

Evidence of osmoregulation in *Larix decidua* at Alpine treeline and comparative responses to water availability of two co-occurring evergreen species

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Abstract – The water relations of three coniferous species (*Larix decidua*, *Picea abies* and *Pinus cembra*) growing at a treeline ecotone in the Southern Alps were investigated. Sap flux and xylem water potential were measured in two individuals of each of the above-mentioned species during part of summer 1997. Throughout the growing period, *L. decidua* showed a gradual decrease in minimum water potential while for *P. abies* and *P. cembra*, variations were more correlated to actual weather conditions. Daily sap flux was also higher in *L. decidua* than in the two other species. Pressure-volume curves derived for *L. decidua* during July 1997 demonstrated that the species further diminished its minimum water potential through osmoregulation. During dry periods the other species showed an evident reduction in sap flux suggesting a water saving behaviour. The three species seem therefore to have evolved different drought avoidance strategies.

osmotic adjustment / *Pinus cembra* / *Picea abies* / sap flow / pressure-volume curves

Résumé – Évidence d'un ajustement osmotique chez *Larix decidua* à la limite de l'étage forestier alpin et réponses comparées à la disponibilité en eau de deux espèces de conifères co-existantes. On a étudié les stratégies hydriques de trois espèces de conifères (*Larix decidua*, *Picea abies* et *Pinus cembra*) qui poussent dans un écotone à la limite supérieure de l'étage forestier dans le sud des Alpes. On a mesuré le flux de sève et le potentiel hydrique du xylème pour deux individus des espèces citées précédemment pendant une partie de l'été 1997. Durant la période de végétation, *L. decidua* a montré une diminution progressive du potentiel hydrique minimum tandis que les variations de *P. abies* et de *P. cembra* étaient corrélées en grande partie aux conditions atmosphériques. Le flux de sève journalier aussi était plus important chez *L. decidua* que dans les deux autres espèces. Les courbes pression-volume établies pour *L. decidua* au mois de juillet 1997 montrent que l'espèce est en mesure de diminuer ultérieurement son potentiel hydrique minimum à travers un ajustement osmotique. Pendant les périodes de sécheresse, les autres espèces ont manifesté une réduction visible du flux de sève suggérant ainsi un comportement adapté pour limiter la consommation d'eau. Les trois espèces semblent donc avoir développé des stratégies différentes pour éviter la sécheresse.

ajustement osmotique / *Pinus cembra* / *Picea abies* / flux de sève / courbes pression-volume

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Abbreviations

F_d :	Sap flux density ($\text{dm}^3 \text{ dm}^{-2} \text{ h}^{-1}$)
PAR:	Photosynthetic active radiation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
R :	Hydraulic resistance ($\text{MPa dm}^{-1} \text{ h}$)
RTLP:	Relative water content at turgor loss point
RWC:	Relative water content
VPD:	Vapour pressure deficit (hPa)
WPTLP:	Water potential at turgor loss point (MPa)
ϵ_{max} :	Maximum elastic modulus of the cell wall (MPa)
Ψ :	Xylem water potential (MPa)
Ψ_m :	Minimum xylem water potential (MPa)
Ψ_{pd} :	Predawn xylem water potential (MPa)
Ψ_{π} :	Osmotic potential (MPa)
$\Psi_{\pi 100}$:	Osmotic potential at full turgor (MPa)

1. INTRODUCTION

In the last few years a renewed interest in the physiology of plants growing at treeline has been sparked by the realisation that global climate change could have a marked effect on the treeline ecotone [3, 13]. Treelines are controlled by a range of environmental factors in different parts of the world with temperature usually identified as the main one [15]. The treelines of the Alps appear to be determined, at least in part, by winter and spring desiccation of needles when the soil is frozen. This has been attributed to an incomplete development of the needle cuticle during the short growing period [30, 37], although this is not usually the case in more maritime regions [10, 11].

Recent evidence suggests that climate changes can affect the distribution of plant communities and shift the range of various alpine species [19, 21] and climate warming has been thought to be the cause of an altitudinal shift upwards in alpine plants [9]. However, no evident effects of recent higher summer temperatures on altitudinal range have been recorded in alpine *Pinus sylvestris* and *Pinus cembra* [14]. A better understanding of tree physiology at the treeline is needed in order to predict possible future scenarios brought about by climate change. Indirect effects (such as the duration of snow cover or the amount of water in the soil) appear to be more important than direct temperature effects on life processes [18]. Climate scenarios suggest lower rainfall and more frequent droughts [36], which may influence species distributions as a consequence of species variability in water relations [7]. It follows that the seasonal monitoring of water status in trees at treeline should increase our understanding over how climate change can affect

their distribution. Recently, drought resistance mechanisms of different species at treeline have been studied in the Southern Alps [2]. Although trees growing at the alpine treeline only rarely undergo severe water stress because of high precipitation during the vegetative period, moderate water deficits may lead to a strong reduction of transpiration due to a high stomatal sensitivity to drought. Tree species found at treeline show a well-developed water-saving behaviour, probably induced by the low soil water content due to the shallow mountain soils. Some species (such as *Larix decidua*) appear to cope with these moderate water deficits better than others (*Picea abies* and *P. cembra*). Studies carried out on a treeline ecotone in the Italian Alps hypothesised the occurrence of osmoregulation in *L. decidua* during periods of drought. Osmoregulation can contribute to the maintenance of turgor during periods of water stress and could therefore increase the chances of this species to compete with the other treeline species for the colonisation of the alpine areas rendered suitable to seedling establishment in the case of climate warming. In this article we will discuss the importance of this phenomenon in relation to drought response and competitive abilities of these three species.

2. MATERIALS AND METHODS

2.1. Study site

The experiments were conducted on a treeline ecotone (*sensu* Crawford [5]) at 2080 m above sea level in the Southern Alps (Italian Dolomites, Cortina d'Ampezzo). The site has a Southern aspect and 30% slope, with shallow calcareous soil. The treeline is formed by mixed stands of relatively young *L. decidua*, *P. cembra* and *P. abies* which are invading edges of recently abandoned pasture [8]. June–September mean precipitation is 450–500 mm.

Six trees (the same ones used in another study [2] during 1996) were used for the experiment, two for each of the above-mentioned species (*table 1*).

2.2. Xylem water potential

Xylem water potential (Ψ) was measured for seven days (from 1 July to 23 August 1997; days 182–235) on 1-year-old shoots. Two shoots were collected at a height of 2 m on each tree from predawn (Ψ_{pd}) to dusk at intervals of 2 hours and measurements were made directly at the site with a pressure chamber within two minutes of collection. Data were then averaged since no significant ($p = ns$) statistical difference was recorded between individuals of the same species (*table III*).

Table I. Main features of the sampled trees including their age as calculated from sample cores the year before the study, their diameter at breast height (1.3 m) and their height.

Tree	Age (years)	Diameter at breast height (cm)	Height (m)
<i>L. decidua</i> #1	38	24.2	10.2
<i>L. decidua</i> #2	59	25.1	9.6
<i>P. abies</i> #1	54	25.1	9.3
<i>P. abies</i> #2	53	30.9	11.1
<i>P. cembra</i> #1	36	27.3	7.2
<i>P. cembra</i> #2	47	33.4	7.9

2.3. Sap flux density

Xylem sap flux density (F_d , $\text{dm}^3 \text{dm}^{-2} \text{h}^{-1}$) was measured in each tree using 2 cm continuously-heated sap flowmeters [12]. Sensors were inserted into the xylem (NW aspect) at 1.5–2 m. Measurements were taken every minute, averaged and stored every 15 minutes using a storage module connected to a datalogger (CR10, Campbell Ltd, Lincoln, Nebraska). Protection from high solar radiation was ensured, both by insulating shields placed over the sensors in the case of *L. decidua* and by the dense tree crowns reaching to the ground for *P. abies* and *P. cembra*. Sap flux density was measured from 17 June to 13 October 1997 (days 168–286). Sapwood area and total tree transpiration were not estimated because of the uncertainty in defining the number of active tree rings and the contribution of each of them to the total water transport.

2.4. Hydraulic resistance

The sapwood-specific hydraulic resistance between soil and needles was calculated from the relationship between needle water potential and sap flux density:

$$R_{\text{soil-needle}} = \frac{(\Psi_{\text{needle}} - \Psi_{\text{soil}})}{F_d}$$

Where $R_{\text{soil-needle}}$ is the sapwood-specific hydraulic resistance between soil and needles ($\text{MPa dm}^{-1} \text{h}$), Ψ_{soil} and Ψ_{needle} are the soil and needle water potential respectively (MPa) and F_d the sap flux density ($\text{dm}^3 \text{dm}^{-2} \text{h}^{-1}$).

2.5. Pressure-volume curves

Ten pressure-volume curves were derived for *L. decidua* at the site and two for *P. cembra* at irregular intervals in the period between 29 June and 2 August (days 180–214). Samples were always taken from the S exposed canopy at a height of 1.5–2.5 m from the ground in the evening hours of the day previous to the day of the measurement, sealed in a polythene bag to reduce evaporative loss of water and taken to the laboratory. Here cut ends of the shoots were immersed in water and the shoots were left rehydrating for 12–15 hours in the darkness for the whole night [26, 34].

The pressure-volume curves were constituted as the standard method described in the literature [33] suggests, collecting data by using a pressure chamber [28]. A wet piece of blotting paper was enclosed in the pressure chamber in order to prevent evaporative loss during the measurements [31, 34]. Pressure was increased slowly (0.01 MPa s^{-1}) during the measurements, until a droplet of xylem sap appeared on the section of the shoot.

In some samples Ψ remained almost constant with tissue dehydration in the region of high turgor potential [25]. This particular ‘‘plateau effect’’ is believed to be an artefact caused by oversaturation of samples [20] even if observed in naturally rehydrated plants [25].

In order to minimise the plateau effect, the raw data were plotted and, after having excluded the points where this effect was evident, the real saturated weight ($\Psi=0$) of the shoots was extrapolated using a linear regression of fresh weight against balance pressure as suggested in the literature [22].

Curves were then analysed using a segmented non-linear regression algorithm [26] fitted on a modified exponential model described in the literature [29]. When the plateau effect was minimum the model used fitted the experimental data very well (figure 1). In other cases a slight difference appeared in the region of high turgor pressure. However, for all curves, the variance explained from the model exceeded 0.972 (table II). All curves and parametric values inferred from them were derived separately and then averaged for display in the figures. This was not possible for *L. decidua* for day 208 and 212, in which only one curve was available.

2.6. Microclimate

Standard meteorological variables above the canopy (global radiation, air temperature, relative humidity, wind velocity and direction, rainfall and photosynthetic active radiation) were monitored every minute, averaged and stored every 15 minutes with a datalogger (Campbell

Ltd CR10) connected to two multiplexers (Campbell AM32). A solar panel (Helios technology 50 W) and batteries (140 Ah) provided power.

2.7. Soil water

Relative soil moisture content was measured with time domain reflectometry (Campbell CS615) at 30 cm depth with a water content reflectometer from 11 June (day 162) to 13 October (day 286). These measurements are expressed as relative values in relation to the maximum value recorded after high precipitation occurred (i.e. relative soil water content compared to soil holding capacity).

3. RESULTS

During summer 1997 (June–September) an above-average rainfall of 652.6 mm was recorded (*figure 2a*). However, an unusually dry period occurred from 9 September (day 252) to 13 October (day 286 and end of the measurements) (*figure 2b*).

The maximum mean air temperature was reached at the beginning of September (about 15 °C), just after a cool spell at the end of August.

3.1. Shoot water potential

Figure 3 shows the seasonal course of predawn water potential (Ψ_{pd}) and minimum water potential (Ψ_m) for the selected trees. *P. abies* was the species with the highest values of Ψ_{pd} , dropping below -0.4 MPa only during August and maintaining a fairly constant value throughout the study period. *L. decidua* and *P. cembra* showed parallel variations for most of July (days 182–204). While in *P. cembra* Ψ_{pd} became less negative at the end of July, in *L. decidua* it continued to decrease to a minimum (-1.07 MPa) at the end of August (day 235).

Minimum water potentials (Ψ_m) of *P. abies* and *P. cembra* displayed parallel time courses during most of July (days 190–211). However, while *P. abies* reached its minimum (-1.48 MPa) at the end of August (day 235), the minimum for *P. cembra* (-1.28 MPa) was reached at the end of July (day 211). *L. decidua* Ψ_m continued to decrease throughout the study period, with a different pattern than in the other two species and reaching its minimum (-2.23 MPa) at the end of August (day 235).

Different statistical tests showed that there was a highly significant effect of species and, in some cases, time of the season on the values of Ψ_{pd} and Ψ_m (*table III*). However, differences between individuals were not significant.

Table II. Values of the variance explained (R^2) of each of the pressure-volume curves drawn. *a* = *Larix decidua*, *b* = *Pinus cembra*.

Date	Day of year	R^2
<i>a</i>		
29-Jun	180	0.998
29-Jun	180	0.99
16-Jul	197	0.972
16-Jul	197	0.98
27-Jul	208	0.992
31-Jul	212	0.998
02-Aug	214	0.972
02-Aug	214	0.986
<i>b</i>		
01-Aug	213	0.999
01-Aug	213	0.998

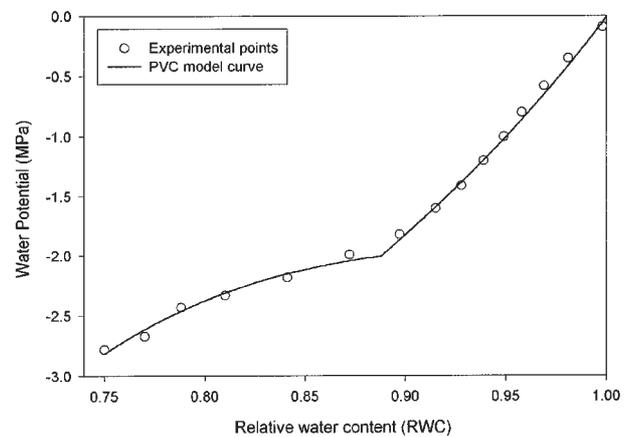


Figure 1. Example of accuracy of model (line) derived pressure-volume curve and experimentally derived data (points) for day 180 (29 June).

3.2. Daily and seasonal variations in sap flux density

Daily fluctuations in water potential, in relation to meteorological parameters and sap flux density, are shown for two representative days in *figure 4*. Because of the frequent and rapid variations in cloudiness at high altitude, air temperature, vapour pressure deficit (VPD) and solar radiation changed abruptly.

Sap flux of all species was visibly coupled with VPD. In *L. decidua* F_d increased sharply and reached the daily maximum by mid morning. Ψ decreased rapidly and Ψ_m was usually reached by 10 AM. Once the minimum was

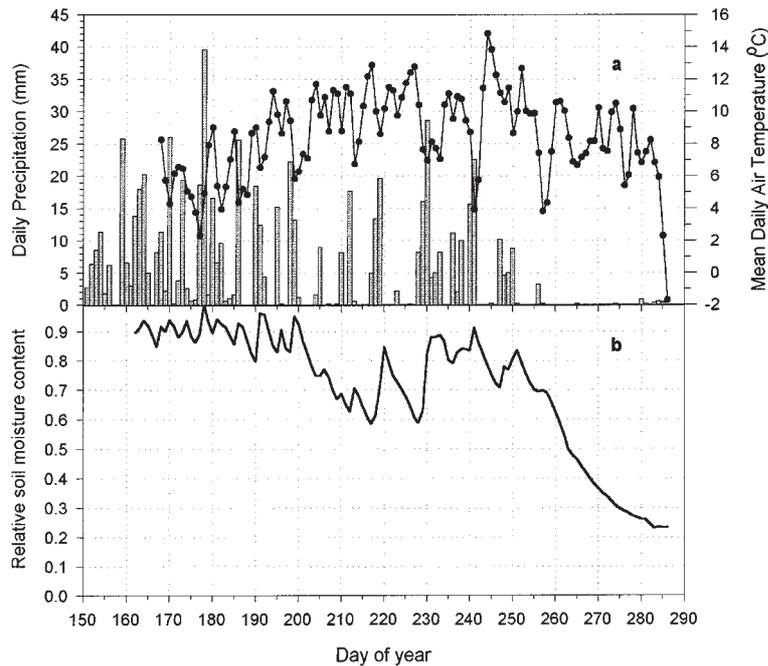


Figure 2. Comparison of seasonal trends in daily precipitation, mean daily air temperature (a) and relative soil moisture content at 30 cm depth (b).

reached, Ψ increased slowly compared to the rapid fall in the morning. F_d in *P. abies* and *P. cembra* increased later and the maximum daily values were much lower than those of *L. decidua*. It is interesting to notice that when VPD was high at night (1–3 hPa) there was a detectable sap flux occurring in *L. decidua* as shown in day 190 in figure 4. The other two species however did not show nocturnal transpiration.

Table III. Results of the statistical tests used to detect significant differences between time of the season (results differ from species to species), species and individuals regarding the data for Ψ_{pd} and Ψ_m .

	Predawn water potential (Ψ_{pd})	Minimum water potential (Ψ_m)
Time of season*		
<i>L. decidua</i>	$p < 0.001$	$p < 0.001$
<i>P. abies</i>	$p = ns$	$p < 0.01$
<i>P. cembra</i>	$p = ns$	$p = ns$
Species*	$p < 0.0001$	$p < 0.0001$
Individuals#	$p = ns$	$p = ns$

* Kruskal-Wallis test, # Wilcoxon test.

3.3. Seasonal variation in hydraulic resistance

Sapwood-specific hydraulic conductance ($1/R_{soil-needle}$) and hydraulic resistance ($R_{soil-needle}$) were calculated for the three species during the study period (figure 5) and showed different trends for each of the species studied. In *L. decidua*, $R_{soil-needle}$ increased constantly throughout the month of July, reaching its maximum (0.6 MPa $dm^{-1}h$) at the end of July (day 211) and then decreasing during August. In *P. abies*, after some initial fluctuations, $R_{soil-needle}$ increased from July to August reaching its maximum (0.45 MPa $dm^{-1}h$) at the end of August (day 235). *P. cembra* showed a highly fluctuating trend reaching its maximum (0.51 MPa $dm^{-1}h$) on day 211 only to decrease sharply in August. Regression lines for $R_{soil-needle}$ were good for all cases of *L. decidua* and *P. abies* but only for two of *P. cembra*.

3.4. Pressure-volume curves

Pressure-volume curves for *L. decidua* were derived during five different days from the end of June to the beginning of August and two curves for *P. cembra* were derived at the beginning of August (day 213).

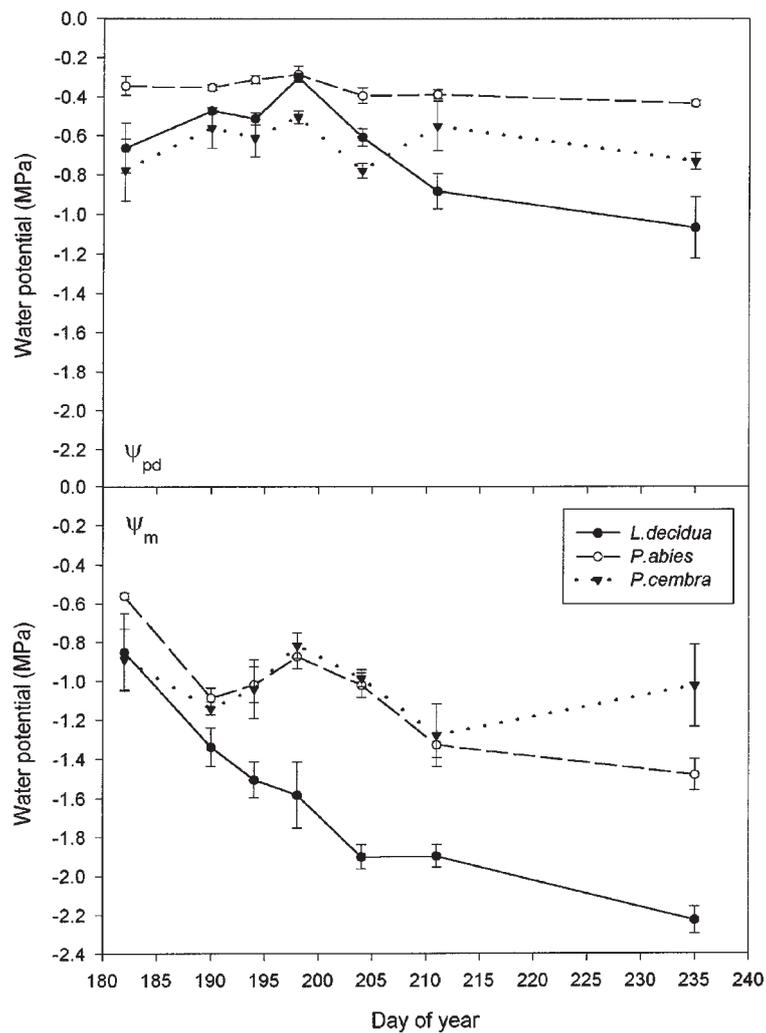


Figure 3. Variations of predawn water potential (Ψ_{pd}) and minimum water potential (Ψ_m) for *L. decidua*, *P. abies* and *P. cembra* during the study period. Bars = $1 \pm SE$.

A number of parameters estimated from the pressure-volume curves are shown in figure 6. Both osmotic potential at full turgor ($\Psi_{\pi 100}$) and water potential at turgor loss point (WPTLP) reached their maximum value on day 197 in *L. decidua*, before decreasing to their minimum at the beginning of August (day 214). The values obtained on day 213 for *P. cembra* were slightly higher.

The relative water content at turgor loss point (RTLTP) and the maximum elastic modulus derived from the pressure-volume curves (ϵ_{max}) in *L. decidua* increased during the study period reaching their maxima at the beginning of August.

P. cembra showed a much lower value than *L. decidua* on day 213 for both, RTLTP and ϵ_{max} .

4. DISCUSSION

4.1. Pressure-volume curves

The main aim of the research was to assess the extent of osmoregulation in *L. decidua* and the compared responses to water availability of two co-occurring ever-green species. We concentrated on *L. decidua* as a previous study [1] on *P. abies* pressure-volume curves had

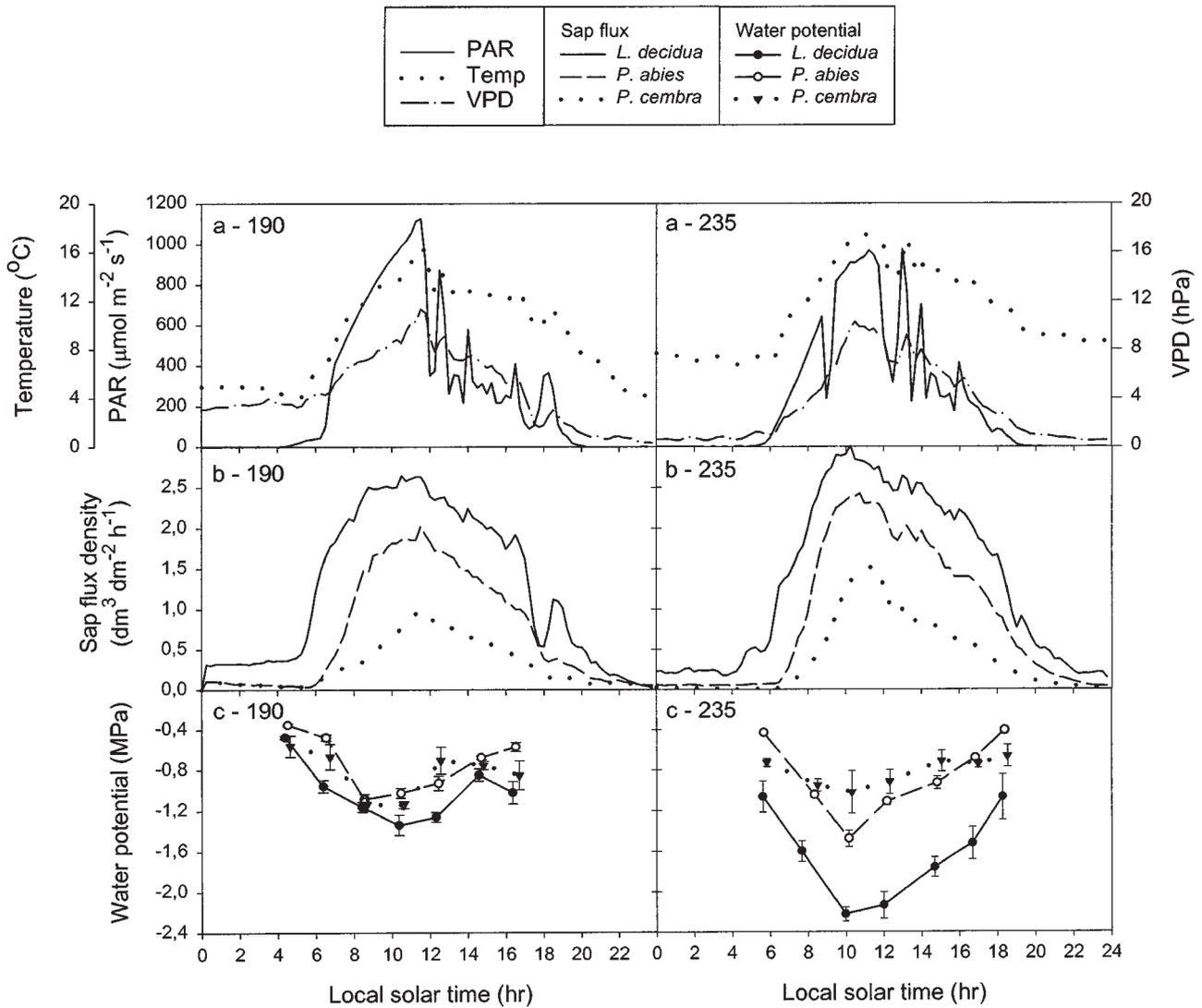


Figure 4. Daily fluctuations of environmental conditions (temperature, PAR, VPD) (a) in relation to sap flux density (F_d) (b) and shoot water potential (Ψ) (c). Days 190 (9 July) and 235 (23 August). Bars = $1 \pm$ SE.

shown that no osmoregulation occurred in this species and no further experiments seemed necessary. In *P. cembra*, pressure-volume curves were very difficult to derive because of very high resin emissions during the dehydration phase and early attempts were unsuccessful.

We realise that the number of curves at our disposal is not enough for an in-depth study of the behaviour of the species. However, comparison of pressure-volume curves of *L. decidua* during the growing season allowed us to suggest whether osmoregulation had occurred or not. The latter is a process by which cell turgor is main-

tained by means of increases in cell solute content (lowering Ψ_π) in response to water stress [17, 24] or when new organs are expanding [24, 32]. It may be a very important mechanism for maintaining physiological activity as Ψ falls, although some authors report it may be of little importance in conifers [16].

The decrease in $\Psi_{\pi 100}$ by about 0.6 MPa was indicative of osmoregulation (figure 6a). This brings about a substantial decrease in WPTLP which in turn could enhance the water extraction capacity of the species (figure 6a).

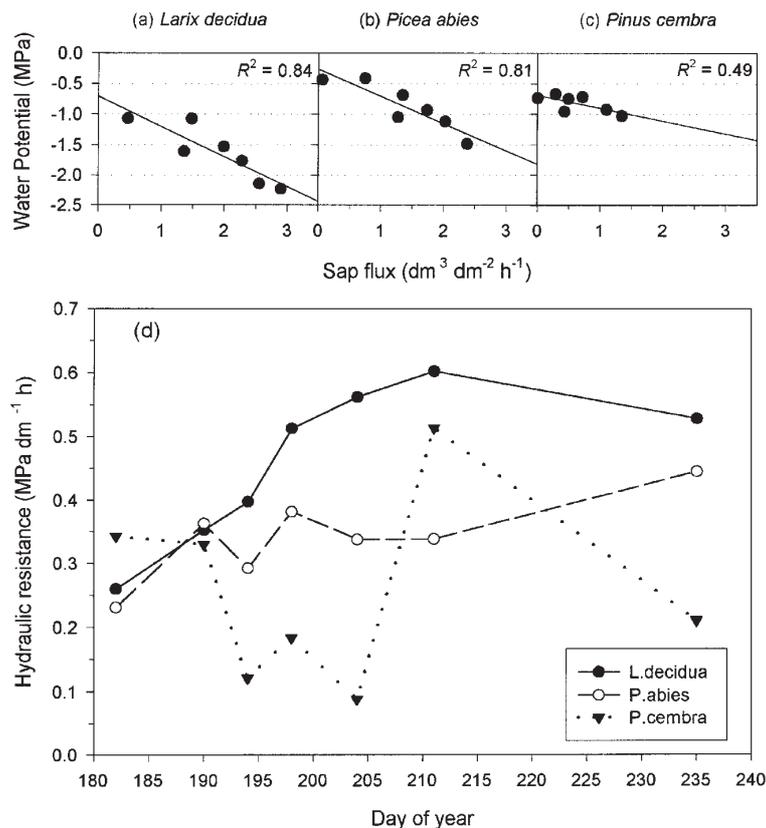


Figure 5. Comparison of hydraulic conductance in *L. decidua* (a), *P. abies* (b) and *P. cembra* (c) on day 235 (23 August). Seasonal variations in hydraulic resistance (R) for *L. decidua*, *P. abies* and *P. cembra* are shown below in (d).

Since stomata conductance is maintained higher also under water deficit, leaf water potential decreases more than in absence of osmoregulation.

A lower leaf water potential means also a stronger decrease in xylem water potential due to the “propagation” of the water potential gradient among different plants compartments. A lower xylem water potential means, in turn, a lower water potential up to the fine roots. Since the water uptake depends also on the capacity to decrease the water potential, osmoregulation, in the end, should have the effect of increasing the water uptake capacity. Moreover, osmotic adjustment should allow to maintain turgor in root cells at lower water potential [27 in 32], leading to a more effective root elongation. Plants can, therefore, explore a greater volume of soil increasing the capacity of water uptake.

At the same time an increase in the elastic modulus of the cell wall (ϵ_{\max}) has been observed, a feature usually associated with the capacity to withstand low water potentials (figure 6c).

It is also important to notice that between day 200 and day 214 there was a progressive decrease in precipitation and relative soil moisture (figure 2b) which is likely to have increased the water stress to which the trees were subjected. Hence the species enhanced its water uptake ability in mid-summer when the occurrence of moderately water deficits is most likely.

It would be risky to draw definite conclusion about the reasons for the occurrence of osmoregulation with the few curves we have derived but nonetheless they allow us to make some considerations. It seems unlikely that osmoregulation be the effect of ontogenetic changes since a parallel experiment conducted the same year [6] clearly showed that needle growth in *L. decidua* finished on days 188–190 well before the beginning of the decrease in Ψ_{π} we have found. In fact on the first day of measurements (day 180) needles and shoots were still expanding [6] but $\Psi_{\pi 100}$ was higher than some weeks later (figure 6a). It should have been the opposite if an ontogenetic cause was involved. Furthermore, it has

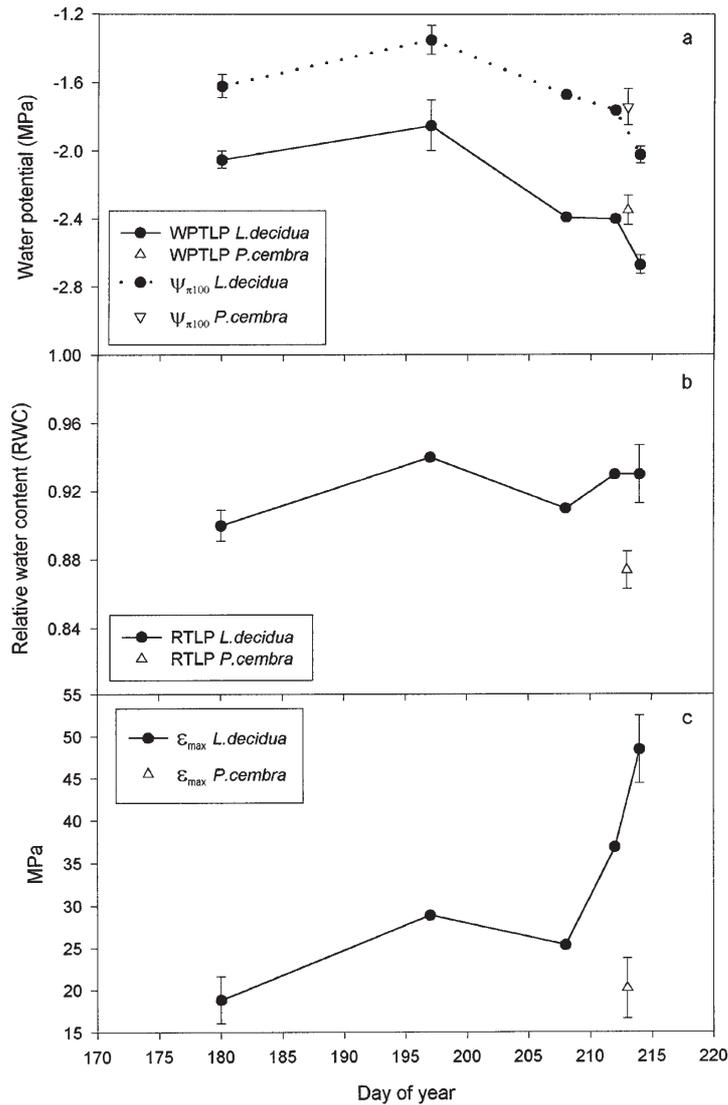


Figure 6. Seasonal trends for WPTLP and $\Psi_{\pi 100}$ (a), RTLP (b) and ϵ_{\max} (c) as obtained from the analysis of the pressure–volume curves. Bars = $1 \pm \text{SE}$ apart from values for day 208 and 212 in which they are absent since only one value was available.

been reported [24] that if plants are hardened by exposure to larger diurnal fluctuation in humidity and solar radiation (as it occurs at high altitude) the capacity of osmoregulation may remain unchanged or increase with age without water stress being involved.

4.2. Daily shoot water potential and sap flux density variations

Values of Ψ_m in *P. abies* were less negative than in similar studies conducted in other parts of the Alps [23]

but more negative than those found at the same site the year before [2]. Moreover, Ψ_m was above the turgor loss point, which at the alpine treeline was found to be relatively constant throughout the growing season at about -2.8 MPa [1]. Relatively high values of Ψ_m suggest that stomatal control may occur well above the threshold of significant loss of xylem functionality in conifers growing under similar environmental conditions, found to be between -2.5 and -3 MPa [4]. Daily variations of VPD and F_d in *L. decidua* were visibly coupled (figure 4). This does not only occur in diurnal hours

but also during the night and early morning provided VPD has a value of 1 hPa or higher. This behaviour might be explained by the fact that cuticle conductance is rather high leading to a detectable nocturnal transpiration in relation to changes in VPD.

In all species F_d appears to be especially well correlated to VPD below the threshold of 7–8 hPa but when VPD is higher, the high stomatal sensitivity leads to a reduction of the expected F_d (see day 190 in *figure 4*) as already observed in a precedent study [2].

Variations of daily Ψ in *P. abies* and *P. cembra* are closely coupled to variations in VPD and photosynthetic active radiation (PAR) (*figure 4*). Daily water potential variations (especially Ψ_m) in *L. decidua* appear to depend on seasonal meteorological trends rather than daily ones as in *P. abies* and *P. cembra*. This is probably ascribable to internal physiological adjustments associated with osmoregulation. This is consistent with the results of another study [35] which concludes that deciduous species (*L. decidua*) use almost exclusively groundwater while evergreen species (*P. abies* and *P. cembra*) use rainwater to a larger extent. The same study demonstrated that *L. decidua* develops a deep root system which allows utilisation of water sources in the deepest and wettest soil layers which are precluded for instance to *P. abies* because of its shallow root system.

The lower Ψ_{pd} measured in *L. decidua* at the end of July and in August might depend on nocturnal transpiration which prevents that an equilibrium between plant and soil be achieved during the night. Therefore the extractive capacity of the tree cannot be inferred from the analysis of Ψ_{pd} only but VPD and F_d must also be taken into account.

As expected, under non-limiting soil moisture conditions, *L. decidua* exhibited a F_d higher than the other two evergreen species.

4.3. Hydraulic resistance

It is unlikely that significant cavitation of water in the xylem occurred in these species. Even in *L. decidua* with the lowest Ψ_m , the measurements of Ψ_m in this study and in an earlier one [2] are all well above the threshold of ~3.0 MPa which is when most (but not all) conifer species undergo a consistent loss in xylem conductivity [4]. The increase in overall hydraulic resistance R in *L. decidua* is likely to be caused by increased resistance at the soil-root interface. It appears that this may be the way that soil moisture influences species also at the tree-line. In function of its lower Ψ_m , *L. decidua* is able to uptake more water in drier conditions than do *P. abies* and *P. cembra* which appear to be more susceptible to

water shortage. Thus the results confirm what had already been found in a previous study [2] that despite high precipitation, soils at high altitude can become physiologically dry because they are shallow, discontinuous and highly permeable.

4.4. Conclusions

Data presented suggests that *L. decidua* is able to accumulate solutes within cells decreasing the osmotic component of water potential. This behaviour may allow the species to maintain a high stomatal conductance at lower water potential. Osmoregulation is rarely documented in conifers but *L. decidua* might be an exception perhaps because of its deciduous habit. We do not know yet whether low altitude ecotypes show a similarly pronounced capacity in accumulating solutes but it might be speculated that the shorter growing season and the lower soil water capacity might lead to an enhancement of the osmoregulation capacity in high altitude trees.

Compared to other two co-occurring conifers, *L. decidua* seems to be more adapted to continue carbon assimilation when mild water deficit conditions occur and seems to be less sensitive to soil water shortage as well.

Although it is not possible to draw definitive conclusions from this study, it can be imagined that if precipitation rate, regimes and cloudiness should change towards more xeric conditions as hypothesised recently [36], *L. decidua* might be advantaged and a change in high altitude forest composition might occur.

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