

# Comparative studies of the water relations and the hydraulic characteristics in *Fraxinus excelsior*, *Acer pseudoplatanus* and *A. opalus* trees under soil water contrasted conditions

Damien Lemoine<sup>a</sup>, Jean-Paul Peltier<sup>b</sup> and Gérard Marigo<sup>b,\*</sup>

<sup>a</sup>Laboratoire de Biologie Forestière, Équipe Écophysiologie Cellulaire et Moléculaire, Université Henri Poincaré, BP 239, 54506 Vandœuvre-lès-Nancy Cedex, France

<sup>b</sup>Écosystèmes et Changements Environnementaux, Centre de Biologie Alpine, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France

(Received 23 March 2001; accepted 2nd July 2001)

**Abstract** – Plant water relationships and hydraulic characteristics were measured for two species of the genus *Acer* that co-occur with *Fraxinus excelsior*, but differ in their habitat preference with respect to soil moisture: *Acer pseudoplatanus* is restricted to wet habitats, whereas *Acer opalus* occurs on drier sites. The data obtained showed significantly lower hydraulic conductance and lower vulnerability to embolism in the drought-tolerant species, *Acer opalus*, than in the water preferring species *Acer pseudoplatanus*. Similar differences in hydraulic conductance and xylem vulnerability to embolism were also found under dry acclimated conditions for *Fraxinus excelsior* trees, indicating that the hydraulic differences observed might be attributable to the contrasting soil water conditions of the sites. The possible physiological and ecological significance of such differences are discussed, in relation to habitat preference and the distribution of each species.

**hydraulic conductance / xylem embolism / drought tolerance / *Acer pseudoplatanus* / *Acer opalus* / *Fraxinus excelsior***

**Résumé** – Étude comparée des relations hydriques et des caractéristiques hydrauliques chez *Fraxinus excelsior*, *Acer pseudoplatanus* et *Acer opalus* dans différents milieux secs et humides. Ce travail concerne l'étude des relations hydriques et la détermination des caractéristiques hydrauliques chez deux espèces du genre *Acer*, présentes fréquemment dans les espaces naturels en compagnie de *Fraxinus excelsior*, mais différant dans leur mode de distribution en fonction de la disponibilité de l'eau du sol : *Acer pseudoplatanus* se rencontre sur des sols bien alimentés en eau, *Acer opalus* a une préférence marquée pour les milieux secs. Les résultats obtenus montrent, chez *Acer opalus*, l'espèce tolérante à la sécheresse, que la conductance hydraulique et la vulnérabilité à la cavitation sont moins fortes que chez *Acer pseudoplatanus*, l'espèce des zones humides. Des modifications identiques de la conductance hydraulique et de la vulnérabilité à la cavitation s'observent également chez *Fraxinus excelsior* pour l'espèce acclimatée aux milieux secs, ce qui semble indiquer que ces changements des caractéristiques hydrauliques pourraient être associés aux conditions hydriques des milieux. Ces résultats sont analysés au plan physiologique et écologique en relation avec le mode de distribution de ces espèces dans leur environnement respectif.

**conductance hydraulique / embolie du xylème / tolérance à la sécheresse / *Acer pseudoplatanus* / *Acer opalus* / *Fraxinus excelsior***

\* Correspondence and reprints  
Tel. (33) 04 76 51 46 74; Fax. (33) 04 76 51 44 63; e-mail: gerard.marigo@ujf-grenoble.fr

## 1. INTRODUCTION

Water availability is one of the most important factors which influence not only the growth and development of plants, but also the spatial distribution of species in their appropriate habitat [8]. Cyclic droughts favor the establishment of species which are able to acclimate to water deficits, the resulting selection tending, in contrast, to eliminate species that are not able to do so.

There is ample evidence indicating that the structure of the plant hydraulic system – the hydraulic architecture – has the potential to limit water flow through plants, thus restricting their water balance, their gas exchange, and their growth [18]. A number of studies have shown that the hydraulic architecture of trees may be related to the processes of drought adaptation [20, 22]. Consequently, studying the differences in the hydraulic architecture of plants may help us to understand species habitat preferences with regard to water availability in soils.

In this study, we were interested in the mechanisms of water status regulation in two coexisting species from the highly diverse genus *Acer*, with respect to their spatial distribution. These are *Acer pseudoplatanus*, which is found only to fresh and wet habitats (alluvial flood plains) or very moist microsites such as ravines in the mountains, up to 1800 m, and *Acer opalus*, which is found in lower mountain areas subject to pronounced dry seasons, and which tolerates relatively dry and hot microsites such as hillslopes. For a comparative study, these experiments were also extended to include *Fraxinus excelsior* trees, which have been found to occur with *Acer pseudoplatanus* or *Acer opalus*, depending on the environmental conditions [11]. In fact, the common ash is a mesophilic species that usually thrives on well-watered alluvial soils, but which can also survive the strong water deficit on hillslopes [7]. These different species are common and widespread throughout the North Alpine region [11].

The objectives of this study were to assess the water status of the plants by monitoring the diurnal changes in stomatal conductance and leaf water potential during hot sunny days. These experiments were carried out on trees of the different species growing at three sites with different soil moisture conditions. Some properties of the hydraulic system, such as the hydraulic conductance and the vulnerability to cavitation, were characterized to determine if species with different habitat preferences had different hydraulic architecture characteristics and also to see if differences in hydraulic architecture between

species might explain the habitat preferences. There is evidence from the literature that xylem conductance is sensitive to drought conditions [1, 5, 12] but there is little information available on the effect of drought acclimation on xylem vulnerability to embolism.

## 2. MATERIALS AND METHODS

### 2.1. Site and plant material

This study was carried out on three different species, *Fraxinus excelsior* L., *Acer pseudoplatanus* L., and *Acer opalus* Mill., on three different sites. The first site, which is located along the Isere river on the Campus of the University of Grenoble (45° 20' N, 5° 30' E, elevation 200 m), is well-watered [10]. Ash trees (15–20 years old, 13 m tall) and *Acer pseudoplatanus* trees (10–15 years old, 10 m tall) occur in this place, mixed with other coexisting tree species (*Tilia cordata* Mill.), on an alluvial soil with a water table at a depth of between 2.20 and 2.50 m, on average [10]. The second site is situated between Saint-Georges de Commiers and Grenoble, along an affluent of the Drac river which dried up partially, some ten years ago, due to the presence of a dam across the upper part of the stream (Saint-Georges de Commiers dam). On this plain, (45° 4' N, 5° 43' E, elevation 280 m) the coarse texture of the substrate (shingle, gravel, rough sand) explains the dryness of the soil [2]. This water-deprived area has been colonized by xeric and mesoxeric species (*Astragalus monspessulanus*, *Festuca duriuscula*, *Sedum album*, *Plantago cynops*, *Helichrysum stoechas*), and *Fraxinus excelsior* is found in this area in association with *Acer opalus*, instead of *Acer pseudoplatanus*. Some other hydraulic characteristic measurements were also carried out on trees growing in a mesoxerophilic mountain stand (site 3) in the intermediate zone of the North-western Alps (45° 4' 34" N, 6° 3' 21" E, elevation 1350 m). Vegetation, soil and climate at this station have been described in detail by Carlier et al. [3] and Peltier et al. [13]. Compared to the alluvial floodplains, the size of *Fraxinus excelsior* and *Acer opalus* trees present on the dry sites is smaller (4–6 m tall). For *Fraxinus excelsior*, analysis of chloroplastic DNA showed that the floodplain and the mountain species were genetically similar [6]. In most of the experiments carried out in all three stations, two trees per species were studied for each population.

## 2.2. Water potential, transpiration and stomatal conductance

Leaf water potential ( $\psi_w$ ), stomatal conductance (Gs) and transpiration (E) were monitored periodically throughout the day, at different times, as indicated in the legends of the tables and figures. Leaf water potentials were assessed by a Scholander pressure chamber [15]. Predawn leaf water potential ( $\psi_{wp}$ ), was measured at sunrise (4h00 solar time; GMT). Stomatal conductance and transpiration were measured hourly from 6h00 to 17h00 hours GMT with a Li-Cor-1600 diffusive resistance porometer (Li-Cor, Lincoln, Neb.). Five south-facing leaves taken randomly from the same position, and which had been submitted to the same illumination level, were used in the different species. Since the diurnal changes of stomatal conductance and transpiration were similar, the values of the transpiration indicated in tables and figures were the maximum values ( $E_{max}$ ). All of these measurements were made during the summers of 1999 and 2000, on two sunny days in each season.

## 2.3. Hydraulic conductivity analysis

Xylem hydraulic conductivity was determined on 1- to 3-year-old twigs from 1 to 2 m long branches collected in the morning from mature trees. The branches were enclosed in black airtight plastic bags to reduce water loss through transpiration, and brought rapidly to the laboratory for hydraulic analysis. In the laboratory, the branches were recut under water. After rehydration, segments about 2–3 cm long were excised under water from different growth units of each branch, shaved at both ends with a razor blade, and then fitted to plastic tubes at the basal end. The segments were then perfused with filtered (0.2  $\mu$ m) deionized water with a pressure difference of 0.1 MPa through each sample. Any air embolisms were eliminated by successive water pressurization for 10–15 min in order to restore the full capacity of the xylem. After removing the gas bubbles in the water, maximum conductivity ( $K_{max}$ ,  $\text{mmol s}^{-1} \text{m MPa}^{-1}$ ) was determined by forcing distilled water, with a pressure difference of 3.7 kPa, through each sample. The resulting flow rate ( $\text{mmol s}^{-1}$ ) was measured using an analytical balance (Sartorius). At the end of the measurement, the segment diameter was measured (m, bark not included) to determine the specific conductivity ( $\text{mol s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ ) which takes into account vessel diameter and the number of vessels in the samples [9, 21].

Hydraulic efficiency was also characterized in leaf blades. The principle of the measurements is similar to that used for branch segments. The leaf used was first perfused with deionized water under a pressure of  $P = 0.1$  MPa in order to restore the full capacity of the water conducting vessels. At this stage, some free water appears at the stomata level. The leaf was then fixed on a plate of an analytical balance and the water flow was induced by forcing distilled water through the leaf with a pressure difference of 0.1 MPa. The water flow was determined by measuring the changes of the leaf weight when the flow became constant. The specific conductivity of the leaf was calculated as the ratio between F and P, and related to the leaf area ( $K_s$ ,  $\text{mmol s}^{-1} \text{MPa}^{-1} \text{m}^{-2}$ ).

## 2.4. Vulnerability curves

Vulnerability curves (VCs) were established for excised well-watered branches in which embolism was induced in a long pressure chamber (0.4 m), as described by [4]. Air pressure in the chamber was maintained at the designated values (between 1 and 5 MPa) using nitrogen, until sap exsudation ceased (after 10 to 60 min, depending on the pressure applied). For each pressure treatment, the percentage loss of hydraulic conductivity (PLC) was measured for 6 to 8 randomly rachise segments (ash) or petiole segments (maple) and 6 shoot internodes. The shape of the sigmoid curve was characterized by two critical points,  $\psi_{cav}$  and  $\psi_{100}$  which indicated the water potential values that induced the start of the embolism, and 100% of the maximal hydraulic conductivity, respectively  $\psi_{cav}$  and  $\psi_{100}$  were measured graphically from each VC. VCs were produced for two trees of each population.

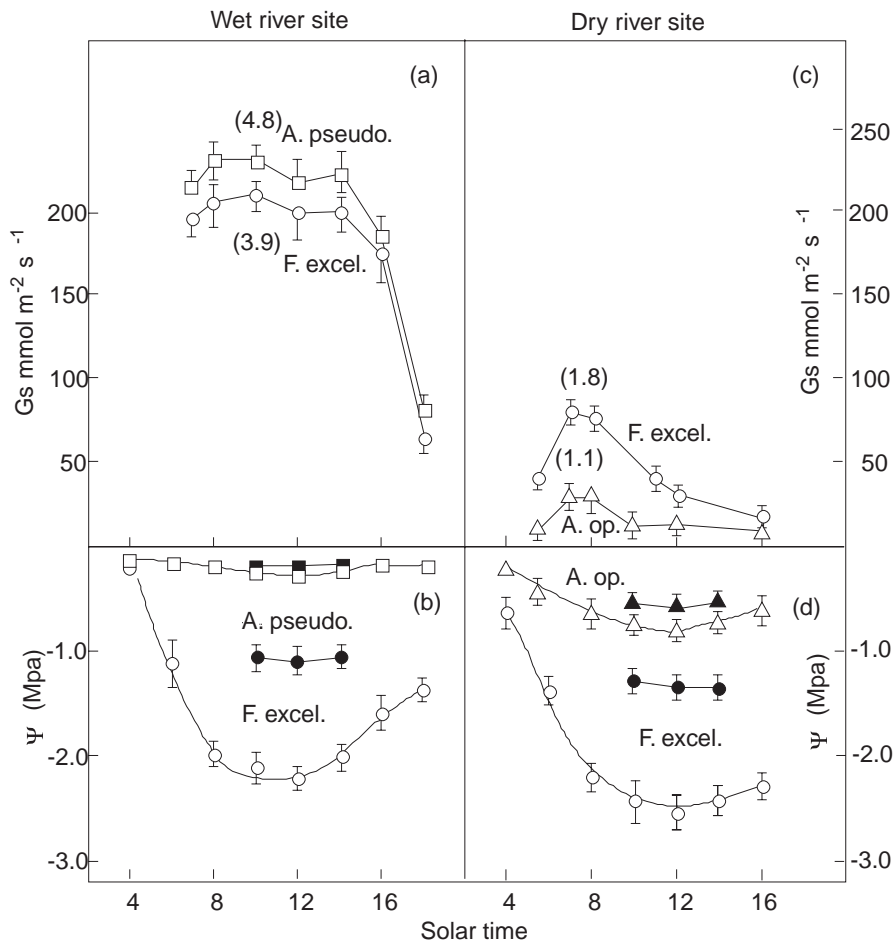
## 3. RESULTS

### 3.1. Comparative study of diurnal regulation of the water status in *Acer pseudoplatanus* and *Fraxinus excelsior* trees growing in well-watered floodplains (site 1)

The experiments were carried out in June 1999 and 2000, for expanded leaves in a high solar radiation environment. Daily irradiance followed a bell-shaped curve. The riparian water table was constantly refilled with water originating from a tributary of the Isere river. This situation provides a massive water supply and extensive

water availability to the trees. Under these conditions, the leaves of ash and *Acer pseudoplatanus* trees did not present significant differences in their diurnal change in stomatal conductance (figure 1a). For both species, stomatal conductance tended to remain close to its maximum value during the morning and the beginning of the afternoon, allowing a high transpiration rate (4.8 and 3.9 mmol m<sup>-2</sup> s<sup>-1</sup> for maple and ash trees, respectively, in June, figure 1a). In ash trees, the water potential of leaves exposed to the sun gave a sinusoidal curve over time: it decreased sharply in the morning and sometimes fell as low as -2.2 MPa, with a minimum around solar noon,

when the transpiration rate was high. This trend appeared to be a general pattern for ash trees, as indicated by similar diurnal  $\psi_w$  curves on expanding leaves determined in other years [10]. In contrast to ash leaves, the leaf water potential of *Acer pseudoplatanus* showed low diurnal variations. During the first part of the morning,  $\psi_w$  remained similar to the predawn leaf water potential ( $\psi_{wp}$ ), at a value of about -0.1 MPa, then declining slowly to the minimum value ( $\psi_m$ ) reached at solar noon. No matter what experiments were performed under conditions of extensive water availability,  $\psi_m$  never decreased below -0.3 MPa.



**Figure 1.** Daily course of stomatal conductance ( $G_s$ , mmol m<sup>-2</sup> s<sup>-1</sup>) and leaf water potential ( $\psi_w$ , MPa) in leaves of *Fraxinus excelsior* (○) and *Acer pseudoplatanus* (□) trees growing on the wet river site (a, b) or in leaves of *Fraxinus excelsior* (○) and *Acer opalus* (△) trees growing on the dry river site (c, d). The values of the maximal transpiration (mmol m<sup>-2</sup> s<sup>-1</sup>) are given in parenthesis. The full symbols represent the values of the xylem water potentials. Data represent mean value of two sunny days in June 2000. Errors bars indicate standard deviation ( $n = 10$ ). Identical experiments repeated the previous year (June 1999) led to the same variations.

### 3.2. Regulation of water status in *Fraxinus excelsior* and *Acer opalus* trees growing in low-watered floodplains (site 2)

During these experiments, most days were completely sunny with high temperatures, and no extensive nightly precipitation. In comparison to the changes in stomatal conductance and leaf water potential observed in well watered flood plains for *F. excelsior* and *A. pseudoplatanus*, the dry conditions of the floodplains led to a decrease in the leaf water potentials for *F. excelsior* and *A. opalus* (figure 1d). This decrease in water potential was always larger, however, in *F. excelsior*. The first sign of soil water depletion in this site was given by the predawn leaf water potential ( $\psi_{wp}$ ) value in *F. excelsior*, which decreased noticeably ( $-0.6$  MPa, figure 1d) compared to the wet site ( $-0.2$  MPa, figure 1b). This drop in  $\psi_{wp}$  was increased in *F. excelsior* with the length of the drought period (table I). This could also be observed in *A. opalus*, but later on, in the final days of July (table I). It should be noted that this  $\psi_{wp}$  decrease, in *A. opalus*, was lower than that observed in *F. excelsior* (figure 1d, table I).

The drier conditions also drastically limited stomatal conductance and transpiration in ash and *A. opalus* trees, relative to the species found in humid riparian area. Under a low soil water regime, both *F. excelsior* and *A. opalus* in fact showed a decrease in stomatal conductance after the first hours of the morning resulting in low transpiration rates ( $1.8$  and  $1.1$   $\text{mmol m}^{-2} \text{s}^{-1}$  for ash and maple trees, respectively, in June, figure 1c). In comparison of *F. excelsior*, the limitation of stomatal conductance was greater in *A. opalus* (figure 1c). It was especially severe for both species in the last days of July, when the stomata were nearly closed (table I).

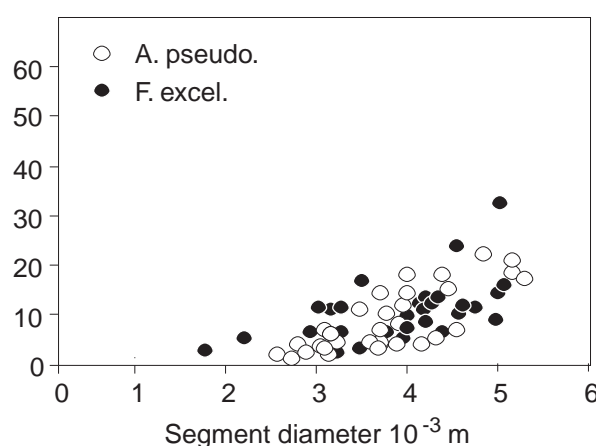
**Table I.** Effect of a summer drought on some plant water relationships in *Acer opalus* and *Fraxinus excelsior* trees growing in the valley of the Drac river. The experiments were carried out in the last days of July 2000. Data are the means of ten determinations ( $\pm$  SD) from two trees.  $\psi_{wp}$  is the predawn leaf water potential,  $\psi_m$  is the minimum midday leaf water potential.  $E_{\max}$  and  $G_{\max}$  are the maximum values for transpiration and stomatal conductance respectively.

	$\psi_{wp}$ (MPa)	$\psi_m$ (MPa)	$E_{\max}$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	$G_{\max}$
<i>F. excelsior</i>	$-2.3 \pm 0.1$	$-3.8 \pm 0.15$	$0.26 \pm 0.01$	$11 \pm 2$
<i>A. opalus</i>	$-0.58 \pm 0.05$	$-1.7 \pm 0.1$	$0.32 \pm 0.05$	$14 \pm 3$

### 3.3. Hydraulic characteristics and vulnerability to embolism

Figure 2 shows the hydraulic conductivity of stem segments taken in *A. pseudoplatanus* and *F. excelsior* trees after embolism dissolution ( $K_{\max}$ ), as a function of stem diameter.  $K_{\max}$  increased with stem diameter, but there was no significant modification between the values of the hydraulic conductivity for each species. The hydraulic properties of the system that conducts water were also analysed in the leaves (table II).  $K_s$  decreased markedly in the rachises and the leaf blades of ash trees when compared with *A. pseudoplatanus* by a factor of 2 and 4, respectively, on average (table II).

Table III shows the hydraulic conductivity for leaf petioles of *A. pseudoplatanus*, *A. opalus* and rachises of *F. excelsior* trees growing in the different habitats. For *F. excelsior* there is a decrease in  $K_s$  under dry conditions



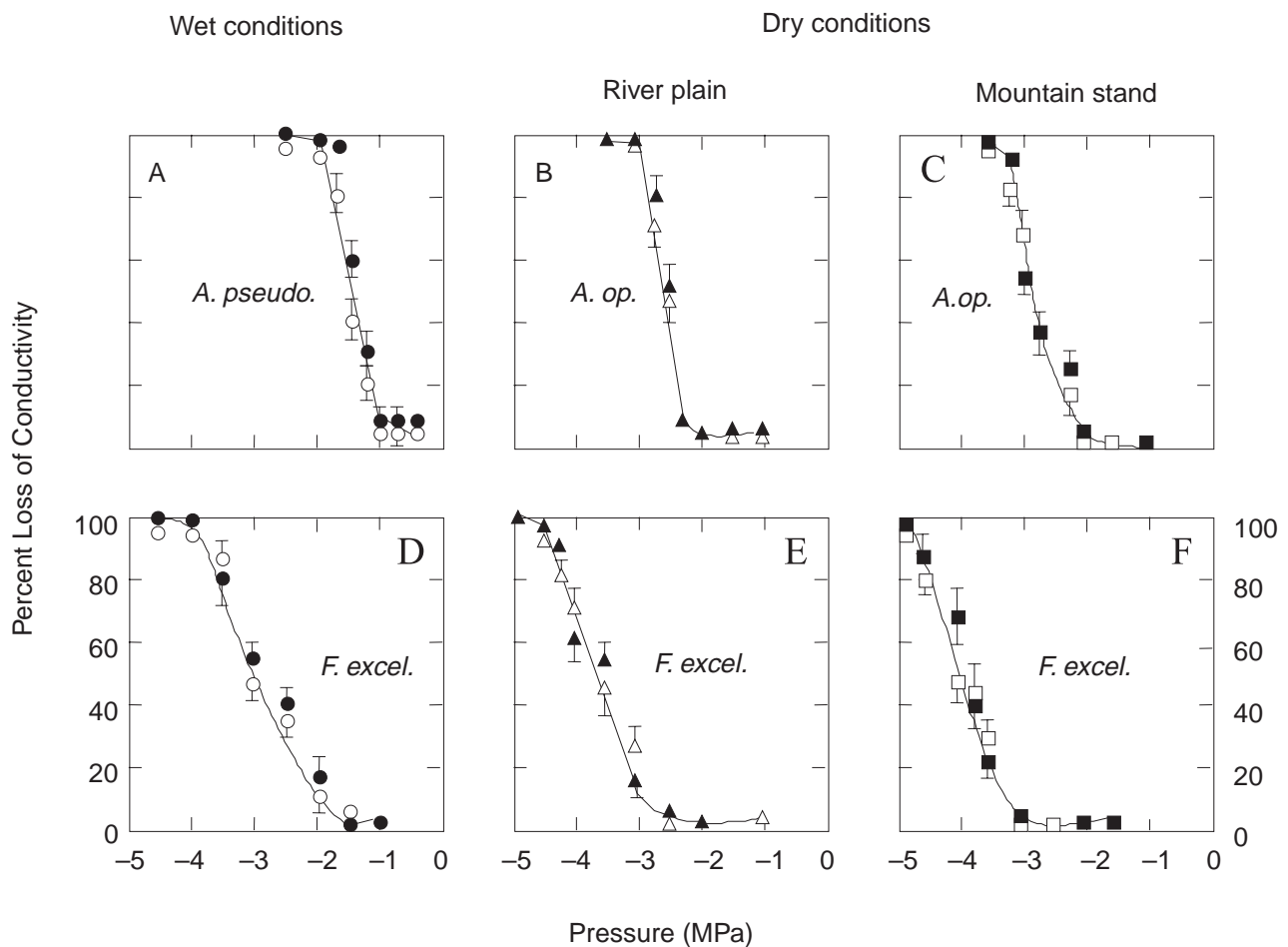
**Figure 2.** Xylem hydraulic conductivity ( $K_{\max}$ ,  $\text{mmol s}^{-1} \text{mPa}^{-1}$ ) versus segment diameter (bark excluded). Xylem segments, 2 cm long were excised from shoot internodes of adult branches taken from *Fraxinus excelsior* (●) or *Acer pseudoplatanus* (○).

**Table II.** Xylem segment and leaf specific conductivity in *Fraxinus excelsior* and *Acer pseudoplatanus* trees. Segments were excised from the rachises (ash) or petioles (maple) of leaves from each species. Data are means  $\pm$  SD with  $n$  being the number of replicates from two individual trees.

	$K_s$ segments $\text{mol s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$	$K_s$ leaves $\text{mmol s}^{-1} \text{MPa}^{-1} \text{m}^{-2}$
<i>A. pseudoplatanus</i>	$2.38 \pm 0.11$ ( $n = 21$ )	$2.08 \pm 0.17$ ( $n = 15$ )
<i>F. excelsior</i>	$1.10 \pm 0.07$ ( $n = 14$ )	$0.50 \pm 0.13$ ( $n = 15$ )

**Table III.** Xylem specific conductivity ( $K_s$ ) for leaf petioles of *Acer pseudoplatanus*, *Acer opalus*, and rachises of *Fraxinus excelsior* trees growing in different habitats. For dry conditions, two different sites were selected, one in the valley of the Drac river, the other in a mountain stand in the Alps. The  $K_s$  ( $\text{mol s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ ) data are means  $\pm$  SD with  $n$  being the number of replicates from two trees of each population.

$K_s$	Wet conditions Isere river plain		Dry conditions			
			Drac river plain		Mountain stand	
	<i>F. excel.</i>	<i>A. pseudo.</i>	<i>F. excel.</i>	<i>A. opalus</i>	<i>F. excel.</i>	<i>A. opalus</i>
	1.1 ( $n = 14$ )	2.4 ( $n = 21$ )	0.34 ( $n = 26$ )	0.087 ( $n = 23$ )	0.24 ( $n = 28$ )	0.15 ( $n = 19$ )



**Figure 3.** Comparison of the vulnerability to embolism in *Acer pseudoplatanus* (A), *A. opalus* (B, C) and *Fraxinus excelsior* (D, E, F) trees growing in wet (A, D) or in dry conditions (B, C, E, F). For dry conditions, two different sites were selected, one in the valley of the Drac river, the other in a mountain stand in the Alps. The experiments were conducted on leaf petioles (full symbols) and branches (empty symbols). These data are obtained from two individual trees of each population. Errors bars represent one standard deviation ( $n = 6-8$ ).

(by a factor of about 4).  $K_s$  also was lower (factor 20 on average) in *A. opalus*, the drought-tolerant species, with respect to the water-demanding one, *A. pseudoplatanus*.

Figure 3 presents the vulnerability curves obtained for stems and petioles taken from *F. excelsior*, *A. pseudoplatanus* and *A. opalus* trees. For both species, there was little or no difference between stems and petioles (or rachises), which showed similar vulnerability to the cavitation processes. Under wet conditions, the branches and petioles of *A. pseudoplatanus* displayed a higher vulnerability to cavitation than those of *F. excelsior* (figure 3A and D), the major differences occurring for low  $\psi$  values ( $\psi_{cav}$  at  $-1.0$  and  $-1.5$  MPa and  $\psi_{100}$  at  $-1.8$  and  $-4.2$  MPa for *A. pseudoplatanus* and *F. excelsior* respectively).

In comparison to a wet habitat, dry conditions are associated with a decrease in vulnerability in *F. excelsior* (figure 3), especially for the low potentials (onset of embolism at  $-1.5$  and  $-2.5$  or  $-2.8$  MPa depending on the dry site, respectively). Vulnerability was also lower for the petioles of *A. opalus* (the dry habitat species) than those of *A. pseudoplatanus* (wet habitat species), with similar differences for  $\psi_{cav}$  and  $\psi_{100}$  (figure 3).

#### 4. DISCUSSION

When soil water availability is not limited (site 1), *F. excelsior* and *A. pseudoplatanus* trees exhibit, together, a high transpiration rate and an absence of stomatal regulation in response to the high evaporative demand. These common characteristics with respect to the water relationships for these two species are accompanied by specific modifications in diurnal leaf water potential, which shows large variations in ash leaves, but which does not decrease in *A. pseudoplatanus* below a value of  $-0.3$  MPa. These  $\psi_w$  variations are related in this study to a higher hydraulic conductance in *A. pseudoplatanus* leaves compared to that of *F. excelsior*. The higher the hydraulic conductance of the leaves, the less negative the leaf water potential is. With regard to its hydraulic properties, *A. pseudoplatanus* may be considered therefore as being water-consuming species. The loss of water by the transpiration is also important in ash leaves, but there are strong hydraulic resistances limiting water transfer from xylem vessels to the evaporative zones.

In the floodplains situated along the affluent of the Drac river (site 2), *F. excelsior* and *A. opalus* exhibit

together some typical responses of droughted plants in term of water relationships (1) a fall in leaf water potential and (2) a reduction of stomatal conductance. The water soil depletion in this site also is demonstrated by the values of  $\psi_{wp}$  in *F. excelsior*, which are lower compared to that in humid riparian area, and which decreases in the dry site with the length of the drought period between June and July. Interestingly, for ash trees growing in a dry habitat,  $\psi_{wp}$  is always lower in ash leaves compared to *A. opalus*, whatever the extent of the drought. From these data, it may be concluded that the root system of the *A. opalus* is more efficient with respect to water uptake than that of ash trees. Facilitation of water uptake in *A. opalus* trees may be due in part to the proliferation of a deep root system, as water is depleted. It has been reported recently that some deep-rooted plants, such as *Acer saccharum*, take in water from lower soil layers and exude this water into the upper soil layers. We suggested that this process, which has been termed the hydraulic lift [14], might also explain the lowest  $\psi_{wp}$  values in *A. opalus* trees observed in dry conditions.

In comparison to humid habitats, the drier conditions of water-deprived floodplains lead to a decrease in hydraulic conductance and an increased resistance to cavitation in the drought-tolerant species, *F. excelsior* and *A. opalus*. Similar relations between the dry conditions and the hydraulic characteristics may be also observed for *F. excelsior* and *A. opalus* species submitted periodically to a summer drought in a mesoxerophilic mountain stand.

In an attempt to find a relationship between the hydraulic architecture and the general ecological behaviour of 7 *Quercus* species, Nardini and Tyree [12] recently found a lower-leaf-specific hydraulic conductance in oak species that are typically adapted to aridity, with respect to those growing in humid areas. The same trends for whole plant hydraulic conductance and leaf-specific hydraulic conductance have also been observed for two co-occurring neotropical understory shrub species of the genus *Piper* which differ in their habitat preference [5]. These authors postulate that, in dry habitats, the ability to tolerate drought is more important than the ability to transport water rapidly, and that it might be more adaptive to optimize for the avoidance of embolisms than for high hydraulic conductance. In dry habitats, the rate of growth is less critical to the survival of plants and the need for water is, therefore, limited. We suggest that the decrease in hydraulic conductance, which helps to limit water flux through the xylem, is in itself an important feature of drought resistance. Indeed, superimposing a decrease in the hydraulic conductance on stomatal

regulation provides an additional means of reducing water use during prolonged drought, as a part of an avoidance strategy.

Another important component of the hydraulic architecture is vulnerability to drought-induced embolism. When the xylem water potential ( $\Psi_{\text{xylem}}$ ) in the water-conducting system exceeds a critical point ( $\Psi_{\text{cav}}$ ), the water columns may be disrupted and become air filled which cause embolism events and a xylem dysfunction [19]. Xylem dysfunction may be characterized by vulnerability curves which represent the changes in embolism level with increasing xylem potential. The determination of these curves, in *F. excelsior*, shows that stem and petiole segments, taken from trees growing on wet site, are more vulnerable than those from dry ones. These data are in agreement with similar observations concerning roots of *Acer grandidentatum* trees growing under contrasted soil water conditions, which are much more vulnerable in wet habitats [1]. When compared to ash trees, *A. pseudoplatanus* exhibits a high vulnerability to drought cavitation, which may be linked to the ecology of this species and its preference for wet habitats. The drought-avoiding species, *A. opalus*, shows a considerably lower xylem vulnerability than *A. pseudoplatanus*. These species suffered 50% loss of hydraulic conductivity when xylem potential fell to  $-1.4$  MPa for *A. pseudoplatanus* and  $-2.5$  MPa for *A. opalus* making the former the most vulnerable. In drier conditions, complete embolism of the xylem should occur for a xylem potential decrease of  $-1.8$  MPa in *A. pseudoplatanus*. A lower susceptibility to cavitation for branches appears to be necessary for the survival of this species at the drier site.

In conclusion, our data show that for two drought-tolerant species, *F. excelsior* and *A. opalus*, which are acclimated to dry conditions, a gain in hydraulic safety is associated with a loss in hydraulic efficiency. These data are in agreement with the trade-off between hydraulic conductance and vulnerability to xylem embolism that was reported earlier [22]. The significance of this trade-off should be investigated through the study of the structural/functional relationships. The mechanism by which xylem vulnerability acclimates to water stress is known to depend directly on pit pore membrane diameter [16, 17, 22], whereas hydraulic conductance is mainly related to conduit diameter [22]. During their development, the different tree organs acclimate to the environmental conditions, and therefore develop structures that acclimate them to environmental changes. Under wet conditions, plants optimize water conductance to accelerate the growth rate and differentiate large diameter conduits

adapted for high water transport. In contrast, plants need to invest less water for their growth in dry habitats, and therefore decreases in xylem vulnerability and in hydraulic conductivity may be advantageous for the avoidance of drought-induced embolism and for the limitation of water transport. These processes may be associated with small pores in the pit membranes and small diameters for water conducting vessels. Therefore, adaptation of the hydraulic conductance and embolism vulnerability seem to play an important role in determining species habitat preference.

**Acknowledgements:** This work was supported by financial assistance from the European Community, Contract N° EVK1-CT-1999-00031 (Proposal N° EVK1-1999-00154 Flobar 2). The authors thank Dr H. Cochard (INRA Clermont-Ferrand) for helpful criticisms of the first draft of this manuscript. They thank also M. Willison for correcting the English, J. Tissier for the assistance in the field and laboratory works, and J.P. Guichard for technical help.

## REFERENCES

- [1] Alder N.N., Sperry J.S., Pockman W.T., Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient, *Ecologia* 105 (1996) 293–301.
- [2] Blanchard E., Fonctionnement hydrologique, fonctionnement géomorphologique et dynamique de la végétation : la plaine d'inondation du Drac à proximité de Grenoble, Thèse Université Grenoble I, Grenoble, 1994.
- [3] Carlier G., Peltier J.-P., Gielly L., Comportement hydrique du frêne (*Fraxinus excelsior*) dans une formation montagnarde mésoxérophile, *Ann. Sci. For.* 49 (1992) 207–223.
- [4] Cochard H., Bréda N., Granier A., Aussenac G., Vulnerability to air embolism of three European oak species (*Quercus petraea* (Matt) Liebl, *Q. pubescens* Willd, *Q. robur* L.), *Ann. Sci. For.* 49 (1992) 225–253.
- [5] Engelbrecht B., Velez V., Tyree M.T., Hydraulic conductance of two co-occurring neotropical understory shrubs with different habitat preferences, *Ann. For. Sci.* 57 (2000) 201–208.
- [6] Gielly L., Taberlet P., Chloroplast DNA polymorphism at the intrageneric level and plant phylogenies, *C. R. Acad. Sci. Paris* 317 (1994) 685–692.
- [7] Guichard P., Peltier J.-P., Gout E., Bligny G., Marigo G., Osmotic adjustment in *Fraxinus excelsior* L.: malate and mannitol accumulation in leaves under drought conditions, *Trees* 11 (1997) 155–161.



- [8] Kozłowski T.T., Water supply and tree growth. Part I. Water deficit, For. Abstr. 43 (1982) 57–95.
- [9] Lemoine D., Granier A., Cochard H., Mechanism of freeze-induced embolism in *Fagus sylvatica* L., Trees 13 (1999) 206–210.
- [10] Marigo G., Peltier J.P., Analysis of the diurnal change in osmotic potential in leaves of *Fraxinus excelsior* L., J. Exp. Bot. 47 (1996) 763–769.
- [11] Marigo G., Peltier J.P., Girel J., Pautou G., Success in the demographic expansion of *Fraxinus excelsior* L., Trees 15 (2000) 1–13.
- [12] Nardini A., Tyree M.T., Root and shoot hydraulic conductance of seven *Quercus* species, Ann. For. Sci. 56 (1999) 371–377.
- [13] Peltier J.-P., Agasse F., De Bock F., Marigo G., Ajustement osmotique chez le frêne commun et stress hydrique, C. R. Acad. Sc. Paris 317 (1994) 679–684.
- [14] Richards J.H., Caldwell M.M., Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots, Oecologia 73 (1987) 486–489.
- [15] Scholander P.F., Hammel H.T., Bradstreet E.D., Hemmingsen E.A., Sap pressure in vascular plants, Science 148 (1965) 119–125.
- [16] Sperry J.S., Sullivan J.E.M., Xylem embolism in response to freeze-thaw cycles and water stress in ring porous, diffuse porous, and conifer species, Plant Physiol. 100 (1992) 605–613.
- [17] Sperry J.S., Saliendra N.Z., Pockman W.T., Cochard H., Cruiziat P., Davies S.D., Ewers F.W., Tyree M.T., New evidence for large negative pressure and their measurement by the pressure chamber method, Plant Cell Environ. 19 (1996) 427–436.
- [18] Tyree M.T., Ewers F.W., The hydraulic architecture of trees and other woody plants, New Phytol. 119 (1991) 345–360.
- [19] Tyree M.T., Sperry J.S., Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model, Plant Physiol. 88 (1988) 718–724.
- [20] Tyree M.T., Sinclair B., Lu P., Granier A., Whole shoot hydraulic resistance in *Quercus* species measured with a high-pressure flowmeter, Ann. Sci. For. 50 (1993) 417–423.
- [21] Tyree M.T., Yang S., Cruiziat P., Sinclair B., A maize-root dynamic model for water and solute transport, Plant Physiol. 104 (1994) 189–199.
- [22] Zimmermann M.H., Xylem Structure and the Ascent of Sap, Springer-Verlag, Berlin 1983.

