Plant, Cell and Environment (1999) **22,** 101–108

The effects of acclimation to sunlight on the xylem vulnerability to embolism in *Fagus sylvatica* L.

H. COCHARD*, D. LEMOINE & E. DREYER

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

ABSTRACT

We assessed the effects of irradiance received during growth on the vulnerability of *Fagus sylvatica* L. xylem vessels to water-stress-induced embolism. The measurements were conducted on (1) potted saplings acclimated for 2 years under 100% and 12% incident global radiation and (2) branches collected from sun-exposed and shaded sides of adult trees. Both experiments yielded similar results. Light-acclimated shoots were less vulnerable to embolism. Xylem water potential levels producing 50% loss of hydraulic conductivity were lower in sun-exposed branches and seedlings than in shade-grown ones (–3·0 versus –2·3 MPa on average). The differences in vulnerability were not correlated with differences in xylem hydraulic conductivity nor vessel diameter. Resistance to cavitation was correlated with transpiration rates, midday xylem and leaf water potentials in adult trees. We concluded that vulnerability to cavitation in *Fagus sylvatica* may acclimate to contrasting ambient light conditions.

Key-words: *Fagus sylvatica*; Fagaceae; acclimation; cavitation; hydraulic conductivity; light; water relations.

INTRODUCTION

Since the introduction of reliable techniques to measure cavitation events (Tyree & Dixon 1983) and air embolism in xylem (Sperry, Donnelly & Tyree 1988a), considerable progress has been made in the knowledge of species vulnerability to water stress and in the understanding of whole plant water relations. We now have evidence that xylem conduits are exposed to cavitation events and that many woody species are operating very close to the point of xylem dysfunction (Tyree & Sperry 1988). Therefore, it has been suggested that the maintenance of xylem integrity may impose a limitation to maximum plant transpiration rates (Jones & Sutherland 1991; Cochard, Bréda & Granier 1996a; Lu *et al*. 1996). This hypothesis has recently been verified for a mutant of *Populus trichocarpa* lacking efficient water loss regulation (Cochard, Ridolfi & Dreyer 1996b).

The mechanism of dehydration-induced xylem embolism has been identified (Sperry & Tyree 1988). Air enters the lumen of water-filled vessels through pores in the pit membrane of the walls when the xylem pressure potential exceeds the maximum capillary pressure sustainable by the pores. Xylem tension, measured by its water potential, Ψ_{xylem}, is therefore the triggering variable for embolism induction. Xylem dysfunction can then be characterized by 'vulnerability curves' (VC) which represent the changes in embolism level with increasing tension in xylem sap. Xylem VCs have been established for a large number of woody species and we now have a better idea of its variability. VCs were first shown to differ considerably between species (e.g. Sperry, Tyree & Donelly 1988b; Cochard *et al*. 1991; Cochard 1992), or genotypes (Neufeld *et al*. 1992; Borghetti *et al*. 1993). Significant differences were also found between organs of a same plant (Tyree *et al*. 1993a; Sperry & Saliendra 1994; Hacke & Sauter 1995) or similar plants growing under contrasted soil water conditions (Jackson, Irvine & Grace 1995; Alder, Sperry & Pockman 1996). It has also been shown that petiole vulnerability varied according to their vertical position in a crown of *Fraxinus excelsior* (Cochard *et al*. 1997).

However, the question of whether the xylem vulnerability of a tree can acclimate to modifications in ambient conditions remains largely unexplored. For instance, forest tree species experience very contrasting light conditions during their life-time, especially shade-tolerant species that initiate their growth in the understory. As light is a major factor determining plant water relations, the degree of xylem tension and therefore the risk of xylem embolism may change with the growing conditions of the tree. Xylem vulnerability acclimation to new irradiance conditions might then determine tree survival. This may also be an important issue in the context of a global climate change because the increasing likelihood of drought may interact with the effects of light. There is evidence from the literature that xylem conductance is sensitive to light (Schultz & Matthews 1993) but there is no information available on the effect of light on xylem vulnerability to embolism.

The objective of this study was to assess the plasticity of xylem vulnerability in *Fagus sylvatica* induced by different ambient light conditions. We chose this species because it is known to grow and develop under both full-light and heavily shaded conditions and to maintain large living branches in the shade of the under-canopy. We compared

Correspondence: Hervé Cochard. Fax: + 3 33 83394069; e-mail: cochard@nancy.inra.fr

**New address: INRA-PIAF, Domaine de Crouël, 63039 Clermont-Ferrand, France.*

shoot internodes VCs (1) of saplings grown under two different irradiance levels and (2) of branches in different light conditions from the same adult trees. Xylem safety was compared to xylem anatomy and xylem hydraulic conductivity to examine if a gain in hydraulic safety was associated with a loss in hydraulic efficiency. We also analysed leaf gas exchange and leaf water potentials to find out if differences in VCs had some impacts on branch water relations.

MATERIALS AND METHODS

Plant material

Two mature, 70-year-old, *Fagus sylvatica* L. trees were chosen in the Arboretum of Amance, near Nancy, in the eastern part of France (48°45' N, 6°20' E, elevation: 255 m). The trees were growing on the periphery of the Arboretum, with southern branches exposed to full sunlight (= light branches), and northern ones heavily shaded by upper crown branches and surrounding trees (= shade branches).

The experiments on potted saplings were conducted in 1994 after the plants were grown for two consecutive years under contrasting light environments. In spring 1993, 80 1-year-old plants were transplanted in 5-L pots containing a mixture of sand and blond peat and fertilizer (Nutricote 100 N/P/K 13/13/13; Nutril, Paris, France). The plants were randomly allocated to each of two treatments: full light (control) and shade. In the shade treatment, the incident irradiance was artificially reduced by shade screens. The microclimate under the screens was continuously monitored for several weeks with a portable weather station and correlated with the nearby weather station of Champenoux. On average, the global radiation (W m^{-2}) for the shade treatment was 0·12, the air temperature (°C) 0·86, and the air vapour pressure deficit (hPa) 0·9 that of the ambient values, respectively. The shade treatment was close to the light environment in *Fagus sylvatica* forest understory (Aussenac & Ducrey 1977) with the difference that the red/far red ratio was not modified by these neutral screens (data not shown). Plants were well watered throughout the experiment. Six full-light, and seven shade-grown saplings were sampled for hydraulic analysis.

Vulnerability curves

Vulnerability curves (VCs) are plots of degrees of xylem embolism versus Ψ_{xylem} that induced the embolism. They are constructed by dehydrating different excised branches to different Ψ_{xylem}. Degrees of embolism were assessed as described by Sperry *et al*. (1988a) by measuring losses of hydraulic conductance caused by air blockages in the xylem conduits of short (2–3 cm) shoot internodes. We established VCs for current-year and previous-years shoot internodes. In August and September 1993, we collected branches from the mature trees in the morning with a 6-m-long pruning pole, enclosed them in an black airtight plastic bag to reduce water loss through transpiration and brought them to the laboratory for hydraulic analysis. In August 1994, VCs were established for saplings. Saplings' root systems were cleaned from their soil in the nursery and brought to the laboratory as described above. In the laboratory, the samples were bench dehydrated for a few hours to a few days, then enclosed for at least 4 h in an black airtight plastic bag to stop transpiration and remove water potential gradients between the leaves and xylem vessels. Ψ_{xylem} was then calculated from the leaf water potential measured on four randomly chosen leaves with a pressure chamber. Xylem tension was then returned to zero by immersing the branches in tap water for 30 min before hydraulic analysis. When the saplings were large enough, one or two branches were cut under tap water from the main axis and the remainder of the saplings allowed to dehydrate anew to lower Ψ_{xylem} values. After rehydration, eight to 15 shoot internodes were excised under water from different growth units of each branch. The initial hydraulic conductivity K_{init} (mmol m s^{-1} MPa^{-1}) was measured by forcing distilled water with 5 kPa pressure difference through each sample and measuring the resulting flow rate (mmol s^{-1}) with five decimal place analytic balances connected to a computer. Air embolism was then removed by successive 0·1 MPa water pressurization until the conductivity no longer increased (K_{max}). The percentage loss of hydraulic conductivity (P) was then calculated as:

$$P = 100\,(1 - K_{\text{init}}/K_{\text{max}}) \tag{1}$$

The following sigmoid function was fitted to the experimental vulnerability curves:

$$P(\Psi_{\text{xylem}}) = P_0 + (100 - P_0)/(1 + (\Psi_{\text{xylem}}/\Psi_{\text{50P}})^s) \tag{2}$$

where P_0 is the native state of embolism, Ψ_{50P} is the Ψ_{xylem} that induces 50 P and s is a slope parameter. Equation 2 was inverted to compute the value of Ψ_{xylem} for which P increased by 10% (Ψ_{10P}). Ψ_{10P} was a rough estimate of the point of runaway embolism, i.e. a threshold water potential below which any slight increase in leaf transpiration will lead to 100 P and shoot desiccation (Tyree & Sperry 1988).

To characterize the xylem hydraulic efficiency to water transport (Tyree & Ewers 1991), we assessed xylem anatomy (see below), segment cross-section area specific hydraulic conductivity (K_s, mol m^{-1} s^{-1} MPa^{-1}) and leaf area specific hydraulic conductivity (K_l, mmol m^{-1} s^{-1} MPa^{-1}). K_s was computed by dividing K_{max} by the segment cross-section (m^2, bark not included). K_s is an integrative parameter determined by vessel diameter and vessel number. K_l was calculated by dividing K_{max} by total leaf area distal to xylem internodes (m^2, one side counted).

Water potential and stomatal conductance

Minimum midday leaf water potentials (Ψ_{leaf}) of the adult trees were assessed with a portable pressure chamber (PMS, Coravalis, Oregon, USA) on two sunny days during the summers of 1993 and 1997. Midday xylem water potentials (Ψ_{xylem}) were estimated in 1997 by measuring the midday water potential of leaves that were previously enclosed in an aluminium foil early in the morning. During the 1994 growing season, we measured sapling midday leaf stomatal conductance, g_s (mmol s^{-1} m^{-2}), and transpiration rate, E (mmol s^{-1} m^{-2}) with a portable porometer (Li-Cor 1600; Lincoln, Nebraska, USA). This was measured on four plants per treatment on 7 d. In 1997, we measured g_s and E for adult trees on leaves randomly taken from representative sunlit and shaded branches.

Xylem anatomy

Vessel diameters were measured for saplings and adult branches on four representative 1-year-old shoots. Thin cross-sections were obtained by hand with a fresh razor blade and observed with a light microscope (400x). On each cross-section we chose a sector delimited by two radial rays and measured at least 50 conduits larger than 10 μm with an micrometric ocular (resolution one µm). For each conduit, we measured the minimum and maximum lumen diameters and computed their geometrical means.

RESULTS

Shade- and full-light-grown branches differed in their anatomy and water relations (Table 1). Leaf mass per unit area (LMA) was higher for leaves grown under high irradiance, but the LMA values for light-acclimated saplings were much lower compared with light-acclimated adult branches. Midday leaf (Ψ_{leaf}) and xylem (Ψ_{xylem}) water potential values were significantly lower for full-light branches than shaded ones. Lower water potential values were associated with higher stomatal conductance and transpiration rates in adult trees. However, saplings of both treatments exhibited similar stomatal conductance (g_s) values.

On mature trees, branches developed under full-light conditions were clearly less vulnerable to water-stress-induced embolism (Fig. 1a & b and Table 2). The difference in Ψ_{50P} and Ψ_{10P} was about 0·8 MPa for both branch age classes and highly significant. Older branches (Fig. 1b) exhibited a higher degree of native embolism (about 40%) because of an incomplete removal of embolism accumulated during the previous winter (Cochard & Lemoine, unpublished). The effect of irradiance levels on xylem embolism was experimentally confirmed on saplings grown in a nursery. Higher light intensity corresponded to lower vulnerability to embolism. However, the differences in Ψ_{50P} between treatments were lower (about 0·4 MPa) and for older shoots the differences were not significant. Overall, a linear relationship ($r^2 = 0{\cdot}97$) was found between Ψ_{50P} of current year shoots and LMA (see also Fig. 5b).

On Fig. 2 we expressed the hydraulic conductivity after embolism dissolution (K_{max}) as a function of stem diameter for saplings and adult trees. The relationships were linear (on a log-log scale) but slopes were greater than two suggesting that segment cross-section area specific hydraulic conductivity (K_s) was increasing with stem diameter. For a given segment diameter, K_{max} was significantly higher for the internodes of shaded saplings (compare open and closed symbols on Fig. 2 lower panel) but K_{max} were identical for different branches in the same mature tree (Fig. 2 upper panel). Within each treatment, leaf specific conductivities (K_l) were significantly higher for current year apical shoots than older shoot internodes (Fig. 3, compare different symbols with same colour). For a given adult tree stem diameter, K_l values were much higher for branches acclimated to full light (Fig. 3 upper, open versus closed symbols) but irradiance had no effect on K_l for saplings (Fig. 3 lower). The frequency distribution of vessel diameters were comparable in 1-year-old shade and light branches of adult trees (Fig. 4). In saplings, the vessels were wider, especially in the full-light treatment. The fact that K_s was lower in full-light saplings although vessels were wider was probably caused by a lower vessel density or a higher production of late wood in this treatment.

On Fig. 5 we expressed Ψ_{50P} as a function of the mean K_s for each treatment. This graph expresses a safety versus efficiency trade-off for xylem vessels. Within the same branch system, there was a tendency for an increase in vulnerability with segment age and therefore K_s (compare data connected by a dotted line) but the increase in xylem vulnerability under low light conditions was not correlated with changes in K_s (compare data with same symbol and different colours).

Table 1. Anatomy and water relations of shade and light grown *Fagus* branches or saplings. Leaf characteristics included leaf mass per unit area (LMA) and individual leaf area. E represents leaf transpiration rates, g_s stomatal conductance to vapor water and Ψ_{xylem} and Ψ_{leaf}, xylem and leaf water potentials, respectively. Data are means ± SE with n the number of replicates. Water potential values were not available for saplings

	Adult trees				Saplings			
	Light		Shade		Light		Shade	
LMA (g m^{-2})	79·20 ± 1·6	$n = 54$	39·27 ± 0·52	$n = 54$*	58·00 ± 1·9	$n = 300$	34·70 ± 1	$n = 300$*
Leaf area, cm^2	24·27 ± 0·9	$n = 54$	36·82 ± 1·8	$n = 54$*	9·56 ± 0·48	$n = 300$	4·15 ± 0·48	$n = 300$*
vessel diameter (μm)	17·66 ± 0·28	$n = 218$	17·86 ± 0·24	$n = 203$	27·42 ± 0·34	$n = 208$	20·06 ± 0·27	$n = 204$*
E (mmol s^{-1} m^{-2})	3·66 ± 0·10	$n = 21$	0·55 ± 0·27	$n = 20$*	4·17 ± 0·19	$n = 28$	5·03 ± 0·44	$n = 28$*
g_s (mmol s^{-1} m^{-2})	218·20 ± 28·5	$n = 20$	33·60 ± 5·6	$n = 21$*	183·9 0± 8·41	$n = 28$	234·00 ± 20·5	$n = 28$*
Ψ_{xylem} (MPa)	–1·12 ± 0·14	$n = 9$	–0·64 ± 0·07	$n = 9$*	–	–		
Ψ_{leaf} (MPa)	–2·37 ± 0·16	$n = 19$	–1·39 ± 0·18	$n = 19$*	–	–		

*, $P < 0{\cdot}001$.

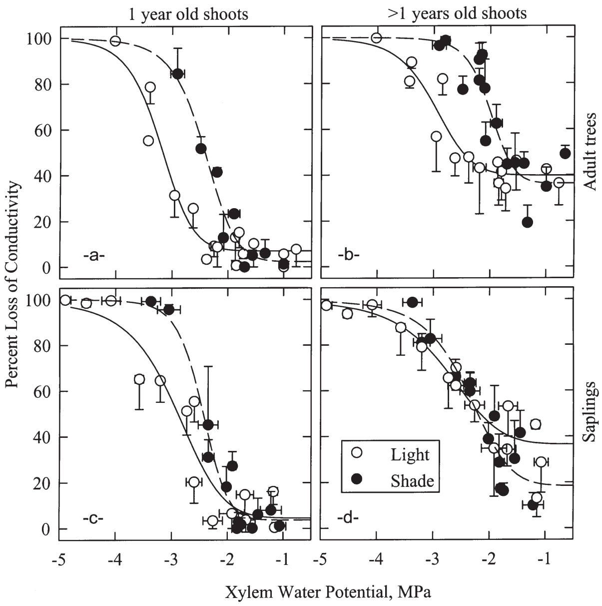

Figure 1. Vulnerability curves of *Fagus sylvatica* shoot internodes acclimated to shade- (closed circles) or full-light (open circles) conditions. Internodes were taken from current year (left, a and c) and previous years shoots (right, b and d) on adult trees (upper a and b) and potted saplings (lower c and d). Error bars represent one standard deviation ($n = 4$ for x, $n = 4$–8 for y). Solid and dashed lines are logistic regressions for light and shade treatments, respectively. In all treatments, full-light condition was associated with lower vulnerability to cavitation.

DISCUSSION

In this study we showed that the irradiance level received during growth had strong impacts on the xylem vulnerability to water-stress-induced embolism in *Fagus sylvatica*. Branches developed under shaded conditions were more vulnerable than sun-exposed ones. These patterns were reproduced experimentally by growing saplings under two different light regimes. However, saplings acclimated to full irradiance levels were more vulnerable than branches from adult trees. These saplings also exhibited lower leaf LMA values so we do not know if these patterns were age-related or due to differences in growth conditions between 1993 and 1994.

Differences in xylem vulnerability were correlated with the differences in Ψ_{leaf} and Ψ_{xylem} measured at midday during sunny days for the two types of adult branches. Ψ-values were higher in the shade because the air evaporative demand, and thus transpiration rates, were much lower. The most negative Ψ_{leaf} values were very close to the $\Psi_{10\text{P}}$ values for both shaded and full-light branches. However, it did not signify that xylem conduits were operating close to their point of dysfunction because Ψ_{xylem} was much higher than Ψ_{leaf}. This result occurred because, in *Fagus* (Tyree & Cheung 1977; Cochard & Lemoine, unpublished) and other species (Tyree *et al*. 1993b), most of the branch resistance to the sap pathway is extra-vascular and located in the leaf blades. Under adequate water availability, most of

Table 2. Xylem vulnerability to embolism. Logistic functions (see Eqn 2 in the text) were fitted to experimental P versus xylem water potential (Ψ_{xylem}) curves. Parameters of the functions were: (1) the native state percentage loss of conductivity (P_0) (2) Ψ_{xylem} for 50% increase of P above P_0 ($\Psi_{50\text{P}}$) and (3) s, a slope parameter. Ψ_{xylem} below which P increased 10% above P_0 ($\Psi_{10\text{P}}$), was then computed as a theoretical value for catastrophic xylem dysfunction. We distinguished 1-year-old shoots from older shoots because P_0 values were very different. Values are given ± SE. Data having a letter in common are not significantly different at $P = 0{\cdot}01$

	Mature trees				Saplings			
	1-year-old		> 1-year-old		1-year-old		> 1-year-old	
	Light	Shade	Light	Shade	Light	Shade	Light	Shade
P_0	7·60 ± 2·45b	2·36 ± 4·9b	39·80 ± 3·1a	36·30 ± 5·18ac	4·57 ± 5·36b	3·70 ± 3·45b	36·50 ± 4·24a	18·50 ± 8·8bc
$\Psi_{50\text{P}}$	−3·22 ± 0·07a	−2·43 ± 0·07df	−2·99 ± 0·1ab	−2·00 ± 0·08 h	−2·92 ± 0·12bc	−2·45 ± 0·06de	−2·74 ± 0·13cde	−2·38 ± 0·15efg
s	−10·74 ± 2·22a	−8·22 ± 0·92ac	−8·89 ± 2·55ac	−9·16 ± 3·40ac	−6·67 ± 1·68ac	−10·66 ± 2·73a	−4·66 ± 1·25bc	−6·01 ± 1·77ac
$\Psi_{10\text{P}}$	−2·64	−1·86	−2·49	−1·67	−2·12	−2·00	−2·03	−1·72

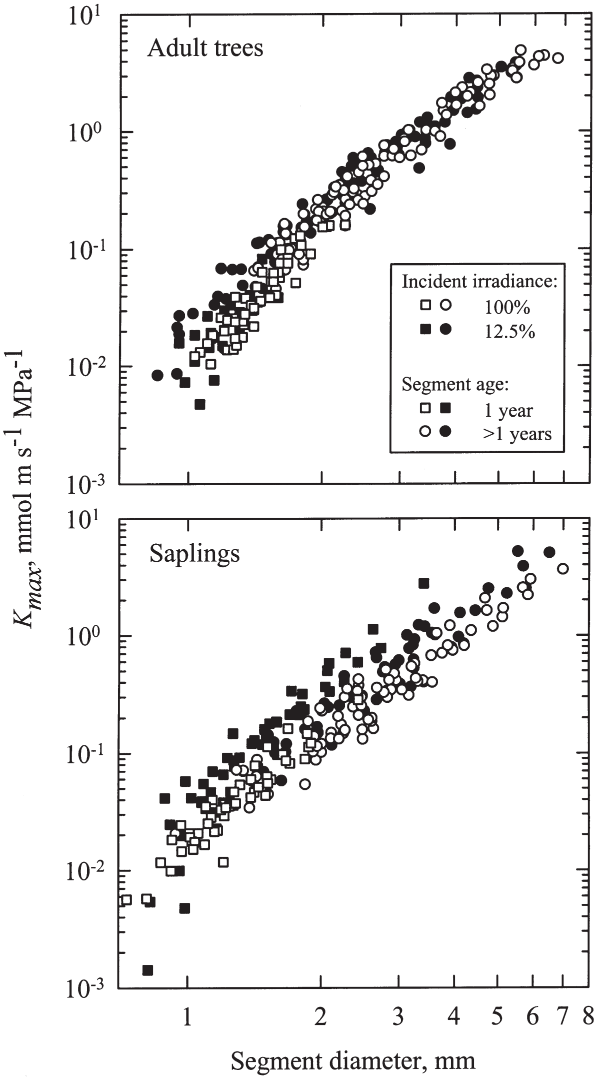

Figure 2. Xylem hydraulic conductivity (K_{max}, mmol m s^{-1} MPa^{-1}) versus segment diameter (bark excluded). Xylem segments, 2–3 cm long, were excised from current year (squares) and previous year (circles) shoot internodes of adult branches (upper) and saplings (lower) grown in full light (open symbols) or shade (closed symbols). Note that scales are logarithmic. For a given stem diameter, saplings acclimated to shaded conditions exhibited higher K_{max} but shade- and lightgrown branches on mature trees did not differ.

the leaf water potential drop will then be in the leaf blade itself. However, when soil resistances are high and transpiration rates low because of a soil drought, Ψ_{leaf} may match Ψ_{xylem} more closely and Ψ_{xylem} is more likely to approach Ψ_{10P} (Cochard *et al*. 1996a; Lu *et al*. 1996).

Our results suggest that within a crown, branch xylem vulnerability correlates with branch leaf transpiration rates and prevailing xylem water potentials. We were surprised to find comparable and high g_{s} and E-values (and stomatal densities, data not shown) for saplings acclimated to shade or light because these parameters were very different for the branches of adult trees. However, individual leaf and total branch leaf areas were much higher for shaded tree branches than saplings so that transpiration rate may not have been very different for branches versus saplings of comparable xylem areas. Schultz & Matthews (1993) suggest that in grapevine acclimated to low light, the xylem transport capacity was uncoupled from leaf area. This was the case only for adult *F. sylvatica* branches in this study, where shade grown branches exhibited lower K_{l} values. However, the xylem transport capacity was uncoupled to a lesser extent from water loss capacities because leaf E and g_{s} were greatly reduced in the shade. Uncoupling leaf area from leaf transpiration rate might be a strategy to maximize light interception and water use efficiency in the shade.

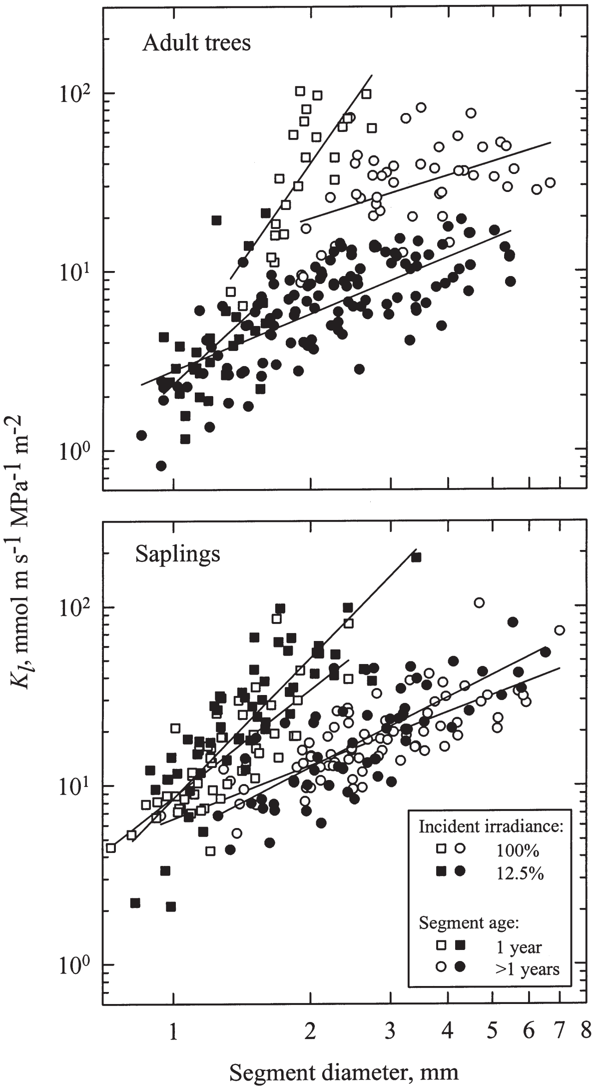

Figure 3. Xylem leaf specific hydraulic conductivity (K_{l}, mmol m s^{-1} MPa^{-1}) versus segment diameter for adult branches (upper) and saplings (lower). Same symbols as in Fig. 2. For a given stem diameter, adult branches acclimated to shaded conditions exhibited lower K_{l} values but shade- and light-grown saplings did not differ.

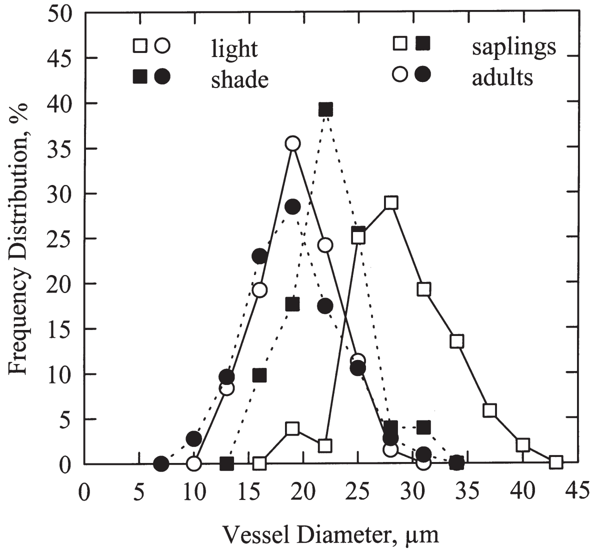

Figure 4. Frequency distribution of vessel diameters in xylem of 1-year-old shoots from shade and light branches. Higher xylem vulnerability in shade grown branches was not correlated with a difference in vessel size.

Low xylem vulnerability might be advantageous for full-light branches because they experience higher and more variable transpiration rates than shaded branches, which can result in lower Ψ_{leaf} and Ψ_{xylem}. The lower susceptibility to cavitation was not correlated with a decrease in xylem hydraulic efficiency (Fig. 5). There is no tradeoff of hydraulic efficiency for vulnerability to embolism in *Fagus* branches acclimated to different light conditions. Tyree, Davis & Cochard (1994) came to the same conclusion when comparing the hydraulic properties of many woody species. A lower efficiency would have enhanced the water potential drop along the sap pathway which would have lessened the gain in cavitation resistance. A benefit associated with an increase in the vulnerability for shaded branches is less clear. However, because xylem conduits can acclimate to new environmental conditions probably only over the long-term (until new vessels are formed), we can predict that shade-grown branches or saplings suddenly exposed to full light (after forest thinning for instance) may experience xylem embolisms if transpiration rates are not efficiently regulated (Tognetti, Michelozzi & Borghetti 1994).

We know from other studies that, within a species, plants acclimated to different habitats may differ in their vulnerability. For instance, Alder *et al*. (1996) found that root xylem in *Acer grandidentatum* was more vulnerable for plants in a wetter site. However, vulnerability to drought-induced embolism of *Rhodendendron maximum* was not affected by the light environment (Lipp & Nilsen 1997). Cochard *et al.* (1997) established that in *Fraxinus excelsior*, the leaf rachis from upper crown branches was more vulnerable in comparison with lower crown branches. In their study, the decrease in xylem vulnerability correlated with a decrease in Ψ_{xylem} induced by higher xylem resistances in lower branches. Altogether, these results indicate that vulnerability to cavitation can exhibit a high degree of plasticity and can respond to light (present study), soil water availability (Alder *et al.* 1996) or vertical position in a crown (Cochard *et al*. 1997). These variations can actually be as large as between species or genotypes. From a methodological point of view, this suggests that, for comparisons of VCs of species or genotypes, plants must have experienced strictly similar ambient conditions during growth.

An important issue of this work is the mechanism by which xylem vulnerability acclimates to irradiance levels. The mechanism of water-stress-induced embolism has been largely documented (Sperry & Tyree 1988; Cochard, Cruiziat & Tyree 1992; Jarbeau, Ewers & Davis 1995) and, according to the current understanding of the phenomenon, differences in vulnerability originate from size differences in inter-conduits pit pores. This explains why xylem vulnerability was clearly not related to vessel size in this study and many others (see Tyree *et al*. (1994) for a review). However, the mechanism by

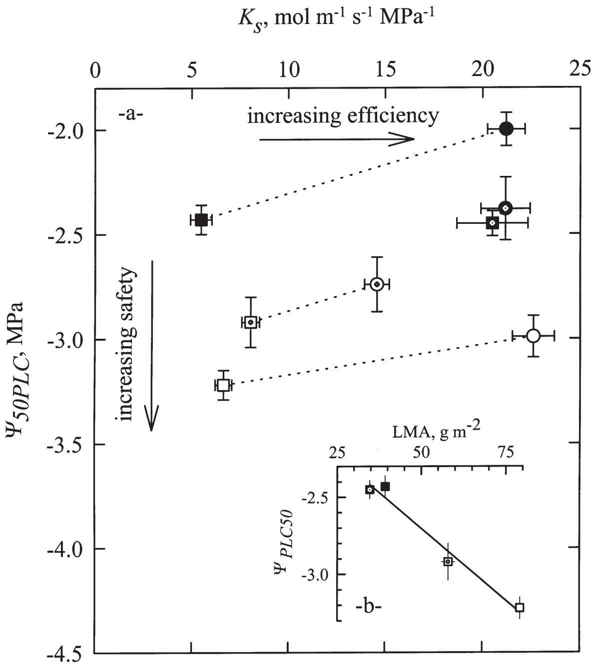

Figure 5. a, Xylem efficiency versus xylem safety in *Fagus*. Xylem hydraulic efficiency is estimated by the cross-section area specific hydraulic conductivity (K_s, mol m^{-1} s^{-1} MPa^{-1}) and xylem safety by the water potential inducing 50% loss of conductivity (Ψ_{50P}, MPa). Closed symbols: shade; open symbols: light; dotted symbols: saplings; squares: 1-year-old shoots; circles: two- or more year-old shoots; Error bars represent one standard error. The increase in xylem efficiency was associated with a slight decrease in safety within a branch system (symbols linked by a dotted line) but there was no tradeoff of hydraulic efficiency for safety between shade- and light-acclimated branches. b, Ψ_{50P} versus leaf mass per unit area (LMA, g m^{-2}) for 1-year-old shoots. Same symbols as in Fig. 5a. Xylem safety was increased for shoots with more xerophytic leaves.

which the light environment could induce microanatomical modifications in vessel walls remains to be explained. Because mature vessels and tracheids contain no cytoplasm, the pit pore dimensions are probably determined during conduit maturation. This suggests that when vessels differentiate during spring, the size of the pores in the pit membrane is already adapted to the Ψ_{xylem} the vessel will experience days or weeks after. It is well-known that light availability can affect plant growth through feedback mechanisms involving water transport or internal carbon balance (Kaufmann 1990). Shoot morphogenesis is also known to be changed by a modification in the far red : red ratio (Ritchie 1997). In the present study we found that under neutral shade (saplings) there were differences in the diameter distribution of vessels, whereas under natural shade and thus altered far red : red ratio there were no differences. So the possibility exists that light quality or quantity may have an effect on pit membrane structure.

In conclusion, our study suggests that xylem conduits of *Fagus sylvatica* grown under different light conditions are functionally adapted to contrasted xylem water potentials and transpiration rates. The high plasticity we found in *Fagus* correlates with its shade tolerance and its ability to maintain living branches in different light climates. We believe that these findings represent a new step in the understanding of tree–water relations. Studies on plant cavitation have already revealed that xylem dysfunction was a critical phenomenon and plant water loss must adjust to plant water transport vulnerability (Jones & Sutherland 1991; Cochard *et al*. 1996a). We now have evidence for an adaptation of xylem vulnerability to changing water loss intensity. The change in vulnerability with growing conditions might be an important parameter to consider in order to understand plant adaptation to its habitat.

ACKNOWLEDGMENTS

We thank T. Améglio, P. Cruiziat, F. Ewers, A. Granier, R. Huc and two anonymous referees for helpful reviews of the manuscript. We are grateful to J.C. Hervé for assistance with the statistics.

REFERENCES

Alder N.N., Sperry J.S. & Pockman W.T. (1996) Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia* **105,** 293–301.

Aussenac G. & Ducrey M. (1977) Etude bioclimatique d'une futaie feuillue (*Fagus sylvatica* L. et *Quercus sessiliflora* Salisb.) de l'Est de la France. 1. Analyse des profiles microclimatiques et des caractéristiques anatomiques et morphologiques de l'appareil foliaire. *Annales Des Sciences Forestières* **34,** 265–284.

Borghetti M., Leonardi S., Raschi A., Snyderman D. & Tognetti R. (1993) Ecotypic variation of xylem embolism, phenological traits, growth parameters and allozyme characteristics in *Fagus Sylvatica. Functional Ecology* **7,** 713–720.

Cochard H. (1992) Vulnerability of several conifers to air embolism. *Tree Physiology* **11,** 73–83.

Cochard H., Bréda N. & Granier A. (1996a) Whole tree hydraulic conductance and water loss regulation: evidence for stomatal control of embolism? *Annales Des Sciences Forestières* **53,** 197–206.

Cochard H., Ridolfi M. & Dreyer E. (1996b) Responses to water stress in an ABA-unresponsive hybrid poplar. 2. Hydraulic properties and xylem embolism. *New Phytologist* **134,** 455–461.

Cochard H., Cruiziat P. & Tyree M.T. (1992) Use of positive pressures to establish vulnerability curves further support for the air-seeding hypothesis and implications for pressure-volume analysis. *Plant Physiology* **100,** 205–209.

Cochard H., Bréda N., Granier A. & Aussenac G. (1991) Vulnerability to air embolism of three European oak species (*Quercus petraea, Q. pubescens, Q.robur*). *Annales Des Sciences Forestières* **49,** 225–233.

Cochard H., Peiffer M., Le Gall M. & Granier A. (1997) Developmental control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L. impacts on water relations. *Journal of Experimental Botany* **48,** 655–663.

Hacke U. & Sauter J.J. (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* **46,** 1177–1183.

Jackson G.E., Irvine J. & Grace J. (1995) Xylem cavitation in two mature Scots pine forests growing in a wet and a dry area of Britain. *Plant, Cell and Environment* **18,** 1411–1418.

Jarbeau J.A., Ewers F.W. & Davis S.D. (1995) The mechanism of water-stress-induced embolism in two species of chaparral shrubs. *Plant, Cell and Environment* **18,** 189–196.

Jones H.G. & Sutherland R.A. (1991) Stomatal control of xylem embolism. *Plant, Cell and Environment* **14,** 607–612.

Kaufmann M.R. (1990) Ecophysiological processes affecting tree growth: water relationships. In *Process Modelling of Forest Growth* (ed. R. Dixon) pp. 64–76. Timber Press, Portland.

Lipp C.C. & Nilsen E.T. (1997) The impact of subcanopy light environment on the hydraulic vulnerability of *Rhododendron maximum* to freeze-thaw cycles and drought *Plant, Cell and Environment* **20,** 1264–1272.

Lu P., Biron P., Granier A. & Cochard H. (1996) Water relations of adult Norway spruce (*Picea abies* (L) Karst) under soil drought in the Vosges mountains: whole-tree hydraulic conductance, xylem embolism and water loss regulation. *Annales Des Sciences Forestières* **53,** 113–121.

Neufeld H.S., Grantz D.A., Meinzer F.C., Goldstein G., Crisosto G.M. & Crisosto C. (1992) Genotypic variability in vulnerability of leaf xylem to cavitation in water-stressed and well-irrigated sugarcane. *Plant Physiology* **100,** 1020–1028.

Ritchie G.A. (1997) Evidence for red: far red signaling and photomorphogenic growth response in Douglas-fir (*Pseudotsuga menziesii*) seedlings. *Tree Physiology* **17,** 161–168.

Schultz H.R. & Matthews M.A. (1993) Xylem development and hydraulic conductance in sun and shade shoots of grapevine (*Vitis vinifera* L) – evidence that low light uncouples water transport capacity from leaf area. *Planta* **190,** 393–406.

Sperry J.S. & Saliendra N.Z. (1994) Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis. Plant, Cell and Environment* **17,** 1233–1241.

Sperry J.S. & Tyree M.T. (1988) Mechanism of water stress-induced xylem embolism. *Plant Physiology* **88,** 581–587.

Sperry J.S., Donnelly J.R. & Tyree M.T. (1988a) A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* **11,** 35–40.

Sperry J.S., Tyree M.T. & Donnelly J.R. (1988b) Vulnerability of xylem to embolism in a mangrove vs an inland species of Rhizophoraceae. *Plant Physiology* **74,** 276–283.

Tognetti R., Michelozzi M. & Borghetti M. (1994) Response to light of shade-grown beech seedlings subjected to different watering regimes. *Tree Physiology* **14,** 751–758.

Tyree M.T. & Cheung Y.N.S. (1977) Resistance to water flow in *Fagus grandifolia* leaves. *Canadian Journal of Botany* **55,** 2591–2599.

Tyree M.T. & Dixon M.A. (1983) Cavitation events in *Thuja occidentalis* L.? Ultrasonic acoustic emissions from the sapwood can be measured. *Plant Physiology* **72,** 1094–1099.

Tyree M.T. & Ewers F.W. (1991) The hydraulic architecture of trees and other woody plants. *New Phytologist* **119,** 345–360.

Tyree M.T. & Sperry J.S. (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.

Tyree M.T., Davis S.D. & 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 M.T., Cochard H., Cruiziat P., Sinclair B. & Ameglio T. (1993a) Drought-induced leaf shedding in walnut – evidence for vulnerability segmentation. *Plant, Cell and Environment* **16,** 879–882.

Tyree M.T., Sinclair B., Lu P. & Granier A. (1993b) Whole shoot hydraulic resistance in *Quercus* species measured with a new high-pressure flowmeter. *Annales Des Sciences Forestières* **50,** 417–423.

Received 19 March 1998; received in revised form 25 July 1998; accepted for publication 25 July 1998