



Vulnerability of xylem to embolism in relation to leaf water potential and stomatal conductance in *Fagus sylvatica* f. *purpurea* and *Populus balsamifera*

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Abstract

The vulnerability of xylem vessels to water stress-induced cavitation was studied by measuring hydraulic conductivity and ultrasound acoustic emissions (AEs) in *Fagus sylvatica* L. f. *purpurea* (Ait.) Schneid. and *Populus balsamifera* L.. The occurrence of xylem embolism in summer was investigated in relation to leaf water potential and stomatal conductance. *Populus* was extremely vulnerable to cavitation, losing functional vessels due to embolism at water potentials lower than -0.7 MPa. *Fagus* experienced embolism when water potential fell below -1.9 MPa. Midday water potentials often approached these threshold values. When evaporative demand increased rapidly on sunny days, water loss became limited by low stomatal conductance. Thus water potentials fell only slightly below the threshold values inducing cavitation. Despite the differences in vulnerability, both species tolerated a similar embolism rate of about 10% in the summer. There was no embolism reversal during prolonged periods of rain. AEs were predictive of loss in hydraulic conductivity, indicating that AEs were mainly confined to vessels. Finally, vessel length distribution, vessel diameter (tangential axis), vessel density, and vessel wall thickness had been determined for both species investigated. *Populus* had longer and wider vessels than *Fagus*, whereas vessel wall thickness was similar in both species.

Key words: Acoustic emissions, *Fagus*, *Populus*, stomatal closure, xylem embolism.

Introduction

Xylem sap of plants is usually under a high tension in the growing season. Therefore, water columns may be

disrupted (cavitation). Cavitation leads to an air-filled (embolized) xylem conduit (Zimmermann, 1983). As a result of embolism, hydraulic conductance and possibly stomatal conductance is reduced. Some grasses (Poaceae) produce enough root pressure to reverse embolism over-night, so a high embolism rate on a given day can be tolerated (Tyree *et al.*, 1986; Neufeld *et al.*, 1992). In trees, however, there is usually no embolism repair during the growing season (Sperry *et al.*, 1988a; Tyree *et al.*, 1994). Thus, water potential (Ψ) should not fall significantly below the threshold-value inducing cavitation (Ψ_{Cav}).

Trees differ widely in their vulnerability to drought-induced cavitation (Tyree and Ewers, 1991; Zotz *et al.*, 1994). While moderate embolism rates in late summer have been reported for *Acer saccharum* (Sperry *et al.*, 1988a), *Betula occidentalis* (Sperry and Sullivan, 1992) and *Alnus cordata* (Tognetti and Borghetti, 1994), several species of *Populus* have been described as extremely vulnerable, losing a large amount of the conducting tissue throughout the growing season by embolism (Tyree and Ewers, 1991; Tyree *et al.*, 1992, 1994). It has been suggested that stomata play an important role in limiting cavitation (Tyree and Ewers, 1991). Jones and Sutherland (1991) argued that tolerance of a slightly reduced hydraulic conductance might be beneficial in order to maximize stomatal aperture and hence short-term productivity, but this remains to be tested.

We report experiments made on *Fagus sylvatica* f. *purpurea* and *Populus balsamifera*. We evaluated the vulnerability of both species to water stress-induced cavitation and characterize the relationship between xylem vulnerabilities and the operating ranges of Ψ . Measurements indicated that water potentials in *Fagus* were often much lower (more negative) than in *Populus*.

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We also studied if stomatal closure occurred when evaporative demand was high and if this prevented Ψ from falling below Ψ_{Cav} . In addition, the seasonal pattern of xylem embolism in trees growing in the usually humid climate of Schleswig-Holstein in northern Germany was monitored.

Materials and methods

Plant material and site

Experiments were carried out on *Fagus sylvatica* L. f. *purpurea* (Ait.) Schneid. and *Populus balsamifera* L., two temperate tree species growing in the Botanical Garden of Kiel University. Measurements were conducted from May to October 1994. Trees of *Fagus* received direct sunlight throughout the day, whereas *Populus* clones were growing in an experimental field and were partially shaded by other trees. Trees were at least 15 years of age. Plants were not watered during dry weeks in July and August. Diffuse-porous species were chosen because the usually short vessels (see Results) allowed a better determination of xylem vulnerability than in ring-porous trees.

Monitoring seasonal occurrence of embolism

Xylem embolism can now be quantified by determining the hydraulic flow through stem segments before and after removal of air emboli by 'flushing' water at high pressure through the sample (Sperry *et al.*, 1988b). Hydraulic conductivity (k_h) as defined by Tyree and Ewers (1991) was measured on 6–11 branch segments about 15 cm long and 0.7–1.3 cm in diameter cut from 3–5-year-old branches sampled in the early morning. Segments were cut under water and were located >40 cm from the original cut end of the branch to avoid including vessels embolized during collection. The cut surfaces were shaved smooth with a razor blade and fitted to numbered plastic tubes at the basal end. Segments were perfused with degassed and filtered (0.2 μm) tap water. Water was degassed by agitating it with an electric shaker for 30 min under vacuum. Oxalic acid (Sperry *et al.*, 1988b) was not used, because microbial growth should not be an important factor during the measurements which only lasted for some hours. Moreover, in our opinion, the possibility can not be excluded that oxalic acid elevates the porosity of pit membranes. Flow rate through the segments was measured under gravity gradient with a maximum pressure head of 4 kPa using a pipette and stopwatch. After determination of the initial conductivity, six samples were flushed at once under a pressure of 0.1 MPa for 10 min followed by a brief (2 min) vacuum perfusion in an opposite flow direction. Conductivity of each segment was measured again, and the process repeated until conductivity could not be further elevated. Maximum conductivity was usually achieved after two flushes. The terms 'per cent loss in k_h ' and 'per cent embolism' are used synonymously in this paper.

Measurement of hydraulic conductivity as a function of Ψ

Per cent loss in k_h can be expressed as a function of the minimum Ψ reached during a dehydration (Sperry *et al.*, 1988c; Tyree *et al.*, 1992). Several branches were successively air-dehydrated on the laboratory bench over different periods. After the desired Ψ had approximately been achieved, a branch was wrapped in a large plastic bag into which a wet towel had been placed. The branch was left overnight to promote equilibration of Ψ and, in particular, to allow air to diffuse into cavitated conduits. At the end of the equilibration period

Ψ was determined on three to four leaves (*Populus*) or small twigs (*Fagus*) with a pressure chamber (Scholander *et al.*, 1965). Conductivity was measured as described above. Results obtained by bench-top dehydration appear to be similar to those produced by *in situ* dehydration (Tyree *et al.*, 1992). Measurements were conducted in May and June, when native state loss in k_h was 0% due to a complete recovery from winter embolism (data not shown).

Some of the water-stressed segments were perfused with 0.1% (w/v) aqueous safranin under a pressure of 2 kPa to identify functional (stained) conduits.

Measurement of acoustic emissions as a function of Ψ

Collected branches 1–1.5 m long and approximately 1.5 cm in basal diameter were immersed with their cut ends in a water bucket and brought into the laboratory. An ultrasonic transducer (model I151, Physical Acoustics Corp., Princeton, NJ, USA, see Tyree and Sperry, 1989) was attached in the centre of a branch to exposed wood (about 2 cm²) with a spring-loaded clamp. Wood was coated with 'water-soluble acoustic couplant' (Dunegan Corp., Irvine, CA, USA) to prevent local water loss and to facilitate transmission of ultrasound to the transducer. Ultrasonic acoustic emissions (AEs) were monitored using a model 4615 drought stress monitor (PAC). When Ψ was near 0 MPa and background AE rate was close to zero, dehydration of the branch was initiated by removing the water. Ψ was measured periodically on two or three leaves or small distal twigs using the pressure chamber. When the second leaf (*Populus*) or small twig (*Fagus*) was cut from the branch, the cumulative number of AEs, as displayed by the drought stress monitor, was taken and was plotted versus Ψ . Measurements were conducted in August and September, when both species had experienced water stress. The detection of AEs was stopped when water potential reached a value inducing an 80–90% loss in k_h .

Anatomical measurements

Vessel length were measured using the paint infusion method of Zimmermann and Jeje (1981). Five vessel length distribution measurements per species were made, and one representative result is shown. A 1000:1 water:paint suspension (Royal Sovereign Graphics, London, UK) was filtered to remove all particles greater than 7 μm . The suspension was gravity-fed into a stem segment from a 2 m column for 1 week. After completion of the paint infusion the axis was cut into 3 cm segments. These were dried overnight, the ends were cut smooth, and paint-filled vessels were counted in the 1993 growth ring. Zimmermann and Jeje (1981) reported that results for individual growth rings were similar in their experiments.

Vessel densities, vessel diameters (tangential axis) and wall thicknesses were determined using segments which were employed previously in the embolism studies. Transverse sections, 40 μm thick, were cut from the middle of these segments with a sliding microtome. A transparent foil was placed on the projection screen of a microscope (Reichert, Austria) and lumen diameters of vessels in randomly chosen sectors in the 1993 and 1994 growth rings were marked. Tangential vessel diameters and wall thicknesses were determined in the same sectors. Wall thickness was measured only where two vessels contacted one another and was calculated by the distance between the luminae divided by two (Sperry *et al.*, 1988c).

In order to measure the number of vessels per mm², all vessels within sectors reaching from pith to cambium were

marked on the transparent foil. Each sector had a known area of several mm².

Field measurements of Ψ and stomatal conductance

On sunny days in July and August 1994 diurnal courses of stomatal conductance (g_s) were monitored on four leaves per plant at approximately hourly intervals with a LI-1600 steady-state diffusion porometer (LiCor Inc., Lincoln, NE, USA). *P. balsamifera* is amphistomatous, so stomatal conductance of both leaf surfaces was measured, and total stomatal conductance as defined by Ceulemans *et al.* (1988) is given. *F. sylvatica* f. *purpurea* is hypostomatous. For this reason, measurements were restricted to the abaxial leaf surface. Photosynthetically active radiation (PAR), leaf and air temperatures as well as relative humidity were measured with the LI-1600 porometer. Ψ was estimated with the pressure chamber. Reported Ψ -values usually are means of two measurements. When values differed by more than 0.1 MPa, a third measurement was conducted. Field measurements of Ψ can be in serious error due to water loss of rapidly transpiring leaves in the first 30 s after excision (Turner and Long, 1980). In preliminary experiments we found water potentials of uncovered leaves up to 0.3 MPa lower than water potentials of leaves that were covered with a small plastic sheath just prior to their excision. Therefore, the sheath was placed on to the sample some seconds before excision and it was kept on the leaf while in the pressure chamber. The time from excision of the sample to pressurization was always less than 1 min.

Results

Hydraulic conductivity and AEs as a function of Ψ

Figure 1 shows vulnerability curves for *Fagus* and *Populus* shoots obtained by measuring the relationship between per cent loss in k_h and water potential. Both species had 0% embolism when fully hydrated (see Discussion). *Populus* began losing k_h at $\Psi_{Cav} = -0.7$ MPa and had 50% embolism at -1.8 MPa. The lowest Ψ observed in the field was -0.9 MPa. A typical midday Ψ on a sunny day was -0.7 MPa. These values refer to the Ψ of leaves, which was estimated to be 0.1 MPa lower than the Ψ in branches. *Fagus* branches lost conductivity due to water stress at water potentials below $\Psi_{Cav} = -1.9$ MPa and had 50% embolism at -2.9 MPa. The lowest midday Ψ observed was -2.15 MPa. Usually Ψ did not fall below -1.9 MPa in the field.

Figure 2 shows the relative number of AEs as a function of Ψ . The value of 1.0 corresponds to the sum of AEs recorded when Ψ reached the value inducing 50% loss in k_h (Sperry *et al.*, 1988c). In both species there was a distinct threshold- Ψ for AE activity. AEs were detected in *Populus* when Ψ fell below -0.9 MPa. In *Fagus*, AE activity sharply increased at water potentials lower than -1.85 MPa. One of the six *Populus* branches had not been excised from the tree. Instead, water supply was irreversibly blocked by freezing a basal stem segment with liquid nitrogen. Even though water loss was much faster

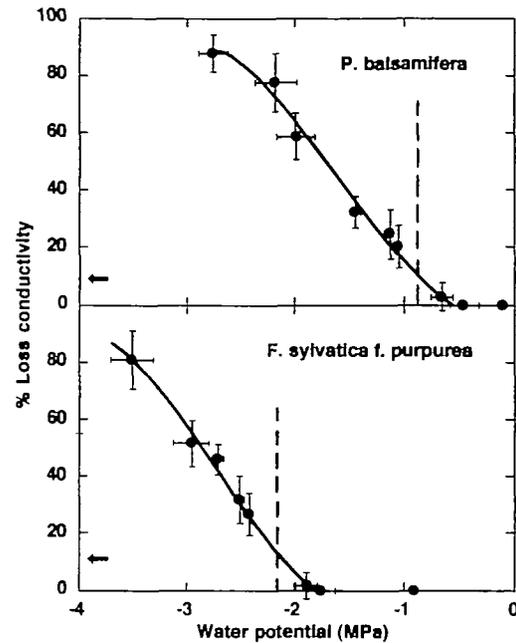


Fig. 1. Relationship between per cent loss in hydraulic conductivity (a measure of xylem embolism) and water potential. Bars represent standard deviations; vertical error bars are based on means of $n=6-9$ segments, and horizontal error bars are based on means of $n=3-4$ pressure chamber measurements. Dashed vertical lines indicate lowest water potentials observed in the 1994 growing season. Arrows indicate predicted loss in native state hydraulic conductivity.

in the field, this branch produced a very similar result to branches dehydrated in the laboratory.

Seasonal pattern of xylem embolism

Both species experienced serious winter embolism (data not shown), but had recovered completely by June, when the embolism rate was 0% (Fig. 3). In July and August air temperature often exceeded 30°C and there was an 8% and 11% loss in k_h in *Populus* and *Fagus*, respectively. In late August and in the rest of the growing season it was raining more or less regularly and Ψ did not fall below Ψ_{Cav} . Even in periods of rain there was no embolism reversal. In late October, after the beginning of leaf fall, and after night temperatures had occasionally fallen below 0°C, there was a sharp increase of embolism rate in *Populus*.

Daily courses of g_s and Ψ

The results shown in Fig. 4A compare the behaviour of stomata of *Fagus* leaves on a hot cloud-free day (4 August) and a day when evaporative demand remained moderate (9 August). The leaves were exposed to the sun. The maximum water vapour concentration difference between the leaf air spaces and the external air (WD) on 4 August was 23 mg l⁻¹, while on 9 August WD did not exceed 15 mg l⁻¹. On 4 August, leaves showed a strong tendency to limit water loss. The low g_s appeared to slow

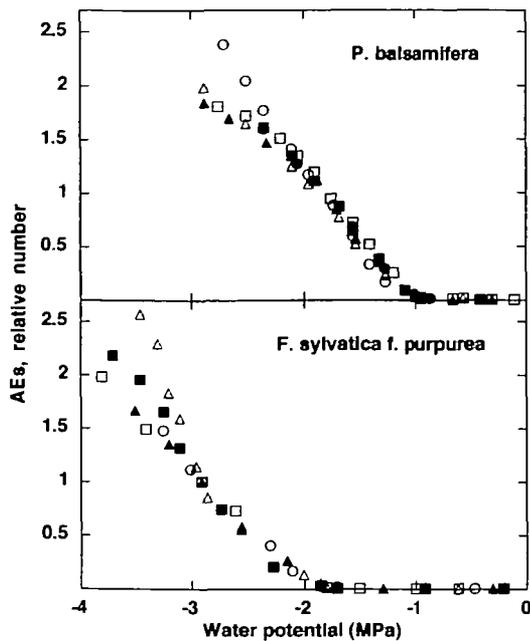


Fig. 2. Relationship between relative number of AEs and water potential. Data are for five and six replicates in *F. sylvatica f. purpurea* and *P. balsamifera*, respectively. One of the *Populus* branches (●) was dehydrated in the field by freezing a basal branch segment with liquid nitrogen. The other branches were excised from the tree and dehydrated in the laboratory. A relative value of 1.0 corresponds to the sum of AEs recorded when water potential reached the value inducing a 50% loss in hydraulic conductivity. Water potential values are means of $n = 2-3$ measurements.

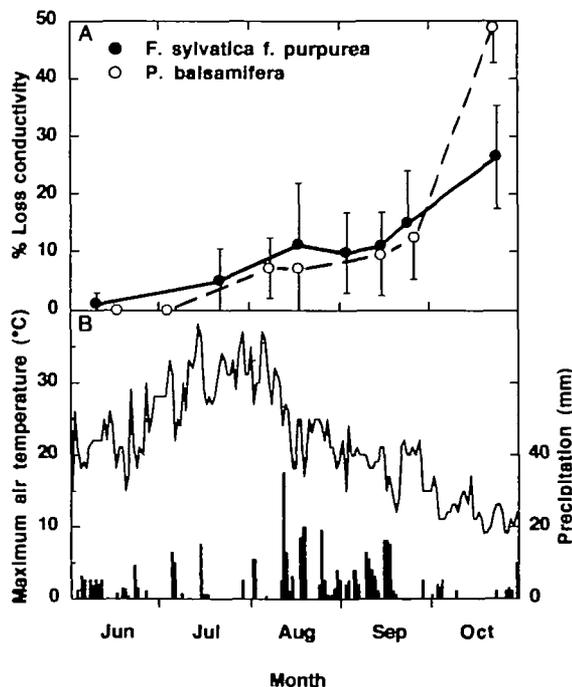


Fig. 3. (A) Seasonal progression of native embolism rate, expressed as per cent loss in hydraulic conductivity. Error bars are standard deviations ($n = 6-11$ segments). (B) Daily measured maximum air temperatures and precipitation at the study site.

the decrease in Ψ . At noon and in late afternoon though, Ψ fell below Ψ_{Cav} . On 9 August, the daily time-course of g_s was more or less two-peaked, and g_s followed variations in PAR caused by intermittent cloud cover. In the morning g_s was about three times higher than on 4 August. Between 11 a.m. and 6 p.m. Ψ remained relatively constant. Minimum Ψ equalled Ψ_{Cav} on that day.

The stomatal behaviour of *Populus* leaves during one of the hottest days in 1994 (28 July) is shown in Fig. 4B. Water vapour concentration difference increased to 26 mg l^{-1} at noon. Stomata closed in the morning and remained closed for the rest of the day. The leaves were occasionally shaded by other trees, but received direct sunlight at noon. At that time Ψ reached the minimum value of -0.9 MPa . Stomatal closure probably prevented Ψ from falling further below Ψ_{Cav} . In comparison, a typical daily pattern of g_s and Ψ is shown, using 22 August as a representative day. WD did not exceed 9 mg l^{-1} . There was a slight reduction of g_s at noon, but g_s remained much higher throughout the day than on 28 July. Ψ did not fall below $\Psi_{\text{Cav}} = -0.7 \text{ MPa}$.

Anatomical data

Vessel length distribution histograms are presented in Fig. 5. In the *Fagus* segment, the longest vessels were in the 27–30 cm class, but over 90% of the vessels were shorter than 12 cm. The longest vessels in the *Populus* branch fell into in the 33–36 cm class. More than 90% of the vessels were shorter than 15 cm. Table 1 summarizes some anatomical data of segments used in the embolism studies. *Populus* had wider vessels and a lower vessel density than *Fagus*. Vessel wall thicknesses were similar in both species.

Discussion

Both hydraulic (Fig. 1) and acoustic (Fig. 2) vulnerability curves characterize *Populus* as extremely vulnerable to water stress-induced cavitation. This is in agreement with results obtained by Tyree *et al.* (1994). In *Fagus*, Ψ_{Cav} was approximately 1 MPa lower than in *Populus* (Figs 1, 2). Despite these differences, native state loss in k_h was similar. Both species tolerated an embolism rate of about 10% in the summer (Fig. 3). Values of native state embolism rate were in close agreement with those predicted by the hydraulic vulnerability curves (compare Figs 1 and 3).

Based on our failure to obtain an increased conductivity after the flushing treatment we concluded that both species had 0% embolism in June. Dye perfusions confirmed that all vessels in the sapwood had been refilled in spring. At present, we do not know if root pressure played an important role in embolism reversal in the species investigated. The subject of conductivity recovery deserves additional work.

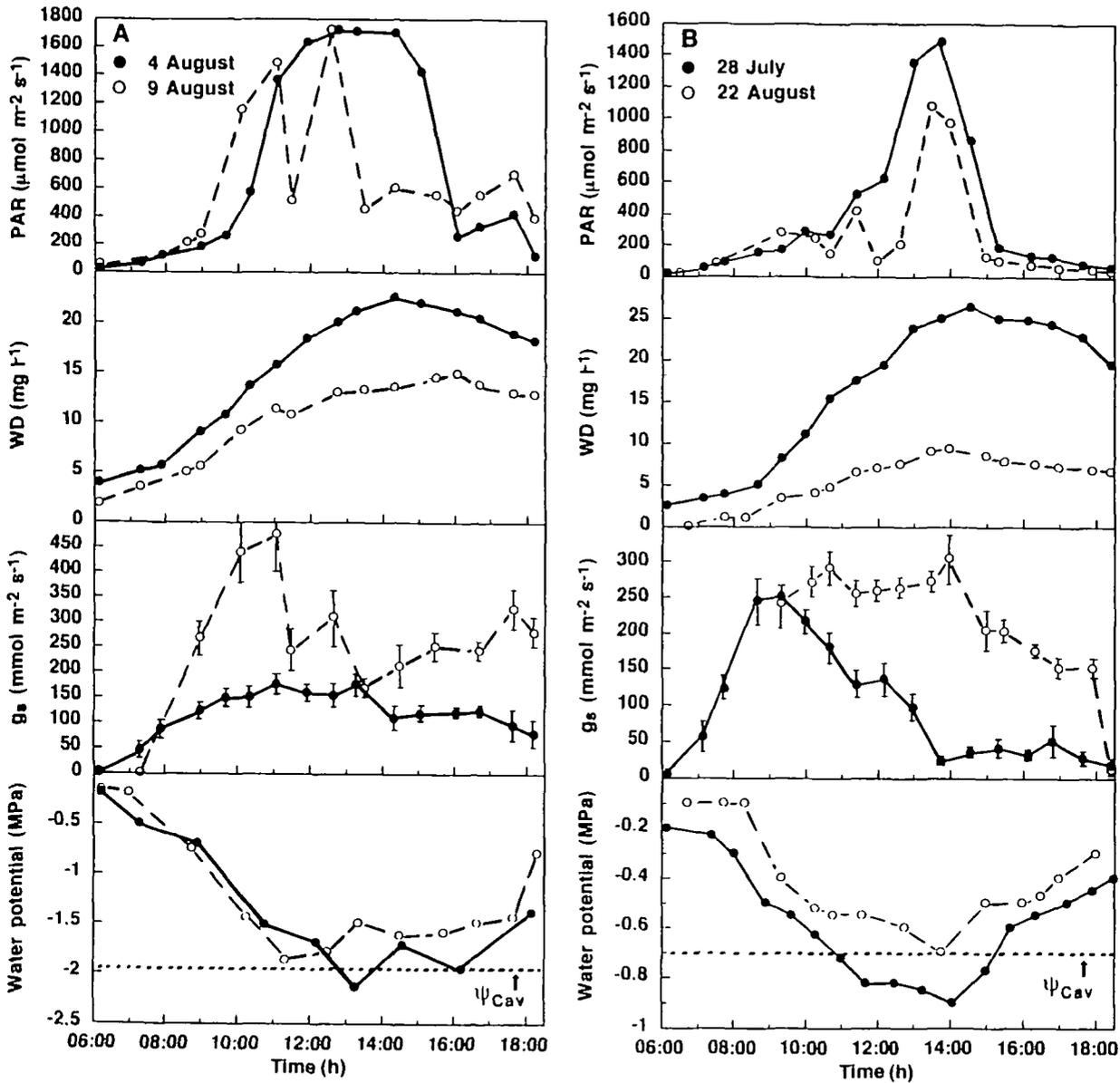


Fig. 4. Diurnal changes in photosynthetically active radiation (PAR), water vapour concentration difference between leaf air spaces and external air (WD), stomatal conductance (g_s), and water potential of *F. sylvatica* f. *purpurea* (A) and *P. balsamifera* (B) on days when evaporative demand was very high (●) and on days when evaporative demand was moderate (○). Each point is the mean of $n=4$ measurements of g_s and $n=2-3$ pressure chamber measurements. Error bars indicate standard deviations. Dashed lines denote the threshold water potentials inducing cavitation (Ψ_{Cav}).

Field measurements (Fig. 4) indicated that stomata closed before excessive embolism occurred. How did stomata sense that hydraulic conductance in branches might be lost? Sperry *et al.* (1993) suggested that stomata are responding to a threshold leaf water potential coincident with the upper end of the cavitation range. While this might be true in many cases, it does not explain the stomatal response found in *Fagus* and *Populus*. On 4 August, the control of g_s was probably via a direct response to environmental conditions since the decrease in Ψ was similar on 4 and 9 August (Fig. 4A). Furthermore, on 4 August (*Fagus*) and 28 July (*Populus*)

g_s was reduced before Ψ had reached Ψ_{Cav} . The direct response of stomata to changes in humidity is well documented (Lange *et al.*, 1971; Schulze, 1986). Such a control loop is advantageous because it allows an early limitation of water loss.

Acoustic and hydraulic vulnerability curves of both species were in good agreement, but it should be noted that hydraulic vulnerability curves were recorded when native state loss in k_h was 0%, whereas acoustic measurements were conducted later in the season, after plants had lost the most vulnerable conduits due to embolism. AEs are predictive of loss in k_h if they are restricted to

Table 1. Vessel diameter (tangential axis, μm), vessel wall thickness (μm), and vessel density (vessels per mm^2) in 3–7-year-old branch segments of *Fagus sylvatica* f. *purpurea* and *Populus balsamifera*

Values are means \pm standard deviation with number of measurements given in brackets.

Species	Vessel diameter (tangential axis)	Vessel wall thickness	Vessel density
<i>F. sylvatica</i> f. <i>purpurea</i>	23.4 \pm 5.2 (186)	2.7 \pm 0.4 (106)	294.3 \pm 58.9 (8)
<i>P. balsamifera</i>	33.6 \pm 10.6 (195)	2.6 \pm 0.6 (92)	181.4 \pm 18.7 (8)

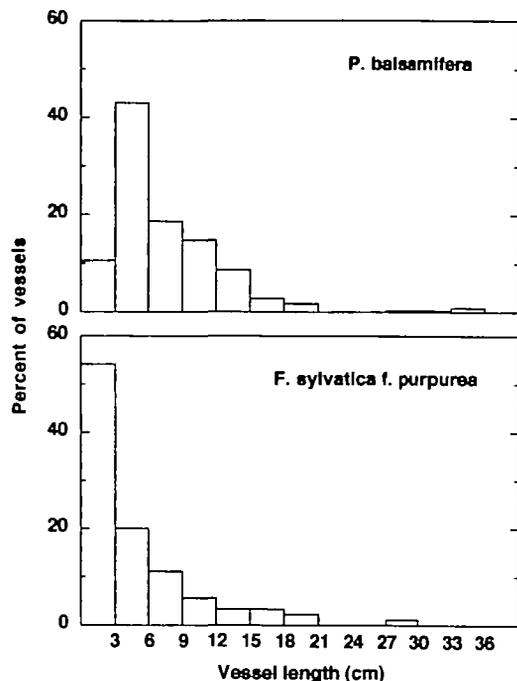


Fig. 5. Vessel length distributions in branch segments typical of those used in the experiments. Vessel length distribution was estimated using the paint infusion method. Five measurements per species were conducted and one representative result is shown. Branch diameter was between 1.0 and 1.5 cm, and branches were 4–9 years of age.

water conducting conduits. Sauter (1966) reported that the water content of sapwood in *Populus* sp. decreased significantly until the end of the growing season. We regard this as an indication that wood fibres in *Populus* were at least partially embolized in the summer, so AEs were probably mainly confined to vessels. There are fibre-tracheids, but no fibres in the xylem of *Fagus*. Therefore, AEs probably indicated rupturing of water columns in vessels and tracheids.

Staining indicated that many narrow latewood-vessels in *Populus* sustained higher xylem tensions without embolizing than wider earlywood conduits. However, there was no clear staining pattern in *Fagus*. The fact that *Populus* had longer (Fig. 5) and wider vessels than *Fagus* (Table 1) probably does not account for differences in their vulnerability. According to a comparative study with ring-porous, diffuse-porous, and conifer species, conduit volume does not correlate with vulnerability to embolism caused by water stress (Sperry and Sullivan,

1992). It seems that the size of pores in the cell wall (e.g. in the pit membrane) is the most important anatomical feature regarding drought-induced xylem dysfunction (Zimmermann, 1983; Sperry and Sullivan, 1992), but pore diameter is difficult to measure (Ewers and Cruiziat, 1991).

In conclusion, embolism rate in summer remained low in both species, even though water potentials often approached Ψ_{Cav} . On days when evaporative demand was very high, a high hydraulic conductance was maintained via a low stomatal conductance. The benefit of stomatal closure in connection with preventing loss of xylem conduits due to cavitation deserves more study. Stomatal control of xylem embolism (Jones and Sutherland, 1991) is particularly important in trees that usually can not reverse embolism during the growing season.

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