

Responses to water stress in an ABA-unresponsive hybrid poplar (*Populus koreana* × *trichocarpa* cv. Peace)

II. Hydraulic properties and xylem embolism

BY H. COCHARD*, M. RIDOLFI AND E. DREYER

INRA, Unité d'Ecophysiologie Forestière, 54280 Champenoux, France

(Received 25 March 1996; accepted 24 June 1996)

SUMMARY

We compared the xylem hydraulic properties of potted cuttings of two poplar clones (*Populus koreana* × *trichocarpa* cv. Peace and *P.* × *euramericana* cv. Robusta) known to differ in their sensitivity to ABA and in their ability to close their stomata during a period of drought. 'Robusta' can control stomatal aperture, whereas 'Peace' can only close the stomata of immature leaves. 'Peace' did not exhibit any specific hydraulic property that could compensate for its lack of response to a water deficit. The two clones did not differ in their petiole or internode xylem vulnerability to embolism, both being highly vulnerable (onset of embolism observed at -1.2 MPa minimum leaf water potential, Ψ_{wm}). Both clones became embolised rapidly when pots were dehydrated, but the onset of embolism was slightly delayed in 'Robusta'. 'Peace' was nevertheless capable of maintaining low xylem embolism near its apex and we associated this feature with the active stomatal control occurring in immature leaves. We conclude that efficient stomatal regulation is essential for maintaining the integrity of xylem sap flow under drought conditions and that 'Peace' shows an exception to the general rule of stomatal control of embolism.

Key words: *Populus* sp. water relations, xylem embolism, stomatal regulation, drought resistance.

INTRODUCTION

For most plant species, regulation of stomatal opening is, in the short term, the only reversible mechanism that can adjust the rate of water loss from leaves. In the presence of soil drought, stomata usually close to prevent leaves and shoots from reaching damaging water deficits. Moderate water deficits are known to cause turgor loss in plant cells and thus to alter plant growth. Many recent studies have also demonstrated the potentially detrimental effects of moderate water deficits on the xylem water transport capacity (e.g. Tyree & Sperry, 1988; Cochard, 1992; Cochard, Ewers & Tyree, 1994; Tyree, Davis & Cochard, 1994; Zotz, Tyree & Cochard, 1994). Low xylem water potentials, caused by high water deficits, can cause incursion of air into

xylem conduits. This in turn can lead to rapid occurrence of embolism (Sperry & Tyree, 1988; Cochard, Cruiziat & Tyree, 1992).

Although the vulnerability to embolism can vary considerably between species, most plants studied so far have been found to operate at xylem water potentials which are very close to the point of xylem dysfunction (Tyree & Sperry, 1988). Any slight increase in transpiration rate can induce a significant loss of hydraulic conductivity in the xylem leading to a so-called 'runaway-embolism' (Tyree & Sperry, 1988) and, eventually, shoot desiccation. The situation is even more critical under drought stress because the hydraulic conductances along the sap pathway from the soil to the leaves are drastically reduced. This enhances the variation in water potentials owing to changes in transpiration rates (Cochard, Bréda & Granier, 1996; Lu *et al.*, 1996). Therefore, an efficient stomatal regulation seems essential to protect xylem from embolism development.

Some populations of *Populus trichocarpa* do not entirely close their stomata when exposed to soil-drying under natural conditions (Ceulemans, Impens & Imler, 1988; Braatne, Hinckley & Stettler,

Abbreviations: ABA, abscisic acid; PLC, percentage loss of hydraulic conductivity; LSC, leaf specific conductivity ($\text{mmol m s}^{-1} \text{MPa}^{-1} \text{m}^{-2}$); PPFR, photosynthetic photon fluence rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); H_s , soil water content (%); Ψ_{wm} , minimum leaf water potential (MPa).

* To whom correspondence should be addressed.
E-mail: cochard@nancy.inra.fr

1992). This species is more sensitive to water stress than other *Populus* species, but it can survive in the field and seems well adapted to its riparian habitat (Hinckley & Braatne, 1994). Furthermore, a hybrid of *P. trichocarpa* (*Populus koreana* × *trichocarpa* cv. Peace) has stomata unresponsive to exogenous abscisic acid (Furukawa, Park & Fujinuma, 1990), a plant growth regulator supposed to be one of the major molecules triggering stomatal closure in response to soil water deficit. Ridolfi *et al.* (1996), working on the same hybrid, complemented the first observation of Furukawa *et al.* (1990) by demonstrating a leaf-age dependency of stomatal response to drought for this hybrid: the youngest apical leaves exhibit stomatal regulation but partly lose this capacity when they mature. Correlatively, droughted cuttings rapidly shed their mature leaves while the youngest ones survive the drought.

The unusual stomatal behaviour of *P. trichocarpa* and its hybrids might provide insight into stomatal control of xylem embolism. In this paper we report experiments performed on potted cuttings of *P. koreana* × *trichocarpa* cv. Peace exposed to rapid dehydration. As a control, we used the *P. euramericana* cultivar Robusta which displays efficient stomatal closure during drought (Ceulemans *et al.*, 1988; Ridolfi *et al.*, 1996). We characterized the xylem vulnerability to embolism and the hydraulic efficiency of both clones in order to determine whether the lack of stomatal regulation was associated with specific hydraulic properties that reduce the risk of vessel cavitation. We also assessed the ontogenic changes in stomatal regulation and its influence on the control of leaf water potentials and xylem embolism along the shoot.

MATERIALS AND METHODS

Experiments were performed on plants of two clones of *Populus*: *P. koreana* × *microcarpa* cv. Peace and *P. × euramericana* cv. Robusta hereafter termed 'Peace' and 'Robusta'. Stem cuttings were planted in 5 l pots filled with a 1:1 (v/v) mixture of sand and peat fertilized with 25 g of Nutricote® 100 (13/13/13 N/P/K). Plants were grown for *c.* 4 months in a greenhouse and automatically micro-irrigated to field capacity each day. After 4 months, the plants were 1.4–1.6 m tall, unbranched and bore 20–25 leaves.

One week before the onset of the experiments, six 'Robusta' and 12 'Peace' plants were transferred to a climate chamber with the following day/night conditions: 14/10 h; r.h. 60/90%; air temperature, 22/10 °C; PPFR at the top of the plants was around 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Each leaf was identified by its rank number, rank 1 being the youngest fully opened leaf. Leaves 1 to 4 were still expanding. Between replicates, we averaged our data according to this rank number and expressed them as a function of the

distance to the shoot apex. Drought was induced by withholding water for up to 10 d on four 'Robusta' and seven 'Peace' plants, the remainder being well hydrated to serve as controls. We initially expected to induce contrasting levels of xylem embolism according to the duration of water depletion but we found that the development of embolism was extremely rapid, so that plants were either almost fully functional or fully embolised. When plants were embolised, the soil water content was around 10% (g water per g d. wt) for both clones. During the development of drought, leaf stomatal conductance to H₂O vapour (g_w) was measured and will be reported elsewhere (Ridolfi *et al.*, 1996). At the end of the drought period, midday water potentials (Ψ_{wm}) were measured with a pressure chamber on 12–17 leaves evenly positioned along each shoot. Because it was necessary to assess the degree of embolism in the petioles of the same leaves, it was not possible to measure Ψ_{wm} on a whole leaf, because cutting the petiole close to the blade would have induced the entry of air into the remainder of the petiole. Ψ_{wm} was therefore measured on leaf blade subparts including the midrib or a lateral vein. It was verified on a few samples that Ψ_{mw} values of such subparts were the same as Ψ_{wm} values measured on whole leaves. After Ψ_{wm} values were determined, the plants were immediately rehydrated, uprooted and sampled for hydraulic measurements.

The degree of xylem embolism was estimated via its effect on the loss of hydraulic conductivity (Sperry, Donnelly & Tyree, 1987). An average of eight shoot internodes, 2–3 cm long, and eight leaf petioles, 1.5–2 cm long, were excised under tap water all along each shoot. The initial hydraulic conductivity (K_{init}) was computed for each segment by measuring gravimetrically the water flow rate under a water pressure head of 3–4 kPa with a 10⁻⁵ g analytical balance. The saturated conductivity (K_{sat}) was obtained by perfusing the segments with distilled water at 150 kPa for a few minutes. The percentage loss of hydraulic conductivity due to xylem embolism (PLC) was computed as:

$$\text{PLC} = 100(1 - K_{\text{init}}/K_{\text{sat}}).$$

Vulnerability curves were constructed for both clones by relating the PLC of each segment to the Ψ_{wm} of the leaf attached to the same petiole and internode. Data were averaged by 0.2 MPa classes of Ψ_{wm} . Eight 'Peace' and four 'Robusta' shoots were cut at the base, placed in a 80-cm-long pressure chamber with the cut end protruding, and pressurized to a constant air pressure until sap exudation ceased (Cochard *et al.*, 1992). The PLC was then related to the negative of the air pressure in the chamber. This technique was used because the xylem water potential gradients are negligible within pressurized shoots, whereas they may be significant in dehydrating potted plants, and the absence of

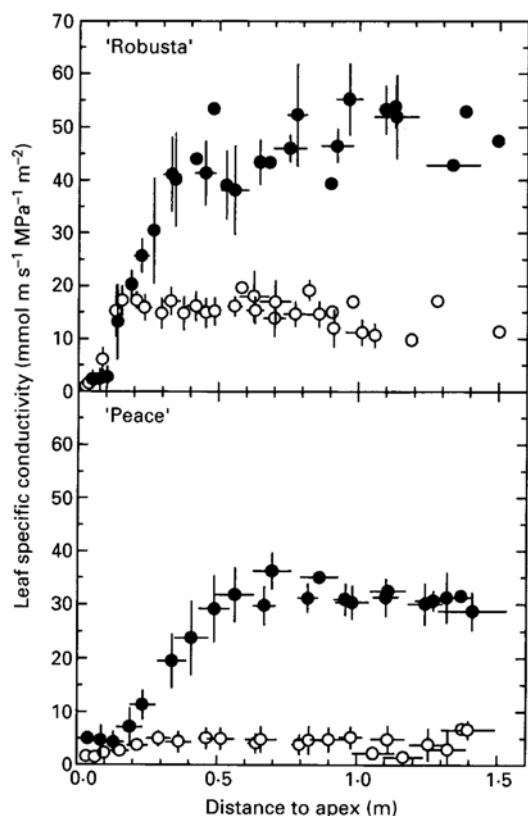


Figure 1. Petiole (○) and internode (●) leaf specific conductivity ($\text{mmol m s}^{-1} \text{MPa}^{-1} \text{m}^{-2}$) as a function of the distance to the shoot apex in unstressed plants of 'Robusta' (upper) and 'Peace' (bottom). Error bars represent one standard deviation.

such gradients is essential for assessing a gradient of vulnerability within the xylem. The efficiency of xylem conduits in conducting sap was estimated by computing the leaf specific conductivity (LSC, $\text{mmol m MPa}^{-1} \text{s}^{-1} \text{m}^{-2}$) of each segment as:

$$\text{LSC} = K_{\text{sat}}/LA,$$

where LA is the total distal leaf area supplied by each segment (m^2 , plan leaf area). This parameter was used because it links the water potential gradient across a segment ($d\Psi \text{ MPa m}^{-1}$) to the water flow F (mmol s^{-1}) through the segment: $d\Psi = F/\text{LSC}$. Plants used for air pressurization were not included in the LSC data set because they were grown later in the season, were slightly younger, and exhibited different leaf sizes.

RESULTS

Along the shoots of unstressed plants, LSC values in both the petioles and internodes were considerably reduced close to the shoot apex (Fig. 1). The reduction was caused by a decrease in hydraulic conductivity (data not shown) probably because these organs were still maturing and large vessels were not yet fully formed and therefore not functional. In the

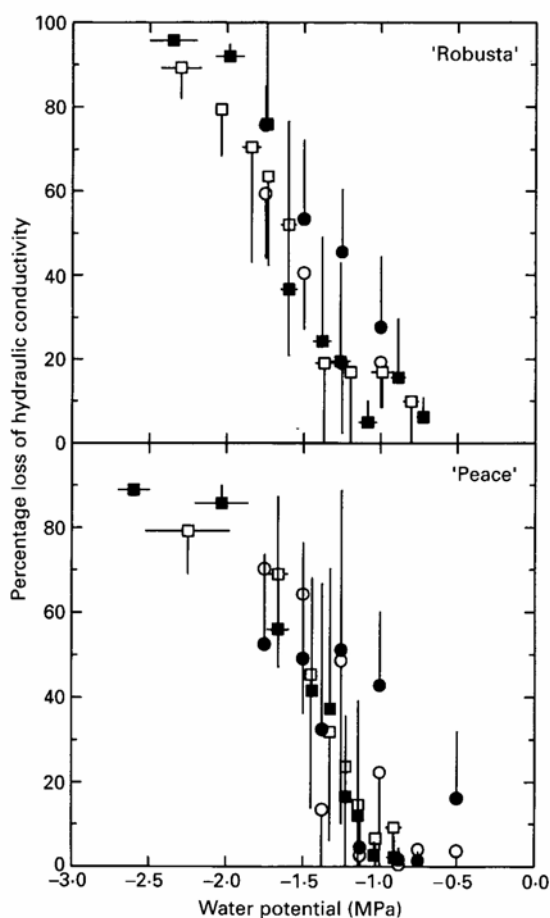


Figure 2. Vulnerability of 'Robusta' (upper) and 'Peace' (bottom) petioles (□ ○) and internodes (■ ●) to water-stress-induced embolism. Embolism was estimated as a percentage loss of hydraulic conductivity (y -axis). Embolism was induced either by pot-dehydration (□ ■) or shoot pressurization (● ○) in a pressure chamber. The x -axis represents, in the first case, the water potential measured on the leaf connected to each petiole or internode, in the latter case, the opposite of the air pressure applied in the pressure chamber. Error bars represent one standard deviation.

remainder of the shoot the LSC was remarkably constant. The petiole LSC values were three and six times lower than those of the internodes for 'Robusta' and 'Peace', respectively, denoting a sharp hydraulic segmentation between these organs. 'Robusta' exhibited significantly higher LSC values, especially for the petioles (3.5 times higher). However, petioles of 'Robusta' were about three times as long as those of 'Peace' ($6.63 \text{ cm} \pm 1.37 \text{ SD}$, $n = 62$ and $2.22 \text{ cm} \pm 0.77$, $n = 52$, respectively; $P < 0.001$). Increasing the path length decreases hydraulic conductance, so values of whole petiole hydraulic conductance in 'Robusta' and 'Peace' were comparable.

The vulnerability curves (i.e. PLC relative to Ψ_{wm}), established either by air dehydration or by air pressurization, were not statistically different (at

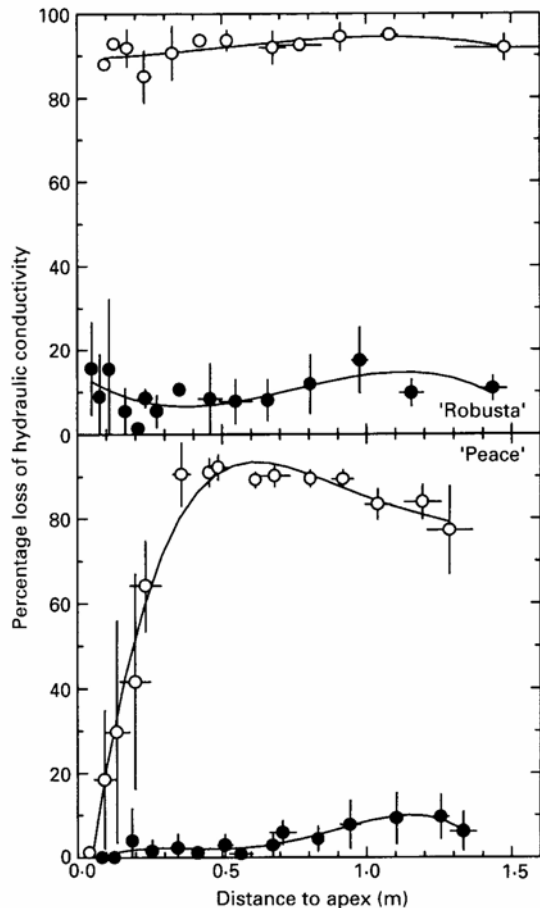


Figure 3. Percentage loss of hydraulic conductivity (y -axis) due to xylem embolism in the internodes of potted 'Robusta' (upper) and 'Peace' (bottom) plants as a function of the distance to the shoot apex. (●) for the unstressed controls plants and (○) for pot-dehydrated plants. The intensity of the soil water stress was comparable for both clones (*c.* 10% relative soil humidity). Error bars represent one standard deviation.

$P < 0.05$) for petioles and shoot internodes of both clones (Fig. 2). The linear regression coefficients and the y intercepts on the x axis for petioles and internodes were compared. Data corresponding to low and high Ψ_{wm} values were not included in the analysis. Vessel cavitation developed when Ψ_{wm} dropped below *c.* -1.2 MPa. At Ψ_{wm} values near -1.4 MPa, the PLC was 50%, and segments approached total embolisation at *c.* -2 MPa. In contrast to the LSC differences between petioles and internodes, there was no segmentation of embolism vulnerability. Nor were differences in vulnerability detected between the xylem near the apex and the xylem in the older part of the shoot (data not shown).

Pot-dehydrated 'Peace' plants exhibited a clear gradient of embolism along the shoot internodes (Fig. 3, bottom). Internodes of all the mature parts of the shoots were almost totally embolised (*c.* 90 PLC) whereas those towards the apex exhibited increasing degrees of conductivity. No loss of

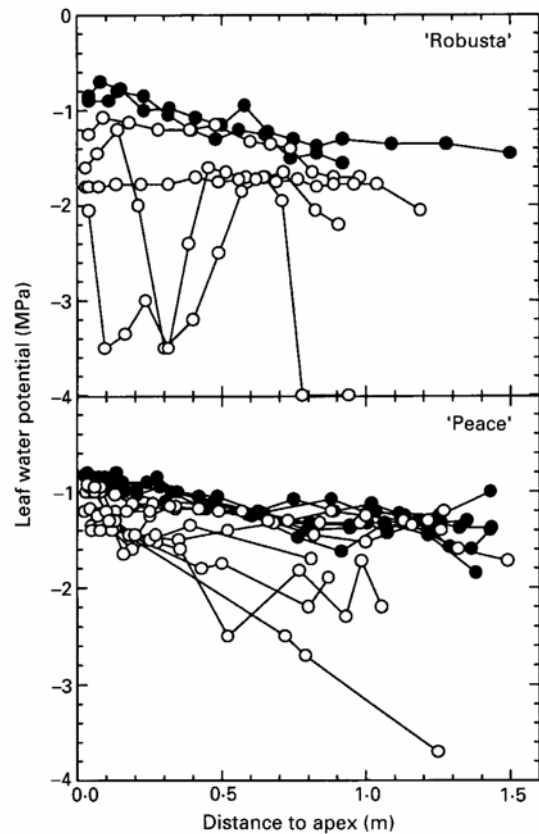


Figure 4. Minimum leaf water potential (y -axis) as a function of the distance to the shoot apex in control (●) and pot-dehydrated (○) plants of 'Robusta' (upper) and 'Peace' (bottom). Lines connect measurements made on the same plant.

conductivity was detectable in the youngest internodes. For 'Peace' controls, there was a significant gradient in embolism (linear regression coefficient different from zero at $P = 0.05$) but the degree of embolism remained low. In pot-dehydrated 'Robusta' plants, embolism was consistently high (90 PLC) along the entire shoot (Fig. 3, top) with no significant gradient (the linear regression coefficient was not different from zero at $P < 0.05$). 'Robusta' controls exhibited low PLC values, with no significant gradient along the shoot. Leaf petioles showed similar patterns (data not shown) suggesting that embolism developed concurrently in the petioles and the internodes in both cultivars.

Longitudinal variations of Ψ_{wm} along the shoots of control and dry 'Robusta' and 'Peace' plants are shown in Figure 4. For the control plants of both clones, Ψ_{wm} values steadily declined from -0.8 MPa at the apex to -1.2 MPa near the base of the shoots ($r^2 = 0.72$ and 0.69 for 'Robusta' and 'Peace' respectively, regression coefficient different from zero at $P < 0.05$). Drought induced a contrast between the two clones in the longitudinal changes of Ψ_{wm} . In 'Robusta', Ψ_{wm} values were reduced for all leaves at the beginning of the drought. This was

particularly evident for one plant that exhibited a constant -1.8 MPa value all along its axes (linear regression coefficient not different from zero at $P < 0.05$). When drought further increased, very low Ψ_{wm} values were recorded and leaves usually withered. In 'Peace', Ψ_{wm} was markedly depleted in the matured leaves that became necrotic, but values became progressively less negative towards the apex. The leaves nearest to the apex did not experience Ψ_{wm} values lower than -1.2 MPa and were still visually turgid after 10 d of drought.

DISCUSSION

The objectives of this study were to analyse the hydraulic properties of a *Populus* cultivar lacking efficient stomatal regulation ('Peace') and to assess the possible consequences for the development of xylem embolism in presence of soil water stress.

Hydraulic properties of Populus

Water potential and hydraulic conductances in the soil and at the soil-root interface are reduced by drought (Nobel & Cui, 1992); consequently a species lacking adequate stomatal regulation is likely to experience very negative water potentials during the day and may undergo a large amount of xylem embolism. It is also now well established that cavitation occurs when Ψ_{wm} drops below a threshold value (Ψ_{cav}) determined solely by the porosity of the bordered pit membranes (Sperry & Tyree, 1988; Cochard *et al.*, 1992; Jarbeau, Ewers & Davies, 1995). It is usually found for field-grown trees that during sunny days Ψ_{wm} values closely approach the Ψ_{cav} value (Tyree & Sperry, 1988). However, most species adjust stomatal conductance to maintain Ψ_{wm} above Ψ_{cav} (Lu *et al.*, 1996; Cochard *et al.*, 1996). Because 'Peace' lacks such a mechanism, it was considered that it might, instead, exhibit xylem hydraulic properties that lessen the development of embolism. Three independent mechanisms were proposed for minimizing xylem embolism: (1) increased xylem safety due to a lower vulnerability to cavitation; (2) increased xylem efficiency (higher LSC) resulting in less negative water potentials; (3) efficient xylem segmentation restricting the development of embolism to the petioles and maintaining the xylem integrity in the shoots.

None of the proposed mechanisms appeared to be present in the 'Peace' cultivar. First, 'Peace' was as vulnerable to embolism as the control cultivar 'Robusta' (Fig. 2) and other *Populus* species studied before (Cochard *et al.*, 1992; Lo Gullo & Salleo, 1992; Tyree, Alexander & Machado, 1992; Tyree *et al.*, 1994; Hacke & Sauter, 1995). Xylem vessels in 'Peace' did not, therefore, exhibit the intrinsic capacity to sustain higher xylem tensions than other *Populus* sp. These plants were actually highly

vulnerable, being among the most vulnerable temperate tree species studied so far. Second, 'Peace' internodes were about 30% less efficient in conducting water than 'Robusta', but the minimum leaf Ψ_{wm} values were nevertheless comparable for both clones. This was probably due to the hydraulic segmentation we observed between the shoots and petioles. Because petiole LSC values were much lower than those of the internode, the internode Ψ_{wm} gradient is negligible compared with that in the petioles and in the leaf blades. Third, embolism developed concurrently in the petioles and the internodes of the two clones, probably because the hydraulic segmentation does not achieve a gradient of vulnerability. A previous study of walnut (a species that also sheds its leaves when exposed to drought) showed that higher vulnerability of petioles than of stems can very efficiently prevent any embolism to shoots (Tyree *et al.*, 1993). This was not the case for either of the two clones we analysed: when leaves were being shed, the shoot was already suffering a large amount of embolism.

Stomatal control of embolism in Populus

The gradient of xylem embolism found along the shoots in droughted 'Peace' plants appears to provide further evidence of the role of stomata in the control of embolism (Jones & Sutherland, 1991; Sperry & Pockman, 1993). It was found that embolisms did not develop near the apices (Fig. 3); and Ridolfi *et al.* (1996) have established, on the same plant material, that drought induced a complete stomatal closure in the youngest leaves, whereas there was a lack of regulation in mature leaves. A gradient of embolism might actually result from a gradient of Ψ_{wm} or a gradient of vulnerability to embolism. In the present experiment, no difference in vulnerability could be detected along the shoots. However, as hydraulic conductivities were low for petioles and internodes near the apex, measures of PLC were not very precise. The contrasting development of embolism can thus probably only be ascribed to differences in Ψ_{wm} . This was confirmed by the Ψ_{wm} measurements. For the youngest leaves, Ψ_{wm} values never dropped below the threshold potential at which cavitation develops (*c.* -1.2 MPa), whereas much lower values were recorded for the mature leaves. The control of Ψ_{wm} was therefore essential in 'Peace' for maintaining xylem integrity near the shoot apices. Because the variations in Ψ_{wm} are reflected in variations in stomatal conductance (Ridolfi *et al.*, 1996), it can be concluded that 'Peace' was able to maintain low xylem embolism in the shoot apices only because the active stomatal closure in the terminal leaves prevent Ψ_{wm} from dropping below the point of xylem dysfunction. By contrast, for the mature leaves, the absence of stomatal regulation led rapidly to Ψ_{wm} values much lower

than the cavitation point, resulting in a high degree of embolisation and leaf death. Leaf death, and leaf fall considerably reduced the transpiring areas (and hence the gradient of water potential) of the droughted plants (Ridolfi *et al.*, 1996) and, after 10 d of water shortage, only the youngest leaves with closed stomata remained attached to the shoots. It was found that such plants could actually survive much longer periods of water shortage and regrow after rehydration (unpublished observations). Although shoots experienced *c.* 90 PLC, the remaining conductivity was probably enough to supply water to the apex. This occurred because the hydraulic conductivity near the apex was *c.* three to four orders of magnitude lower than in the mature part of the shoots. Even with 90 PLC, the mature shoots were still two to three orders of magnitude more conductive than the apices. 'Robusta' plants subjected to similar soil water depletion exhibited a comparable degree of xylem embolism, with the exception that shoot apices also developed embolisms. The observed stomatal regulation in 'Robusta' did not protect the xylem from any embolism damage. However, we observed that the onset of embolism was delayed in 'Robusta' compared with that in 'Peace' (data not shown), probably because the stomatal closure and reduced transpiration maintained higher soil water content for a longer time. The results are consistent with those of Braatne *et al.* (1992) who showed, in a similar experiment, that *P. deltoides* survived longer during drought than *P. trichocarpa* and exhibited less xylem embolism because of greater stomatal control. Furthermore, Hinckley & Braatne (1994) reported that 'under field conditions in which periods of drought develop slowly, stomata of *P. trichocarpa* were found to be responsive to vapor density gradient and soil moisture'. The present experiments were not designed to compare the performance of both clones under 'natural drought' because soil volume for the potted plants was small and drought developed more rapidly than in the field. It can nevertheless be suggested that under field conditions the efficient stomatal closure in 'Robusta' could enable this clone to experience a longer period of drought without developing xylem embolism. 'Peace' trees are likely to become more rapidly embolised and shed their leaves soon after the onset of the drought, but might nevertheless maintain live apices and hence survive the drought period. The ability to achieve stomatal closure in response to drought in the immature leaves might improve the survival of 'Peace' under such conditions.

Populus species studied so far always exhibited higher vulnerability to embolism than other temperate tree species, and results from this study further demonstrate that stomata might not control efficiently the development of xylem embolism. Together, these characteristics reduce plant fitness

and survival under soil drought conditions and might explain why poplar species are associated with riparian habitats.

ACKNOWLEDGMENTS

The 'Peace' clone was provided courtesy of Forest Research Station, Forestry Commission, Farnham, England, and 'Robusta' by the Laboratory of Forest Pathology, INRA, Nancy. We thank A. Granier, D. S. Sandquist and two anonymous referees for comments on an earlier draft of the manuscript.

REFERENCES

- Braatne JH, Hinckley TM, Stettler RF. 1992. Influence of soil water on the physiological and morphological components of plant water balance in *Populus trichocarpa*, *Populus deltoides* and their F1 hybrids. *Tree Physiology* **11**: 325–339.
- Ceulemans R, Impens I, Imler R. 1988. Stomatal conductance and stomatal behavior in *Populus* cultivars and hybrids. *Canadian Journal of Botany* **66**: 1404–1414.
- Cochard H. 1992. Vulnerability of several conifers to air embolism. *Tree Physiology* **11**, 73–83.
- Cochard H, Bréda N, Granier E. 1996. Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism. *Annales des Sciences Forestières* **53**: 197–206.
- Cochard H, Cruziat P, Tyree M. 1992. Use of positive pressures to establish vulnerability curves. *Plant Physiology* **100**: 205–209.
- Cochard H, Ewers FW, Tyree MT. 1994. Water relations of a tropical vine-like bamboo (*Rhipidocladum racemiflorum*): root pressures, vulnerability to cavitation and seasonal changes in embolism. *Journal of Experimental Botany* **45**: 1085–1089.
- Furukawa A, Park SY, Fujinuma Y. 1990. Hybrid polar stomata unresponsive to changes in environmental conditions. *Trees* **4**: 191–197.
- Hacke U, Sauter JJ. 1995. Vulnerability of xylem to embolism in relation to leaf water potential and stomatal conductance in *Fagus sylvatica* f. *purpurea* and *Populus balsamifera*. *Journal of Experimental Botany* **290**: 1177–1183.
- Hinckley TM, Braatne JH. 1994. Stomata. In: Willkinson RE, ed. *Plant-Environment Interactions*. New York: Marcel Dekker, 323–355.
- Jarbeau JA, Ewers FW, Davis SD. 1995. The mechanism of water-stress-induced embolism in two species of chaparral shrubs. *Plant, Cell and Environment* **18**: 189–196.
- Jones HG, Sutherland RA. 1991. Stomatal control of xylem embolism. *Plant, Cell and Environment* **14**: 607–612.
- Lo Gullo MA, Salleo S. 1992. Water storage in the wood and xylem cavitation in 1-year-old twigs of *Populus deltoides* Bartr. *Plant, Cell and Environment* **15**: 431–438.
- Lu P, Biron P, Granier A, Cochard H. 1996. Water relations of adult Norway spruce (*Picea abies*) under soil drought in the Vosges mountains: whole-tree hydraulic conductance, xylem embolism and water loss regulation. *Annales des Sciences Forestières* **53**: 113–121.
- Nobel PS, Cui MY. 1992. Hydraulic conductances of the soil, the soil air gap, and the root—changes for desert succulents in drying soil. *Journal of Experimental Botany* **43**: 319–326.
- Ridolfi M, Fauveau ML, Label P, Garrec JP, Dreyer E. 1996. Responses to water stress in an ABA-unresponsive hybrid poplar (*Populus koreana* × *trichocarpa* cv. 'Peace') 1. Stomatal function. *New Phytologist* **134**: 445–454.
- Sperry JS, Donnelly JR, Tyree MT. 1987. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* **11**: 35–40.
- Sperry JS, Pockman WT. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant, Cell and Environment* **16**: 279–287.
- Sperry JS, Tyree MT. 1988. Mechanism of water stress-induced xylem embolism. *Plant Physiology* **88**: 581–587.

- Tyree MT, Alexander J, Machado JL. 1992.** Loss of hydraulic conductivity due to water stress in intact juveniles of *Quercus rubra* and *Populus deltoides*. *Tree Physiology* **10**: 411–415.
- Tyree MT, Cochard H, Cruiziat P, Sinclair B, Ameglio T. 1993.** Drought-induced leaf shedding in walnut – evidence for vulnerability segmentation. *Plant, Cell and Environment* **16**: 879–882.
- Tyree MT, Davis SD, Cochard H. 1994.** Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA Journal* **15**: 335–360.
- Tyree MT, Kolb KJ, Rood SB, Patino S. 1994.** Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta – a possible factor in the decline of the ecosystem. *Tree Physiology* **14**: 455–466.
- Tyree MT, Sperry JS. 1988.** Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology* **88**: 574–580.
- Zotz G, Tyree MT, Cochard H. 1994.** Hydraulic architecture, water relations and vulnerability to cavitation of *Clusia uvitana* Pittier: a C3-CAM tropical hemi-epiphyte. *New Phytologist* **127**: 287–295.