of variance was tested before ANOVA and found as true.

Differences between meteorological conditions at each aspect were compared by one-way ANOVA after proofing true the assumption of normality and homogeneity of variance (Zar 1999; Crawley 2007).

The significance of seasonal differences (ΔSD) in Ψ_{spd} and Ψ_{smd} was tested with the Wilcoxon's rank sum test (Crawley 2007), comparing a representative dry (Apr-5) and moist (Aug-16/17) sampling date.

Correlation coefficients between water and osmotic potentials (Ψ_{wpd}, Ψ_{wmd}, Ψ_{spd} and Ψ_{smd}) and environmental variables (monthly sum of precipitation, daily mean soil water content, daily mean air temperature, daily mean RH and daily mean VPD, each recorded on the sampling date) were quantified by the Spearman's rank order correlation analyses, since the null hypothesis of normality was rejected at $P < 0.05$. For these analyses, real data of each species, summarizing both plots, were considered on a seasonal base (Zar 1999; Crawley 2007).

On a seasonal basis, regression analysis was performed between averaged soil water content and predawn leaf water potentials (Ψ_{wpd}) considering mean values of each sampling date (Crawley 2007).

All statistical methods were applied according to the R project for statistical computing (free statistic software, R version 2.8.1, The R Foundation for Statistical Computing 2008).

Results

Environmental conditions during the experimental period

Trends of monthly mean air temperatures, relative air humidity, vapour pressure deficit, total precipitation and soil water content are illustrated in Fig. 1. Air temperature increased until April and decreased slightly until the end of the study period. Relative air humidity increased notably from April to August and vapour pressure deficit increased until April but decreased noticeably during the rest of the study period. The sum of precipitation increased in the course of the study. Concerning the total rainfall at the northern aspect, due to technical problems, the monthly rainfall in July had to be estimated by interpolation using registered precipitation of June and August. The comparison of the two sites revealed no statistical differences in meteorological variables (one-way ANOVA: $P > 0.18$).

Averaged soil moisture content decreased along the growing season at both sites, but increased again after the onset of the rainy season in the end of May, especially in the upper soil horizons (Fig. 1). The results of the three-way ANOVA indicated that 'aspect' had the strongest influence on soil water content followed by 'sampling date' as shown by the proportion of explained variance (Table 2). In general, soil moisture content was significantly higher at the northern aspect than at the southern. In comparison, soil depths had no significant influence on soil water content. The ANOVAs demonstrated some significant interactions of factors (Table 2 and Fig. 1). Thus, soil moisture content at different soil depths is influenced by the season interpreting the strongest interaction 'depths × sampling date'. The explained variation by the ANOVA model was not moderate (Table 2).

Variation in leaf water potentials

The results of the three-way ANOVA indicated that the 'sampling date' had the strongest influence on leaf water potential patterns followed by the between-factors 'species' and 'aspect'; see proportion of explained variance in Table 2. Both variables (Ψ_{wpd} and Ψ_{wmd}) showed strong

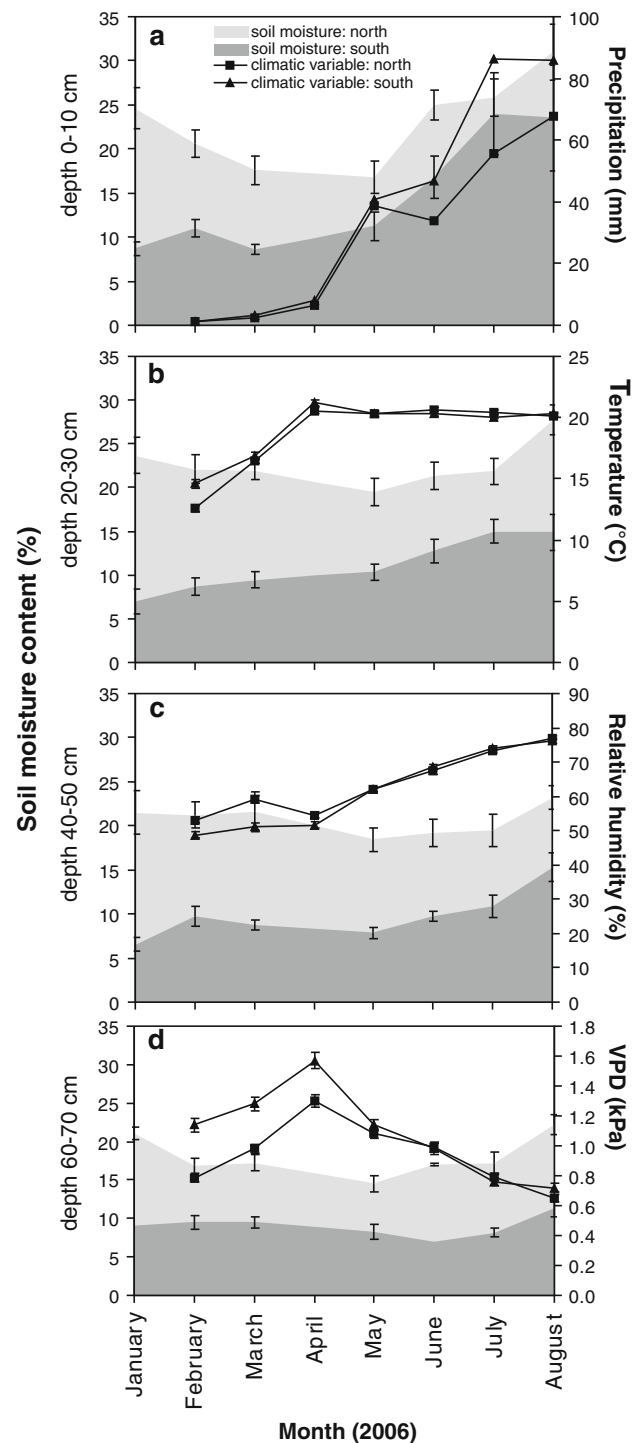**Fig. 1** Seasonal variation in mean air temperature (°C), relative humidity (%), vapour pressure deficit (VPD; kPa), actual precipitation (mm) and mean soil moisture (%) at four soil profile depths ($n = 5$) during the study period from February until August 2006; bars represent standard errors

interactions of all factors (as demonstrated by the ANO-VAs; Table 2 and Fig. 2), reflecting that the influence of 'sampling date' was highly significant on the species

Table 2 Results of the three-way ANOVA with species (between-subject), aspect (between-subject) and sampling date (within-subject) as factors, degrees of freedom (df) and coefficient of determination (r^2)

| Source of variation | df | Ψ_{wpd} | | Ψ_{wmd} | | df | Ψ_{spd} | | Ψ_{smd} | | df | Soil moisture | |
		F	SS_x/SST_c	F	SS_x/SST_c		F	SS_x/SST_c	F	SS_x/SST_c		F	SS_x/SST_c
Species[a]	2	137.9	13.8***	76.7	14.7***	2	9.3	6.5***	11.3	7.3***	2	1.9	1.8[NS]
Aspect	1	210.4	10.5***	164.1	15.7***	1	14.9	5.2***	3.0	1.0[NS]	1	86.7	38.3*
Aspect*Species	2	6.8	0.7**	6.9	1.3**	2	2.3	1.6[NS]	2.9	1.9[NS]	2	9.1	0.9***
SD[b]	11	144.3	38.4***	77.8	30.7***	6	14.9	22.2***	9.9	17.2***	10	4.5	13.9**
Species*SD	22	22.7	12.1***	16.9	13.3***	12	3.4	10.2***	2.1	7.3*	20	6.1	5.9***
Aspect*SD	11	39.8	10.6***	19.4	7.7***	6	4.0	5.9***	4.8	8.4***	10	6.3	3.3***
Aspect*Species*SD	22	12.0	6.4***	6.1	4.8***	12	1.5	4.3[NS]	2.1	7.4*	20	0.3	0.9[NS]
Total	359					209							
ANOVA r^2 (adj.)			0.913		0.871			0.483		0.393			0.555

The F-value, proportion of the explained variance (SS_x/SST_c) and the level of significance (*NS*, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) for each factor and the interaction are indicated

[a] In the case of soil moisture, the factor 'species' is replaced by 'soil depth'; [b] Sampling date

J. flaccida and *Q. canbyi* but less on *P. pseudostrobus*. Or, that the influence of 'sampling date' was highly significant on the water potentials measured at Plot-S and less at Plot-N (Table 2 and Fig. 2). The explained variation by the ANOVA model was high (mean 0.89, range 0.87–0.91).

Fig. 2 Seasonal variation in predawn (Ψ_{wpd}) and midday (Ψ_{wmd}) leaf water potentials as well as the difference between midday and predawn ($\Delta\Psi_w$) leaf water potentials in three tree species at the North (Plot-N) and South aspect (Plot-S); values are means ($n = 5$), bars represent standard error
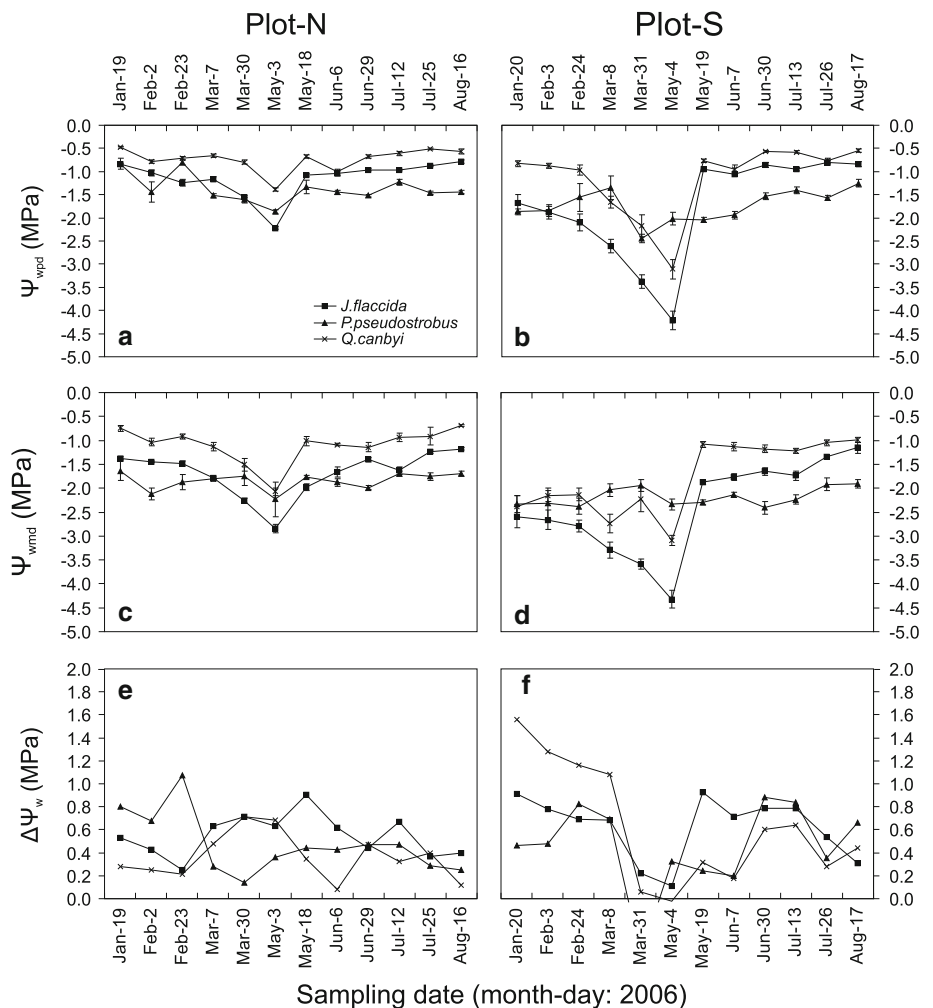
In general, *Q. canbyi* had the highest predawn and midday leaf water potentials at the northern aspect throughout the study period (Fig. 2a, c). At the southern site, in comparison, *P. pseudostrobus* maintained highest values during the dry period from March to May, but was topped by *Q. canbyi* and *J. flaccida* after the onset of precipitation (Fig. 2b, d). *J. flaccida* showed most negative values in both study sites and highest seasonal variation.

Furthermore, water stress appeared earlier in Plot-S than in Plot-N. In Plot-S for instance, Ψ_{wpd} began to decline drastically in early March and in Plot-N towards the end of March. Midday leaf water potentials were more negative but with similar tendencies as observed in predawn potentials (Fig. 2c, d). Moreover, tree species suffered less water stress in Plot-N (Fig. 2e) than in Plot-S (Fig. 2f), where $\Delta\Psi_w$ were close to zero for all species on Mar-31 and May-4.

Variation in leaf osmotic potentials

Leaf osmotic potentials were mainly influenced by 'sampling date' and further by 'species' and 'aspect' as the results of the three-way ANOVA indicated (Table 2). Both variables (Ψ_{spd} and Ψ_{smd}) showed some significant interactions of factors (as demonstrated by the ANOVAs; Table 2 and Fig. 3). For instance, the influence of 'sampling date' was highly significant on Ψ_{spd} of the species *J. flaccida* and *Q. canbyi* but less of *P. pseudostrobus,* and in the case of Ψ_{smd} it was highly significant on the water potentials measured at Plot-S and less at Plot-N (Table 2 and Fig. 2). The explained variation by the ANOVA model was not as high (mean 0.44, range 0.39–0.48) as for leaf water potentials.

In general, midday osmotic potentials were more negative (Fig. 3c, d). Concerning the site comparison, osmotic potentials were much lower at the southern aspect (Fig. 3b, d) than at the northern (Fig. 3a, c). Compared to leaf water potentials, osmotic potentials differed less between species and in time. In Plot-S (Fig. 3d), where differences between species were a little greater, *P. pseudostrobus* maintained generally higher osmotic potentials than *Q. canbyi* and *J. flaccida*. Nevertheless, with increasing water supply at the end of the study period (Fig. 1), the osmotic potentials of the three species draw near (Fig. 3).

Fig. 3 Seasonal variation in predawn (Ψ_{spd}) and midday (Ψ_{smd}) osmotic potential in three tree species at the North (Plot-N) and South aspect (Plot-S); values are means ($n = 5$), bars represent standard error
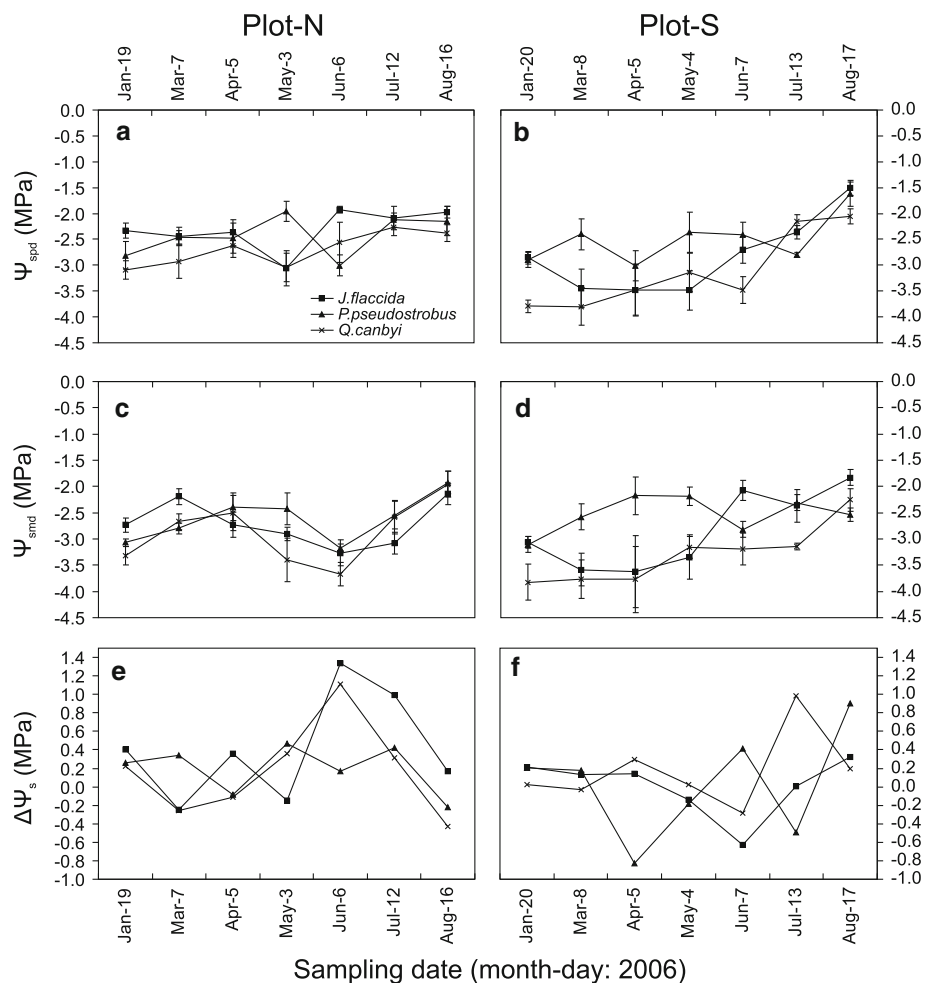
Concerning the $\Delta\Psi_s$, it is difficult to see a clear tendency, especially for *P. pseudostrobus* (Fig. 3e, f) In the case of *J. flaccida* and *Q. canbyi*, $\Delta\Psi_s$ had wide ranges during the moist and small ranges during the dry period (Apr-5) in Plot-N (Fig. 3e). In Plot-S in comparison, *Q. canbyi* and *J. flaccida* had relatively wide $\Delta\Psi_s$ during the dry period (Fig. 3f). Here, the major decrease in $\Delta\Psi_s$ was observed later (Jun-7) recovering wider ranges again in August.

Seasonal differences (ΔSD) in osmotic potentials (Ψ_{spd} and Ψ_{smd}) between a representative dry (Apr-5) and moist (Aug-16/17) sampling date were significant for all species concerning Ψ_{spd} ($P < 0.01$), while Ψ_{smd} were significantly different only for *J. flaccida* (ΔSD = 1.19 MPa; $P < 0.01$) and *Q. canbyi* (ΔSD = 1.03 MPa; $P < 0.05$).

Relationships between plant water potentials and environmental variables

Correlations between environmental variables and predawn water and osmotic potentials (Ψ_{wpd} and Ψ_{spd}) as well as the diurnal depression of both, water and osmotic potentials, are shown in Table 3. In general, highly significant ($P < 0.05$) and positive correlations were found between leaf water potentials (Ψ_{wpd}) and soil water content, whereas correlations were strongest within the first three soil depths. Concerning the meteorological variables, correlations of Ψ_{wpd} were strongest with daily mean relative air humidity (RH) (Table 3) and to a lesser extent with

daily vapour pressure deficit (VPD), monthly precipitation and daily mean air temperature.

Similar tendencies as in water potentials were observed in osmotic potentials (Ψ_{spd}). Nevertheless, osmotic potentials of *P. pseudostrobus* were not correlated with environmental variables (Table 3). *J. flaccida* and *Q. canbyi* in comparison showed significantly strong correlations with soil water content and daily mean relative air humidity ($P < 0.001$).

In the case of the conifers, diurnal depression of leaf water potentials was significantly ($P < 0.05$) correlated with the meteorological variables RH and VPD reflecting mainly the air water status (Table 3). The depression potential of the broad-leaved species *Q. canbyi* in comparison had strong correlations with soil water content, daily mean air temperature and monthly sum of precipitation reflecting rather soil water status (Table 3). Concerning the diurnal depression of leaf osmotic potentials, just one significant correlation with daily mean air temperature was found for *J. flaccida*.

Fig. 4 describes the relationship between soil water content and Ψ_{wpd} for the three tree species. The averaged soil water content in the 0–70 cm soil depth profile explained between ($P < 0.05$) 24% (*P. pseudostrobus*) and 56% (*J. flaccida*) of the variation in Ψ_{wpd} (Table 4). Moreover, it was found that at gravimetric soil water content values above 15%, Ψ_{wpd} values were high and roughly constant; below this threshold value, water potentials declined gradually (Fig. 4).

Table 3 Spearman's correlation coefficient values (*rho*) for predawn potentials (PD) and diurnal depression (DD) of leaf water (observed data of both plots; $n = 2$ aspect × 3 species × 5 replications × 11 SD = 330) and osmotic potential (observed data of both plots; $n = 2$ aspect × 3 species × 5 replications × 6 SD = 180) in relation to mean soil water content at four depths (SWC), daily mean air temperature, daily mean relative humidity (RH) and daily mean vapour pressure deficit (VPD) and monthly sum of precipitation in three tree species (data of the sampling dates were used for the calculation of daily means)

Environmental variable	Water potential at predawn (PD) and diurnal depression (DD)						Osmotic potential at predawn (PD) and diurnal depression (DD)					
	J. flaccida		*P. pseudostrobus*		*Q. canbyi*		*J. flaccida*		*P. pseudostrobus*		*Q. canbyi*	
	PD	DD	PD	DD	PD	DD	PD	DD	PD	DD	PD	DD
SWC: 0–10 cm	**0.79***[***]	0.14[NS]	**0.53***[***]	−0.14[NS]	**0.71***[***]	**0.35***[***]	**0.70***[***]	−0.15[NS]	0.10[NS]	−0.05[NS]	**0.66***[***]	−0.08[NS]
SWC: 20–30 cm	**0.48***[***]	0.17[NS]	**0.44***[***]	0.01[NS]	**0.53***[***]	**0.40***[***]	**0.54***[***]	−0.09[NS]	0.09[NS]	−0.13[NS]	**0.39**[**]	0.14[NS]
SWC: 40–50 cm	**0.40***[***]	0.07[NS]	**0.38***[***]	0.03[NS]	**0.45***[***]	**0.30**[**]	**0.52***[***]	−0.08[NS]	0.06[NS]	−0.10[NS]	**0.34*[*]	0.17[NS]
SWC: 60–70 cm	**0.21*[*]	0.15[NS]	**0.35***[***]	0.08[NS]	**0.25*[*]	**0.24*[*]	**0.50***[***]	−0.20[NS]	0.12[NS]	−0.15[NS]	**0.31*[*]	0.19[NS]
Temperature	**0.25**[**]	0.13[NS]	−0.08[NS]	**0.24*[*]	0.14[NS]	**0.31**[**]	**0.37**[**]	**−0.26*[*]	−0.02[NS]	0.07[NS]	**0.35**[**]	−0.06[NS]
RH	**0.42***[***]	**0.24*[*]	**0.32***[***]	**−0.21*[*]	**0.38***[***]	0.07[NS]	**0.42***[***]	−0.13[NS]	0.24[NS]	−0.09[NS]	**0.50***[***]	−0.11[NS]
VPD	**−0.31***[***]	**−0.22*[*]	**−0.41***[***]	**0.29**[**]	**−0.33***[***]	−0.02[NS]	−0.21[NS]	0.11[NS]	−0.12[NS]	−0.06[NS]	**−0.30*[*]	0.11[NS]
Precipitation	**0.53***[***]	−0.05[NS]	−0.04[NS]	0.03[NS]	**0.30**[**]	**0.24*[*]	0.23[NS]	0.07[NS]	0.20[NS]	−0.01[NS]	**0.35**[**]	−0.14[NS]

Significant correlations are emphasised with bold letters

Due to missing meteorological data in January, the first sampling date was not included in the correlation analysis. Level of significance ($P > 0.05$, NS; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) for each variable
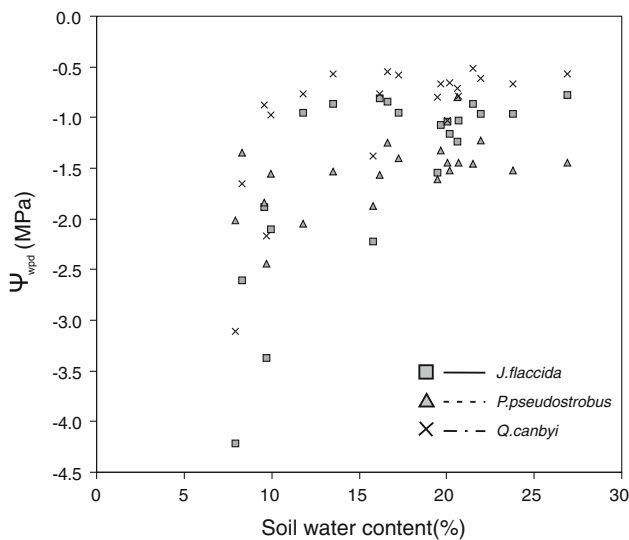
Fig. 4 Predawn (Ψ_{wpd}) leaf water potentials of three native tree species as a function of the averaged gravimetric soil water content in the 0–70 cm soil layer

Discussion

Diurnal water potential values studied in the course of 8 months revealed significant differences between the two study sites, among species, and in the course of time, owing to which species seem to employ different strategies to offset the harmful effect of drought periods. An understanding of these strategies is of importance for the selection of suited tree species for future reforestation of drought-prone areas (Gebrekirstos et al. 2006).

All species presented their highest values at predawn and their lowest during midday, the value that integrates and reflects all environmental influences on the plants' internal water balance, indicating the least favourable condition for the plant (Gebre et al. 1998). The water potential of a fully hydrated plant may be close to zero, while water potentials could reach as low as −12 MPa

under extreme water stress conditions in the field (Zunzunegui et al. 2005).

A plant can make up its water deficit during the night, that is why many authors consider Ψ_{wpd} values as a true equilibrium of soil water potential (not measured in the present study) and plant water status (Mitlöhner 1997; Sellin 1999; Bucci et al. 2004). Furthermore, minimum Ψ_{wpd} values are considered to express the static water stress (Sellin 1998). Nevertheless, some authors report that predawn potentials do not necessarily equilibrate with soil water potentials, especially under well-watered conditions and particularly for woody plants (Sellin 1999; Donovan et al. 2001; Bucci et al. 2004). In the present study, Ψ_{wpd} of all species (Fig. 2) seemed to correspond to seasonal variation in soil water content (Fig. 1) as the strong correlations and regression analyses indicate (Tables 3, 4), although values of *P. pseudostrobus* showed less fluctuations. However, data of all sampling dates were pooled and results might be different analyzing the relationship between soil water content and Ψ_{wpd} for each sampling date separately.

The midday water potential (Ψ_{wmd}) can be split into the base water potential ($\Psi_{wpd,}$) and diurnal depression ($\Psi_{d,}$) which is mainly influenced by atmospheric conditions and plant hydraulic capacity, indicating the level of dynamic water stress (Hinckley and Ritchie 1973; Lassoie et al. 1983; Pothier et al. 1989; Sellin 1998). This was clearly confirmed by the results of the correlation analysis which presented significant correlations between Ψ_d and daily mean relative air humidity, and daily mean vapour pressure deficit in the case of the two conifers. Diurnal depression of *Q. canbyi* in contrast, was significantly correlated with soil water content (Table 3) reflecting the species' dependence on soil water content.

J. flaccida showed highest seasonal fluctuations and presented the lowest minimum values at both sites. *P. pseudostrobus* in comparison presented more balanced values in the course of the study, especially under the drier soil condition in Plot-S. Since isohydric plants reduce

Table 4 Least-squares coefficients for predawn leaf water potential (Ψ_{wpd}) in relation to averaged soil water content (ASWC) in three tree species

Tree species	Least-squares statistics						Adjusted r^2
	Y-axis intercept			Slope of regression model			
	$\hat{\beta}_0$	E.S.E.	P value	$\hat{\beta}_1$	E.S.E.	P value	
J.flaccida	3.13	0.56	<0.001	−1.04	0.20	<0.001	0.56
P. pseudostrobus	1.32	0.33	<0.001	−0.33	0.12	<0.05	0.25
Q. canbyi	2.43	0.57	<0.002	−0.94	0.20	<0.001	0.50

Least-squares estimates have indicated that the best fitted model to relate Ψ_{wpd} as a function of averaged soil water content corresponded to a power mathematical function ($\hat{\Psi}_{wpd} = \hat{\beta} \times ASWC^{\hat{\beta}_1}$, where $\hat{\Psi}_{wpd} = -\Psi_{wpd}$). $\hat{\beta}_0$ and $\hat{\beta}_1$ are the y-axis intercept and slope of the regression model, respectively. Estimated standard errors (E.S.E.'s), P values and adjusted coefficient of determination (r^2) values are provided; $n = 22$

stomata conductance as soil water content declines and atmospheric conditions dry, they maintain relative constant Ψ_{wmd} values regardless of drought conditions. Hence, *P. pseudostrobus* presented a typical pattern of isohydric water regulation, while *J. flaccida* was identified as an anisohydric species that maintain higher stomata conductance and allow Ψ_{wmd} to decline with decreasing soil water content (Tardieu and Simonneau 1998; McDowell et al. 2008). Also other authors mention pine species (*Pinus edulis*) as good examples for isohydric regulation (Lajtha and Barnes 1991; Williams and Ehleringer 2000; West et al. 2008; Breshears et al. 2009) and identified juniper (*Juniperus monosperma*) as an anisohydric species (Loewenstein and Pallardy 1998a, b; Tardieu and Simonneau 1998; Franks et al. 2007; West et al. 2008; Breshears et al. 2009). The course of seasonal Ψ_{wmd} of *Q. canbyi* indicated rather anisohydric water status regulation, since fluctuations of Ψ_{wmd} values corresponded to soil water availability and were very similar to those of *J. flaccida* varying notably over time. Though, in literature several oak species are recognised to regulate efficiently their water status during drought by reduced stomata conductance (Gallego et al. 1994; Cochard et al. 1996; Morecroft and Roberts 1999; Kolb and Stone 2000; Xu and Baldocchi 2003; Otieno et al. 2007) that rather suggests isohydric water status regulation. Nevertheless, *Q. canbyi* apparently lost water under dry conditions as the course of Ψ_{wmd} values indicate (Fig. 2) and therefore seems to exhibit anisohydric behaviour.

In contrast to isohydric species, anisohydric species tend to occur more in drought-prone habitats (McDowell et al. 2008) like *J. flaccida* which inhabits mostly xeric areas. McDowell et al. (2008) discuss various hypotheses on mechanisms of drought related plant mortality and present a theoretical relationship between duration and intensity of (water) stress and the three hypothetical mechanisms of mortality: biotic agent demographics, hydraulic failure and carbon starvation. The type of water status regulation, anisohydric versus isohydric, may be a critical factor for plant survival and mortality during drought (McDowell et al. 2008).

Usually one expects to observe higher water potentials at predawn than at midday and a wide range or positive values of $\Delta\Psi_w$ indicate a high degree of plasticity or high physiological capacity to regulate water loss and maintain high Ψ_w (Mitlöhner 1998; Gebrehiwot et al. 2005). This was the case for *J. flaccida* which presented the widest $\Delta\Psi_w$ under severe drought conditions (Fig. 2e). Conversely, narrow $\Delta\Psi_w$ or even negative values during dry periods, as were found for *P. pseudostrobus* and *Q. canbyi*, indicate a lack of species' capacity to re-saturate during the night (González et al. 2004; Gebrehiwot et al. 2005; Gebrekirstos et al. 2006).

Nevertheless, Sellin (1998) reported that the sensitivity of trees' water status to the atmospheric evaporative demand depended on soil water availability. Furthermore, under drought conditions, more negative predawn values (Ψ_{wpd}) can be observed in comparison to midday Ψ_{wmd} as a consequence of stomata closure, solute enriched xylem concentration, or rather osmotic adjustment (Sellin 1998; Donovan et al. 2003). Similarly, it has been documented for several plant species that stomata do not close completely at night, allowing nocturnal transpiration and thus preventing soil–plant water potential equilibration during night (Kavanagh et al. 2007). Whether or not this mechanism influenced the predawn water potentials responses in studied species remains unknown. However, the trends observed in *P. pseudostrobus* and *Q. canbyi* open a research line for these hypotheses.

Osmotic potentials (Ψ_{spd} and Ψ_{smd}) decreased for all species parallel to the loss of soil moisture content in the course of the study until the onset of the summer precipitations. In general, seasonal declines in Ψ_s of mature leaves reported in several studies including various species, have been interpreted as a response to either drought, shoot or leaf age (see Gebre et al. 1998 for references). Since Ψ_s were always measured on mature leaves or shoots of trees, the decline in Ψ_s is interpreted as water stress. Low osmotic potentials during drought periods indicate higher drought tolerance (Morgan 1984; Aranda et al. 1996; Gebre et al. 1998; Aranda et al. 2004) as observed in *Q. canbyi* and *J. flaccida* (Fig. 3b). Species with high baseline, such as *P. pseudostrobus*, may exhibit osmotic adjustment only under mild water stress being at a disadvantage under severe drought conditions in mixed forest ecosystems, where species with low baseline Ψ_s predominate (Gebre et al. 1998). This could be an explanation for the similar course of the species' Ψ_{spd} and Ψ_{smd} curves in Plot-N compared to the xeric Plot-S, where *P. pseudostrobus* had definitively higher values (Fig. 3).

According to data from literature, American and European oak species in general have shown to be quite drought tolerant, due to their capacity of osmotic adjustment in response to water stress (Bahari et al. 1985; Abrams 1990; Epron and Dreyer 1993; Bréda et al. 1993; Aranda et al. 1996; Corcuera et al. 2002). So far and due to the highly significant difference in Ψ_s comparing a moist and dry sampling date, the higher capacity for osmotic adjustment could be one explanation for the remarkable seasonal fluctuation in Ψ_s and wide ranges in $\Delta\Psi_w$ of *Q. canbyi* (Fig. 3).

Species of the genus *Juniperus* possess quite distinctive responses to drought compared with those of oaks (Bahari et al. 1985). Nevertheless, in the present study, the course of Ψ_s and $\Delta\Psi_s$ showed similar pattern comparing *J. flaccida* with *Q. canbyi* (Fig. 3). In fact, the inherent ability of *Juniperus* species to sustain stomata opening at

low water potentials combined with low capacity for water loss appear to promote the abundance of *Juniperus* in xeric environments. This in turn sustains the theory to categorise the water status regulation of *J. flaccida* as anisohydric (McDowell et al. 2008). Furthermore, species of *Juniperus* seems to possess numerous physiological and morphological characteristics that make them more drought tolerant than others species, such as efficient stem cavitation relationships, transpiration and photosynthetic responses, as well as the capacity to substantially reduce water stress through foliar absorption of intercepted rain (Lajtha and Barnes 1991; West et al. 2007; Breshears et al. 2009).

On a seasonal basis, gradual decrease in Ψ_{wpd} and Ψ_{spd} (Fig. 2) of *J. flaccida* and *Q. canbyi* showed a considerable response to soil–water availability pattern (Fig. 1). In addition, these evidences are sustained by the relationship found within the soil water content in the four soil layers, since it explained (r^2) between 50% (*Q. canbyi*) and 56% (*J. flaccida*) of the variation in Ψ_{wpd} (Table 4), and the correlations with soil moisture at each particular soil depth (Table 3). Soil water content higher than 15% was required to achieve maximum (greater than −1.5 MPa) and constant Ψ_{wpd}; below this threshold value, Ψ_{wpd} decreased gradually, mainly for *J. flaccida* (Fig. 4). A similar pattern of variation in Ψ_{wpd}, depending on the soil water content, has been described for other tree species (Hinckley and Ritchie 1973; Sellin 1998; Montagu and Woo 1999; González et al. 2004), and can be attributed primarily to the decrease in soil water content or rather to static water stress (Sellin 1998).

In contrast, there was no strong relationship found between soil water content and Ψ_{wpd} of *P. pseudostrobus* (Tables 3 and 4), and correlations of Ψ_s with environmental variables were completely missing for this species. Since water potentials curves of isohydric species are more independent of soil water pattern (Tardieu and Simonneau 1998; McDowell et al. 2008), the lack of strong correlations with soil water content sustains further the isohydric behaviour of *P. pseudostrobus*.

The dynamic water stress, expressed by the depression potentials (Ψ_{wd}), was unexceptionally influenced by atmospheric conditions for the two conifers (Table 3). Only for *Q. canbyi*, Ψ_{wd} was mainly correlated with soil moisture content, a behaviour that indicates the species' dependence on soil water availability. So, daily pattern of Ψ_{wd} reflected interaction between soil water dynamics and atmospheric evaporative demands (Sellin 1998).

Conclusions

Water status regulation during periods of drought was quite different comparing three native tree species and their leaf

water and osmotic potentials in the course of 8 months. While *P. pseudostrobus* showed typical isohydric behaviour, *J. flaccida* and *Q. canbyi*, in contrast, seemed to exhibit anisohydric water status regulation. Thus, isohydric behaviour is of advantage during severe but short periods of drought, while anisohydric water status regulation is favourable during long-term drought conditions of minor intensity (Breshears et al. 2009). Detailed knowledge about the type of waters status regulation is crucial in the context of climate change for modelling future changes in forest vegetation. However, for precise conclusions about forest development in the Sierra Madre Oriental, further long-term studies are required including additional plant physiological variables, such as stomatal conductance, photosynthetic activity and carbon assimilation, as well as detailed forest inventories, monitoring spatial distribution, regeneration and tree survival.

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