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Original article

Tree water relations and climatic variations at the alpine timberline: seasonal changes of sap flux and xylem water potential in *Larix decidua* Miller, *Picea abies* (L.) Karst. and *Pinus cembra* L.

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Abstract – Trees growing at the alpine timberline very seldom undergo severe water stress because of high precipitation during the vegetative period. Since trees are adapted to moist conditions, moderate water deficit may lead to a strong reduction in transpiration. Transpiration and xylem water potential were measured in two individuals each of *Pinus cembra*, *Larix decidua* and *Picea abies* growing at the timberline (2 080 m a.s.l.) in the north-eastern Italian Alps. From June to October 1996 predawn water potential was between –0.29 and –1.0 MPa with moderate differences among species. Throughout the growing period *L. decidua* showed a progressive decrease in the minimum water potential (from –0.45 to –1.93 MPa); in *P. abies* and *P. cembra* variations were more correlated to weather conditions with minima (–1.2 and –1.49 MPa, respectively) during a mild drought period. *L. decidua* showed the mean daily maximum sap flux density (about 3.3 $dm^3\ dm^{-2}\ h^{-1}$) while mean maximum values in *P. abies* and *P. cembra* were about 0.9 and 0.7, respectively. High daily fluctuations of sap flow were observed in relation to rapid variations in weather conditions, particularly in *L. decidua*. Regardless of species a very high stomatal sensitivity to vapour pressure deficit was recorded. The three species seem to have evolved different drought avoidance strategies. *L. decidua* maintained a relatively high transpiration even during moderate water deficit periods because of its high water uptake capacity. During the same drought period *P. abies* and *P. cembra* showed an evident reduction in sap flux, suggesting a water saving behaviour. These different responses should be taken into account when considering the effects of global change on timberline trees. (© Inra/Elsevier, Paris.)

water relations / timberline / drought resistance / stomatal sensitivity / climate warming effects

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Abbreviations: Ψ: xylem water potential (MPa); Ψm: minimum xylem water potential (MPa); Ψpd: predawn xylem water potential (MPa); Fd: sap flux density ($dm^3\ dm^{-2}\ h^{-1}$); MWDP: mild water deficit period; HC: hydraulic conductance ($dm^3\ dm^{-2}\ h^{-1}\ Mpa^{-1}$).

Résumé – Relations hydriques des arbres et facteurs du climat à la limite forestière alpine : variations saisonnières du flux de sève et du potentiel hydrique chez *Larix decidua* Miller, *Picea abies* (L.) Karst. et *Pinus cembra* L. Les arbres situés à la limite forestière dans les Alpes sont rarement soumis à des contraintes hydriques sévères, car les précipitations durant la période de végétation sont élevées. Alors que ces arbres sont adaptés à des conditions de forte humidité, une contrainte hydrique modérée peut conduire à une forte réduction de leur transpiration. La transpiration et le potentiel hydrique ont été mesurés sur deux individus de chacune des espèces : *Pinus cembra, Larix decidua* et *Picea abies* dans la zone de la limite forestière (altitude 2 080 m), dans le nord-est des Alpes italiennes. De juin à octobre 1996, le potentiel hydrique de base a varié entre –0,29 et –1,0 MPa, avec peu de différences entre espèces. Au cours de la période de végétation, *L. decidua* a montré une diminution progressive de son potentiel hydrique minimum (passant de –0,45 Mpa à –1,93 Mpa). Chez *P. abies* et *P. cembra,* les variations de ce paramètre étaient plus fortement corrélées aux facteurs climatiques, les valeurs atteintes étant respectivement de –1,2 Mpa et de –1,49 Mpa pour ces deux espèces, lors d'une période de sécheresse modérée. Les valeurs les plus élevées de densité de flux de sève ont été observées chez *L. decidua* (environ 3,3 $dm^3\ dm^{-2}\ h^{-1}$), contre 0,9 $dm^3\ dm^{-2}\ h^{-1}$ chez *P. abies* et 0,7 $dm^3\ dm^{-2}\ h^{-1}$ chez *P. cembra.* Des fortes variations journalières de flux de sève ont été mises en évidence en relation avec les fluctuations rapides des conditions climatiques, notamment chez *L. decidua.* Une forte sensibilité des stomates au déficit de saturation de l'air a été observée pour chacune de ces espèces. Ces trois espèces semblent avoir développé différentes stratégies de réponse à la sécheresse : *L. decidua* a maintenu un taux de transpiration relativement élevé, même lors d'une sécheresse, en relation avec une forte capacité d'extraction de l'eau dans le sol. Au cours de la même période de dessèchement, *P. abies* et *P. cembra* ont montré une nette réduction de leur flux de sève, ce qui indiquerait une stratégie d'évitement. Ces différentes réponses doivent être prises en compte lorsqu'on s'intéresse aux effets des changements climatiques dans cette zone de limite forestière. (© Inra/Elsevier, Paris.)

relations hydriques / limite forestière / résistance à la sécheresse / régulation stomatique / réchauffement du climat

1. INTRODUCTION

The altitude of alpine timberline is mainly controlled by temperature [14]. However, the general statement that heat deficiency during the short and cold growing season affects the carbon budget of trees, decreasing dry matter production [31], is often inadequate to explain why the timberline occurs in different climatic regions. In continental alpine timberlines (e.g. Austrian Alps) an incomplete development of needle cuticles during the short growing period seems to play the most important role in determining severe drought conditions in the following winter [3, 12, 32]. In arctic, temperate-maritime and tropical treelines (Alaska, Washington Cascades, Venezuelan Andes) cold temperatures seem to have the major impact on limiting physiological processes: cold soil, frozen soil or vascular system, subfreezing temperatures during both dormancy and growth periods strongly affect water relations of treeline species determining severe stress conditions [13].

As there is a strong influence of abiotic factors (i.e. temperature, wind, precipitation) on physiological responses of trees at the timberline the effects of climate warming might be particularly pronounced [17].

There is sound evidence that climatic changes can affect the distribution of plant communities and shift the range of various alpine species [21, 22]. Recently, climate warming has been thought to be the cause of an altitudinal shift upwards in alpine plants [8] and for displacement of the arctic treeline as well as for an increase in stem growth in the *Krummholz* zone [24]. Palynological data have outlined the possible migrations of European flora in relation to climatic variations [15].

On the contrary, no evident effects of recent higher summer temperatures on altitudinal range have been recorded in alpine *Pinus sylvestris* and *P. cembra* [11].

Predictions of possible impact of warmer temperatures upon the physiology of plants adapted to cold climates should consider both the effective variations in plant temperature (degree of aerodynamic coupling between the plant layer and free atmosphere) and different aspects of temperature-mediated processes (freezing resistance, soil temperature and mineral nutrient supply, photosynthetic rate, rate of cell division, rate of mitochondrial respiration) [19].

Among these, dark respiration could be crucial since high altitude plants exhibit a much higher respiration rate than lowland species do, and unless acclimation occurs, this can negatively affect the plant carbon balance [23].

Further, predictions are also dependent on the type of temperature values considered: it is important to distinguish annual, seasonal, daily means and extremes [18].

Seasonal monitoring of the water status in timberline trees in the southern Alps has allowed their drought resistance mechanisms to be better defined and to make hypotheses on some possible responses to climate warming.

Our aim is to demonstrate that, despite regularly distributed precipitation (about 400–500 mm between June and September), trees at the timberline may undergo moderate water stresses (i.e. reduction in stomatal conductance) due to their high stomatal sensitivity to drought. Furthermore, these moderate water deficits may have a stronger impact on reducing transpiration in Norway spruce (*Picea abies*) and Stone pine (*Pinus cembra*) than in European larch (*Larix decidua*).

The extent of potential assimilation reduction will also depend on the change in precipitation regime associated with the rising temperature. Since the link between precipitation and temperature in the Alpine region is not yet fully understood [35] and future scenarios are still contrasting, the true effects of higher temperatures on the timberline are as yet uncertain.

Nevertheless, higher summer temperatures may lead, in the long run, to a composition change of timberline forests due to different drought avoidance strategies developed in Alpine timberline species.

2. MATERIALS AND METHODS

Experiments were conducted on a timberline ecotone at 2 080 m a.s.l. in the north-eastern Italian Alps (Dolomites, Cortina d'Ampezzo). The site has S aspect and 30 % slope. Here the timberline is formed by relatively young *L. decidua, P. cembra* and *P. abies* mixed stands invading edges of recently abandoned pasture lands [7]. June–September mean precipitation is about 450 mm.

The experiment lasted from 29 May–6 October 1996. Six similar-featured trees were selected (two each of the above-mentioned species). In each tree a sample core was collected at 1.30 m and height, conventional age and sapwood width were measured *(table I)*. Differences among trees were expected as a result of severe environmental conditions. A quite good growing potential of the specimen appeared comparing tree age and diameter.

Xylem water potential (Ψ) was measured weekly with a pressure chamber on 1-year-old shoots in *L. decidua* and *P. abies* and on 1-year-old bundle needles in *P. cembra*. Four samples were collected at a height of 2 m (two on the south- and two on the north-facing crown) on each tree just before dawn (predawn water potential, Ψpd) until sunset at 2-h intervals. Data were then averaged for each species since no statistical difference was recorded between the two trees and crown aspect.

Table I. Main features of the sampled trees.

Tree	Conventional age (years)	Diameter (cm)	Height (m)	Number of tree rings in the sapwood	Sapwood area (cm^2)
L. decidua #1	37	24.2	10.2	14	238.2
L. decidua #2	58	25.1	9.6	19	291.1
P. abies #1	53	25.1	9.3	17	265.0
P. abies #2	52	30.9	11.1	31	606.5
P. cembra #1	35	27.3	7.2	29	446.2
P. cembra #2	46	33.4	7.9	19	453.2

Xylem sap flux density (Fd, dm^3 dm^{-2} h^{-1}) was measured in each tree using 2-cm-long continuously heated sap flowmeters [9]. Sensors were inserted into the xylem (NW aspect) 1.5–2 m high in the stem. Protection from high solar radiation was ensured both by insulating shields placed over the sensors and for *P. abies* and *P. cembra* by the dense tree crowns, with ground reaching branches.

No alterations in thermal signal due to resin emission or wood desiccation were recorded over the whole monitoring period. Sap flowmeters were heated from 14 June except for two trees in which heating began 20 days later. Measurements were taken every 1 min, averaged and stored every 15 mins.

Sap flux and water potential data were used to estimate the global hydraulic conductance roots–leaves. Neglecting the stem–branch capacitance effect, the equation describing sap transport between roots and leaves can be written as follows [6]:

$$\mathrm{Fd} = (\Psi_0 - \Psi)/r$$

where r is the roots–leaves resistance.

Water potential when sap flux is null (Ψ_0) was deduced from predawn measurements or estimated with linear regressions using water potential data and the corresponding sap flux values.

Specific hydraulic conductance (HC = $1/r$ dm^3 dm^{-2} h^{-1} Mpa^{-1}) was calculated as the slope of the linear regression of sap flux (Fd) versus the drop in the water potential (Ψ) throughout the day. In *L. decidua* data deviated slightly from the regression line, indicating a low stem–branche capacitance [6]. In *P. abies* and *P. cembra* loops were wider showing a less conservative water transport (as indicated from the lower averaged regression coefficients – *table II*)

Table II. Averaged regression coefficients of the Fd/Ψ relationship over the season.

Tree	Averaged r^2	SD	N
L. decidua #1	0.83	0.10	12
L. decidua #2	0.81	0.09	13
P. abies #1	0.60	0.26	11
P. abies #2	0.72	0.21	12
P. cembra #1	0.63	0.25	10
P. cembra #2	0.60	0.19	12

Standard meteorological factors were monitored every minute, averaged and stored every 15 min with a data logger (Campbell Ltd CR10) connected to two multiplexers (Campbell AM32). Power was provided by a solar panel (Helios technology, 50 W) and batteries (140 Ah).

Technical and logistic support was ensured from the Centre of Alpine Environment of the University of Padova located 20 km away in S. Vito di Cadore.

3. RESULTS

In this Alpine area summer is the wettest season (mean precipitation of the last 30 years about 500 mm). In 1996, during the measurement period, we recorded

621 mm *(figure 1)*. At the end of July there was an unusual dry period (10 days with rain less than 0.4 mm d^{-1} that we will call 'mild water deficit period' MWDP) since only four similar periods were recorded from 1960 to 1990.

The maximum mean air temperature was reached at the beginning of June (about 16 °C), followed by a sharp decrease. July and August were moderately cold compared with previous years.

3.1. Shoot water potential variations

Figure 2 shows the seasonal course of the predawn water potential (Ψpd) of selected trees (no ecophysiological mea-

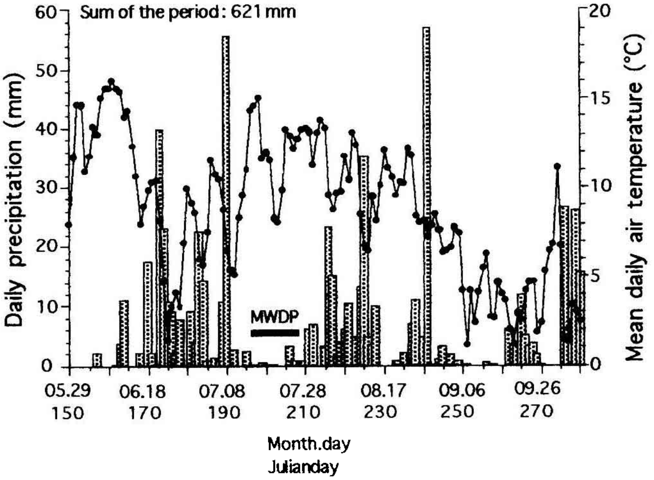

Figure 1. Sum of daily precipitation and daily mean air temperature during summer 1996 at the study site. The mild water deficit period is indicated by a black bar. Bars = precipitation; line = air temperature.

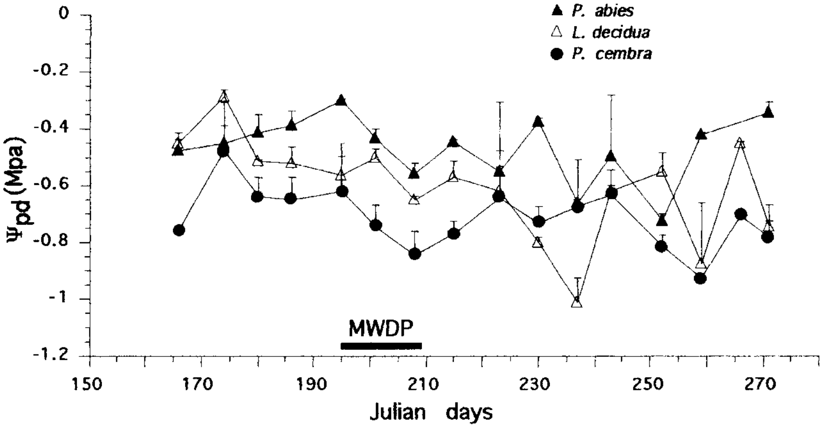

Figure 2. Seasonal variation of predawn xylem water potential in selected trees. Error bars = ± SD

surements were made in the warmest period).

L. decidua reached the highest Ψpd (–0.29 MPa) after high precipitation at the end of June (day 174), it then decreased gradually until the end of August, when the minimum was reached (–1.0 MPa, day 237). In September a new increase in Ψpd was recorded according with the variation in Ψm when high precipitation, high soil water availability and low vapour pressure deficit (VPD) occurred.

P. abies and *P. cembra* showed more parallel variations until the end of the MWDP. In *P. cembra* Ψpd appeared lower than the other two species except at the end of July. In contrast to *L. decidua*, both species exhibited a reduction in Ψpd in relation to the MWDP (about 0.3 MPa) and a slow recovery over 2–3 weeks.

The minimum water potential (Ψm) curves in *P. abies* and *P. cembra* are well related to precipitation variations (*figure 3*). The lowest values (–1.18 and –1.49 MPa, respectively) occurred at the end of the MWDP, the highest (–0.52 and –0.60 MPa) on 22 June (day 174). *P. cembra* also had lower Ψm values probably due to the sampling method (needles instead of twigs).

L. decidua showed a completely different behaviour: Ψm decreased regularly from June (–0.7 MPa) to the end of July (day 215), stabilizing at about –1.9 MPa until the end of August (day 237). Afterwards Ψm again increased, reaching the values of the beginning of the season. In this species no close relationship was found between short-term variations in precipitation and Ψm.

3.2. Daily and seasonal variations in sap flux density (Fd)

Examples of Fd and Ψ courses throughout a typical day at the beginning of August are shown in *figure 4*.

Due to frequent cloudiness variations at high altitude, air temperature (and VPD), as well as solar radiation, change accordingly.

L. decidua appeared strongly coupled with the variations in VPD. Fd increases very sharply reaching the daily maximum

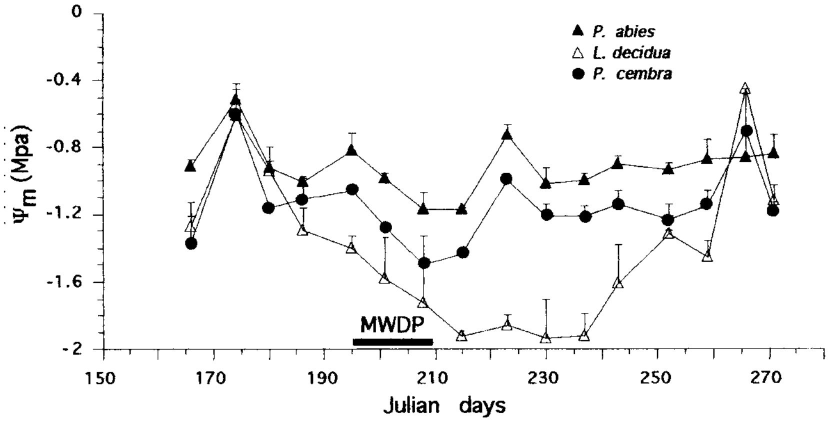

Figure 3. Seasonal variations of minimum xylem water potential in selected tress. Error bars = ± SD

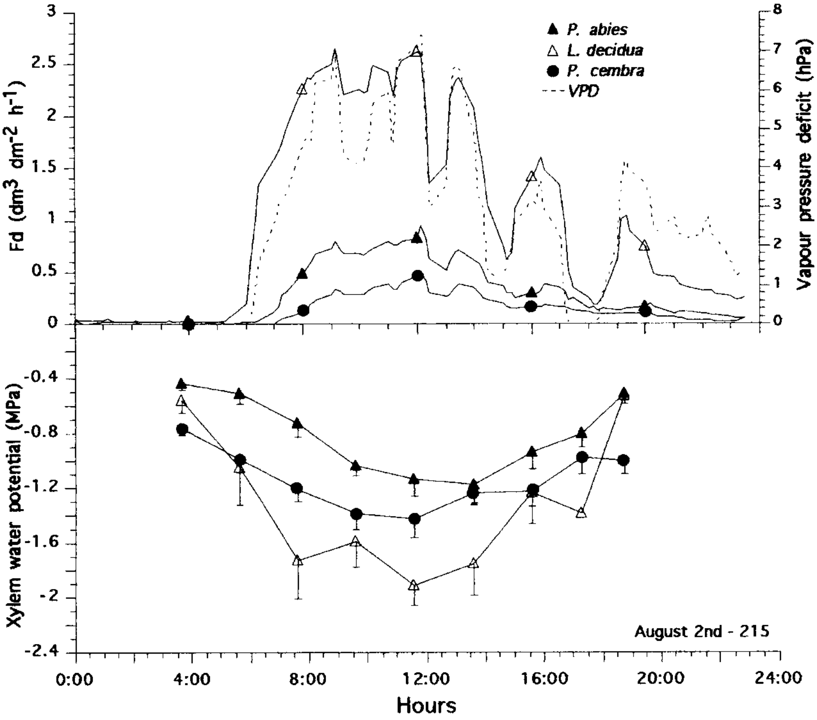

Figure 4. Daily variations of Fd, VPD and Ψ in relation to changing weather conditions.

(mean maximum range 3–3.5 dm^3 dm^{-2} h^{-1}) a couple of hours after sunrise. Ψ decreases rapidly as well: 4 h later it can be 1 MPa lower. Ψm is normally reached after noon and the recovery can be quite fast.

Fd in *P. abies* began later and the maximum value is much lower than *L. decidua* (mean maximum range 0.8–1.0 dm^3 dm^{-2} h^{-1}). Variations in Fd are less dependent on VPD and the course of Ψ appeared more regular.

P. cembra had the lowest Fd values (mean maximum range 0.6–0.8 dm^3 dm^{-2} h^{-1}). Ψm is reached just after noon but subsequent recovery is the slowest among the three species.

Fd daily sum variations and the average diurnal VPD (from 6 a.m. to 8 p.m.) were calculated for the entire measurement period *(figure 5)*.

The mean VPD throughout the growing season was quite low, as expected in a timberline environment. All species showed Fd variations coupled with VPD but, due to high stomatal sensitivity (see below) Fd is well correlated to VPD only below the treshold of 7–8 hPa. When VPD is higher stomatal conductance decreases leading to a reduction in the expected Fd.

During the MWDP no significant changes in Fd were recorded in *L. decidua*. On day 205 (VPD 6.8 hPa) daily Fd was 33.5 dm^3 dm^{-2} d^{-1}; on day 210, at the end of the MWDP (VPD 5.8 hPa), about 32 $dm^3\ dm^{-2}\ d^{-1}$. These values were close to those recorded on similar days (e.g. day 196 Fd = 34; day 222 Fd = 32.5), showing no influence of the soil drying out.

On the contrary, *P. abies* showed an evident reduction in Fd during the MWDP (day 205 Fd = 10 versus day 196 Fd = 12.5; day 210 Fd = 7.5 versus day 222 Fd = 11) reaching about –35 % under the same VPD conditions. The extent to which *P. cembra* Fd was influenced by MWDP appeared slightly different from *P. abies*. At the beginning of the MWDP (day 205) Fd seemed not reduced if compared with day 196: 8.5 versus 9, respectively, but after some days (day 210 versus 222) Fd appeared strongly reduced (–35 %).

In order to better define the effect of MWDP on Fd of studied trees a comparison between the cumulated Fd over a 7-d wet period versus 7 d during the MWDP has been made *(table III)*. The effect of MWDP on cumulated Fd of the evergreen species is expressed in relation to cumulated Fd in *L. decidua* which is the only species not affected by water shortage. Fd is reduced by 25 % in *P. abies* and 32 % in *P. cembra*.

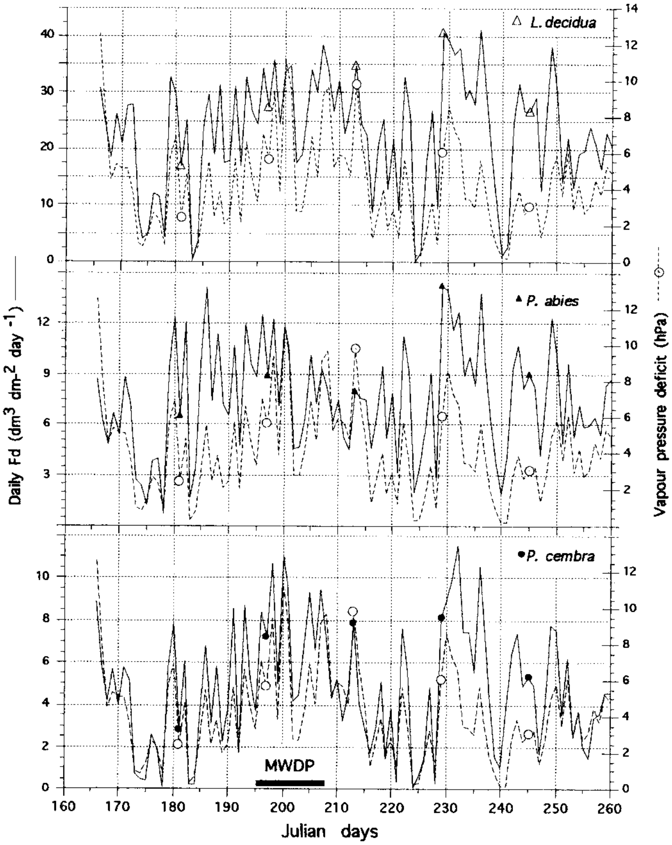

Figure 5. Seasonal variations of Fd for the three measured species and VPD. VPD curve has been drawn in each plot for better visual appreciation.

The seasonal maximum in Fd was on days 230–232 in all species, just after abundant rainfall even if very high transpiration rates were also recorded in July.

Scattergrams of Fd daily highest values versus VPD at the same time highlights the relationship between the former and stomatal control *(figure 6)*. Regard-

Table III. Comparison between Fd cumulated over 7 'wet' days versus 7 days during the MWDP.

Species	Cumulated Fd 'wet' period	Cumulated Fd MWDP	Ratio MWDP / 'wet'	Fd Reduction versus L. decidua
L. decidua	206	211.2	1.03	—
P. abies	74.3	56.8	0.76	0.75
P. cembra	56.9	39.6	0.70	0.68

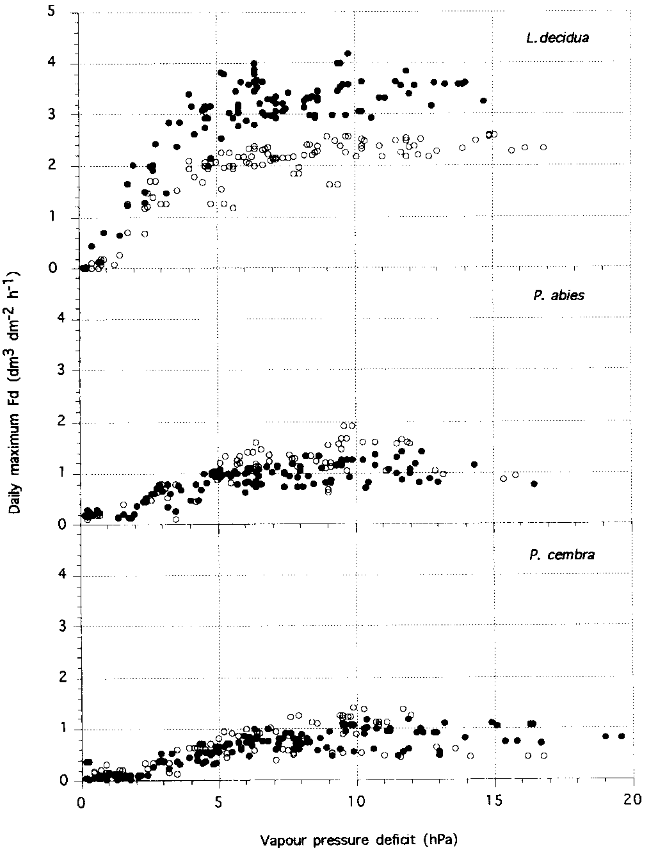

Figure 6. Relation between maximum daily Fd and VPD. VPD values correspond to maximum Fd measurements. Different circles (solid and open) refer to two individual trees.

less of species and tree, Fd increases with increasing VPD from 0 to 4–5 hPa, then tends to stabilize and over 8 hPa no relevant increase was recorded. The shape of the scatters showed clearly that a strong stomatal control occurred, suggesting a very high sensitivity of these species to water deficit.

Differences between Larch #1 and #2 are probably due to the position of the probes in the stem. This may occur using single probe measurements [20].

3.3. Seasonal variation in hydraulic conductance (HC)

Hydraulic conductance showed large variations throughout the season *(figure 7)*. The highest values corresponded to highest precipitation at about the end of June when air temperature was also particularly low and soil evaporation was prevented.

All three species showed a marked depression in HC during the MWDP. HC values in *L. decidua* were always higher than in the other two evergreen species except for two days after the end of the MWDP. In *P. cembra* and *P. abies* HC dropped to minimum values at the end of the MWDP. With the following precipitation HC in *P. cembra* rose quickly while *P. abies* needed 2 weeks to recover values comparable to the beginning of the season.

4. DISCUSSION

Small variations in Ψpd and Ψm both in *P. abies* and *P. cembra* over the season are due to the high frequency of precipitation but also showed that they are able to use the available moisture in an economical way.

Values of Ψm in *P. abies* were significantly higher than in other studies [25] suggesting that a more pronounced water saving behaviour was developed. Moreover Ψm appeared to be much higher than the turgor loss point which, at the alpine timberline, was found to be relatively constant throughout the growing season at about –2.8 MPa [2]. Stomatal control

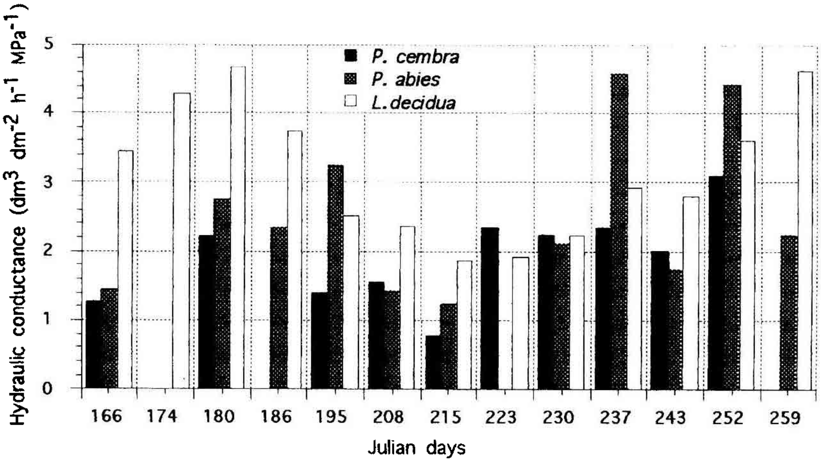

Figure 7. Seasonal variations of HC in selected trees. Bars indicate averaged values for each trees.

therefore occurred well above the threshold of both incipient plasmolysis and of significant loss of xylem functionality in conifers (at least 2.5 MPa [5]).

The roughly constant decrease in Ψpd and Ψm from the beginning of June until the end of July in *L. decidua (figure 3)*, followed by the increase at the end of the season could be due to an osmotic adjustment (even if it seems to have little importance in conifers) [16]. Osmoregulation should allow maintenance of physiological activity (i.e. turgor maintenance) as Ψ falls [28]. Hence, the species enhanced its water uptake ability in the mid-summer when it is more likely that moderate water deficit occurs. In *L. decidua* the value of Ψm also appeared above the threshold for inducing xylem dysfunctions.

It is well known that *L. decidua* develops a deep root system which allows it to utilize water sources in the deepest and wettest soil layers as also demonstrated using hydrogen stable isotope analysis [34].

As expected, under non-limiting soil moisture conditions, *L. decidua* exhibited a Fd higher (up to about three times) than the other two evergreen species. This depends mainly on its deciduous strategy, since the shorter assimilation period [26, 32] must be associated with a higher photosynthetic capacity and hence with a more effective stomatal gas exchange.

A high level of coupling between canopy and atmosphere was demonstrated for coniferous stands [27] and this is particularly true in a less dense stand as occurs at the timberline. In our trees, VPD appeared to be the major factor determining Fd, and among the species *L. decidua* showed the best degree of coupling *(figure 4)*. This may be due both to the less dense crown structure which determines a more efficient air mixing and to the lower stem–branch capacitance (in *L. decidua* and *P. abies* water is stored mainly in branches as demonstrated by Schulze et al. [30]). In fact, if the stem and branches have little capacity to store water and desaturate the reservoirs the variations in Fd measured at 1.3 m will be strongly dependent on stomatal behaviour. This is also partially confirmed looking at the quite good coherence between variations in Ψ measured in shoots and Fd *(figure 4)*.

Less variability in Fd of *P. abies* and *P. cembra* also suggests a more efficient water loss control. The lowest Fd are found in *P. cembra* and this is consistent with the widespread belief that *P. cembra* is the most drought resistant species (with a water saving strategy) at the alpine treeline [32]. A bigger time lag between the start of sap flow and the decreasing of twig water potential confirmed a higher stem–branche capacitance of the two evergreen species.

The course of seasonal Fd highlighted a strong impact of MWDP on *P. abies* and *P. cembra (figure 5; table III)*. Both species seemed unable to maintain an adequate water supply to the leaves after a few days without rainfall. This led to a decrease in the assimilation rate when the supposed most ‘favourable’ weather conditions (high temperature and radiation) occurred.

Stomatal sensitivity appeared particularly pronounced since stomatal control began at 4–5 hPa VPD. Lower sensitivity to soil drought and higher drought resistance has been demonstrated in lower elevation species compared to high mountains species [4, 25]. Values of HC in *P. abies* appeared similar to other measurements at the same Ψpd conditions [10].

During the MWDP the HC decreased sharply in all three species but remained generally higher in *L. decidua*. Since trees did not experience xylem water potential below the threshold of significant loss of xylem functionality in conifers, at least 2.5 MPa [5] the drop in HC seemed mainly to be due to an increase of hydraulic resistance between soil and root interface. Hence, it appeared that soil moisture could play an important role in determining water stress conditions in some species at the timberline. Due to the lowering of Ψm *L. decidua* was able to take up water in drier conditions than did *P. abies* and *P. cembra,* which appeared more susceptible to water shortage. The results showed that, despite high precipitation, soils at high altitude could become physiologically dry because they are shallow, discontinuous and highly permeable.

High temperatures and VPD not associated with an adequate water supply appeared to have a negative effect on *P. abies* and *P. cembra* growth. Since, in this zone, the growing period (considered as a period of wood formation at DBH) is about 50 d [1], any break in assimilation processes could have a considerable impact on total annual growth.

Moreover, since trees adapted to cold climates have a relatively low temperature optimum for photosynthesis (between 10 and 14 °C [33]) high temperatures are not necessary to develop maximum assimilation rate.

In fact no significant variations in Fd were recorded on bright and warm days as compared to relatively cloudy days. Trees seemed unable to make the most of the fine weather conditions. The early stomatal control when VPD approaches 4–5 hPa, irrespective of species studied, undoubtedly affects growth potential. This high stomatal sensitivity was also reported in other spruce species [13].

The different response recorded in *P. abies* and *P. cembra* as compared with *L. decidua* allows us to speculate that in the case of an increase in air temperature (and VPD) the latter could be favoured in competition against the former. Predictions on a change in stand composition must be carefully evaluated considering possible future scenarios of precipitation and cloudiness due to climate warming as well as the effect of higher CO_2 concentration on tree growth [29].

If precipitation rate, regimes and cloudiness should change towards more xeric conditions, as has been hypothesized [35], in the long term, a change in species composition in timberline should not be exluded.

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