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Damien Lemoine, Hervé H. Cochard, André A. Granier. Within crown variation in hydraulic architecture in beech (*Fagus sylvatica* L): evidence for a stomatal control of xylem embolism. *Annals of Forest Science*, 2002, 59, pp.19-27. 10.1051/forest:2001002 . hal-01097901

HAL Id: hal-01097901

<https://hal.science/hal-01097901>

Submitted on 8 Jan 2015

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Within crown variation in hydraulic architecture in beech (*Fagus sylvatica* L): evidence for a stomatal control of xylem embolism

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(Received 13 March 2001; accepted 6 July 2001)

Abstract – The stomatal control of embolism in *Fagus sylvatica* L. was analysed in response to crown position and experimental changes of trunk hydraulic resistance. On one mature beech tree deep cuts were made in the trunk to increase the resistance to water transfert. We followed the changes in leaf and xylem water potential and stomatal conductance after the cuts at three levels within the canopy. We characterised vulnerability to cavitation for branches taken from two levels of irradiance (sun-exposed branches and shaded ones). Some differences appeared between shade and sun-exposed branches. When the leaf water potential dropped, stomatal conductances decreased earlier and faster in the shade branches. These results are well correlated with vulnerability to cavitation, shade branches being more vulnerable than sun-acclimated branches. Xylem water potential levels producing fifty percent loss of hydraulic conductivity were lower in sun-exposed branches than in shade grown ones (–3.1 MPa vs. –2.5 MPa on average). Xylem water potentials that induced stomatal closure were above the threshold-value inducing cavitation both for shade and sun-exposed branches. We confirmed that vulnerability to cavitation in *Fagus sylvatica* can acclimate to contrasting ambient light conditions, and we concluded that stomatal response to water stress occurred early and sufficiently fast to protect xylem from dysfunction.

beech (*Fagus sylvatica* L.) / xylem embolism / stomatal regulation / irradiance / acclimation

Résumé – Variations de l'architecture hydraulique du hêtre (*Fagus sylvatica* L.) : contrôle de l'embolie du xylème par les stomates. Nous avons analysé le contrôle stomatique du développement de l'embolie chez *Fagus sylvatica* L. en fonction de l'éclaircissement des branches et suite à un changement de la résistance hydraulique du tronc. Nous avons fait des entailles dans le tronc d'un hêtre de façon à augmenter la résistance au transfert de l'eau. Nous avons suivi les variations de potentiels hydriques foliaire et de xylème et la conductance stomatique à trois niveaux dans le houppier. Nous avons caractérisé la vulnérabilité à la cavitation de branches de pleine lumière et d'ombre. Lorsque le potentiel hydrique a diminué, la conductance stomatique des branches d'ombre a diminuée le plus tôt et le plus fortement. Ce résultat est bien corrélé avec la vulnérabilité à la cavitation des branches. Les branches d'ombre sont plus vulnérables que les branches de lumière ; ainsi le potentiel hydrique de xylème induisant 50 % d'embolie est plus négatif en plein éclaircissement qu'à l'ombre (–3,1 MPa contre –2,5 MPa). Le potentiel de xylème induisant la fermeture des stomates est supérieur au potentiel induisant la cavitation à la lumière comme à l'ombre. Nous avons confirmé que la vulnérabilité du hêtre s'acclimate aux conditions d'éclaircissement et que les stomates protègent le xylème d'un dysfonctionnement.

hêtre (*Fagus sylvatica* L.) / embolie / régulation stomatique / éclaircissement / acclimatation

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1. INTRODUCTION

Xylem sap of plants is usually under tension during the growing season. Thus, water columns may be disrupted (cavitation) and become air-filled (embolised) when tensions increase too much during water stress [31]. There is ample evidence to indicate that cavitation induced by water stress or excessive transpiration are common events in vascular plants [24]. A large stomatal opening that induces transpiration is a necessary consequence of the plant's need to maintain gas exchange in leaves for photosynthesis. To maintain a favourable water balance, an efficient water flux in the xylem is needed to replace the water loss by the leaves. Embolism causes a reduction in xylem transport and thus induces an imbalance on the plant water status. During four years, we regularly measured embolism in beech trees and we did not observe embolism repair during the growing season (data not shown). Thus, water potential should not fall significantly below the threshold-value inducing cavitation: Ψ_{cav} . It has been suggested that stomata play an important role in limiting cavitation [25]. Decrease of hydraulic conductance following embolism, directly contributes to the limitation of water fluxes through the stem [22]. This induces stomatal closure that limits transpiration to avoid runaway embolism [15, 17, 19]. Sperry [17] noticed an early limitation of embolism by stomatal closure in some species. However only few experiments exhibit a stomatal regulation which occurs after embolism is induced [15]. The vulnerability to cavitation of several woody species has been measured. Large differences were shown among tree species and within a given species due to environmental adaptation. However genetic and site induced variations inside tree crowns had been poorly studied. Cochard et al. [5] showed a relation between vulnerability to cavitation and irradiance in beech: shaded saplings presented an higher vulnerability than sun-exposed ones. However, these authors did not study effects of irradiance on stomatal functioning. In this paper, we were interested to replace the observations made on potted saplings [5] within the forest environment and to observe irradiance impacts on stomatal behavior during increasing hydraulic resistances. *Fagus* trees exhibit a strong vertical light gradient within the crown and could be a good model to explain impacts of light gradient in shade-tolerant species. Thus, for a given tree, differences in xylem vulnerability and stomatal responses to water demand might be induced by diverse microclimate conditions (light, vapour pressure deficit...). In this experiment, we artificially induced water shortage in a beech tree growing under natural conditions.

Concomitant variations in leaf water potential and stomatal conductance were studied in relation with vulnerability to cavitation.

2. MATERIALS AND METHODS

2.1. Plant Material

Five 30-year-old *Fagus sylvatica* L. trees were chosen within the dominant trees in the State Forest of Hesse, in the eastern part of France (48° 40' N, 7° 05' E, elevation: 300 m). Leaf area index estimated from litter collection was close to 7.3. More details can be found in Granier et al. [7], Lebaube et al. [12] and Le Goff and Ottorini [13]. Trees were growing in a closed stand, with upper branches exposed to full sun light ("sun branches"), lower ones heavily shaded by upper crown branches and surrounding trees ("shade branches") and with an intermediate part of the crown with intermediate characteristics ("medium branches").

2.2. Light measurement into the crown

To characterize the vertical light gradient into the crown, we measured the fraction of incident irradiance with a line quantum sensor (LI-191SA, LiCor, Lincoln, Nebraska, USA), during 3 days at 9 levels in the crowns from the top canopy to the soil. Measurements were made on cloudy days to avoid shade projection on the quantum sensor. Thus, we calculated the fraction of incident irradiance as the ratio between the irradiance measured at a given place and irradiance above canopy. We completed these data with measurements made during sunny days close to the studied branches (see *table I*).

Table I. mean values of vapor deficit pressure (*VPD*) and photosynthetically active radiation (*PAR*) during the experiment near the sun and the shade branches and mean leaf area of these branches.

	<i>VPD</i> (hPa)	<i>PAR</i> ($\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$)	Leaf area (m^2)
Sun branches	2.130 ± 0.312	1850 ± 50	0.80 ± 0.15
Shade branches	1.393 ± 0.337	255 ± 55	1.15 ± 0.45

2.3. LSC measurement

The efficiency of branch xylem in conducting water was estimated by measuring the leaf specific conductivity (*LSC*, mmol s⁻¹ MPa⁻¹ m⁻²). This parameter links water potential gradient across a branch ($d\Psi$, MPa m⁻¹) to water flow (mmol s⁻¹) through the branch: $d\Psi = F / LSC$. We used a high pressure flow meter (*HPFM*, [27, 28, 29]) to measure whole branch conductivity, K_{branch} , in a steady state mode. K_{branch} was estimated by applying a positive pressure, P (MPa), and forcing distilled water into the base of the branch. The water flow, F (mmol s⁻¹), was measured when flow became in a steady state and K_{branch} was calculated as the ratio between F and P :

$$K = F / P.$$

The *LSC* of the branch was calculated as the ratio between K_{branch} and the leaf area of the branch. Following this procedure, K_{branch} and *LSC* were measured in 36 branches from three trees.

2.4. Vulnerability curves

Vulnerability curves (*VCs*) are plots of degree of xylem embolism versus Ψ_{xylem} that induced the embolism. They were constructed by dehydrating different excised branches to decrease Ψ_{xylem} . Degrees of embolism were assessed as described in Sperry et al. [18] by measuring losses of hydraulic conductance caused by air blockages in xylem conduits of short (2–3 cm) shoot internodes. We established *VCs* for current-year shoot internodes and petioles of sun-exposed branches and shade branches. In July and August 1998, we collected 66 branches from 11 trees in the morning with a six meter long pruning pole, enclosed them in a black airtight plastic bag to reduce water loss through transpiration and brought them rapidly to the laboratory for hydraulic analysis. In the laboratory, the samples were dehydrated by pressurization for 30 to 45 mn [1, 2, 3] until sap exudation ceased, then enclosed for at least one hour in a black airtight plastic bag to stop transpiration and to remove water potential gradients between leaves and xylem tissues. Xylem tension was then returned to zero by immersing the branches 30 minutes in tap water before hydraulic analysis. After rehydration, 15 shoot internodes from current year growth units of each branch were excised under water. The initial hydraulic conductivity K_{init} (mmol m s⁻¹ MPa⁻¹) was measured by forcing distilled water under 6 kPa pressure difference through each sample and measuring the resulting flow rate (mmol s⁻¹) with a five decimal place analytic balance connected to a computer. Air em-

bolism was then removed by successive 0.1 MPa water pressurizations until the conductivity no longer increased (K_{max}). The percent loss of hydraulic conductivity (*PLC*) was then calculated as:

$$PLC = 100 (1 - K_{init} / K_{max}).$$

The sigmoidal shape of a vulnerability curve can be characterized by two critical water potential values: Ψ_{cav} and $\Psi_{50\%}$. We define Ψ_{cav} as the water potential that induces a significant loss of hydraulic conductivity. Embolism rate under well watered conditions is about 5 to 10% and increases quickly from this point when decreasing Ψ_{xylem} . The second values is $\Psi_{50\%}$, which is the water potential that induces a loss of 50% of the maximal hydraulic conductivity.

2.5. Water potential and stomatal conductance

Leaf water potentials (Ψ_{leaf}) of two 30-year-old trees were assessed with a portable pressure chamber (PMS, Corvallis, Oregon, USA) on 12 sunny days during 1998 summer (days 218 to 231 as described in the following paragraph) directly from a scaffolding. Predawn leaf water potential was measured at 3h00 AM (solar time) i.e. one hour before sunrise. Measurements were made every 90 min from 7h30 AM (i.e. after dew evaporation) to 7h30 PM (the sunset). Xylem water potentials (Ψ_{xylem}) were estimated by measuring the water potential of leaves that had been previously enclosed in an aluminum foil early in the morning [5, 23]. At the same time, we measured stomatal conductance, g_s (mmol s⁻¹ m⁻²) with a portable porometer (Li-Cor 1600, Lincoln, Nebraska, USA). Leaf water potential and g_s measurements were done on six leaves randomly taken from the three canopy levels previously described.

2.6. Increase of the trunk hydraulic resistance

For five days we measured the water status of the trees (days 218 to 222). During this time, we made sure that no soil water stress developed. Then, on day 223, deep cuts were made in the trunk of one tree to increase the trunk xylem hydraulic resistance, sap flux density was reduced by 60% (data not shown). A second cutting was done on day 229 to increase the resistance even more, sap flux density was totally stopped. The experiment finished on day 231. The stand was used for eddy covariance measurements so only one tree was cut to limit disturbance in global CO₂ and water fluxes [7, 8, 12].

2.7. Xylem anatomy

Vessel diameters and densities were measured for one-year-old twigs at two levels in the trees. Thin cross sections were made by hand with a razor blade and examined with a light microscope (8×25). On each cross section we chose randomly four sectors which were defined by the radial rays and measured all the vessels within these sectors with a micrometric ocular (resolution $1 \mu\text{m}$). For each vessel we noticed the minimum and maximum lumen diameters and computed their means. Vessel densities were measured by counting all the vessels in the selected sectors.

3. RESULTS

3.1. Light measurement

Irradiance from the top to the base of the crowns decreased due to the high density of branches and leaves (*figure 1*). Below the crowns there was only 10 to 15% of incident irradiance. Shade branches were characterised by an incident irradiance close to 20%, sun-exposed branches close to 100% and medium ones between 40 and 60%. Light intensity near the sun-exposed branches

was height times higher than the shade branches (see *table 1*).

3.2. LSC pattern within the crown

The LSC distribution within the crown can be described as a linear function of the height of the branch (*figure 1*). Thus, the highest branches in the crown were three times more conductive per unit of leaf area than the lowest ones. Differences between sun-exposed and shade branches could be explained by an higher hydraulic conductance, differences in leaf area being weak (see *table 1*). As a consequence, a given transpiration rate induces a larger water potential drop in the shade that in the sun-exposed branches.

3.3. Vulnerability curves

Figure 2 presents vulnerability curves of one-year-old beech twigs taken from light and shade branches as described above. Significant differences occurred between the shade and sun twigs as well for Ψ_{cav} as for $\Psi_{50\%}$. $\Psi_{\text{cav}} / \Psi_{50\%}$ were $-1.5 / -2.25$ MPa, and $-2.5 / -3.1$ MPa, for shade and sun-exposed branches, respectively. Shade branches displayed therefore a higher vulnerability to cavitation than sun branches.

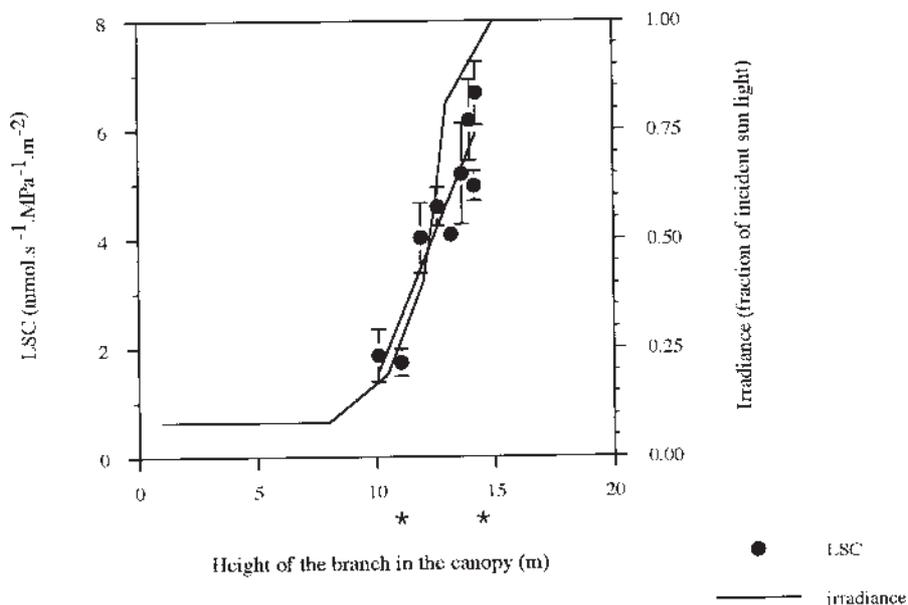


Figure 1. Leaf Specific Conductivity (LSC) distribution and light interception in the crown of three beech trees ($n = 4$ for LSC). Stars indicate where branches used for vulnerability curves were cut.

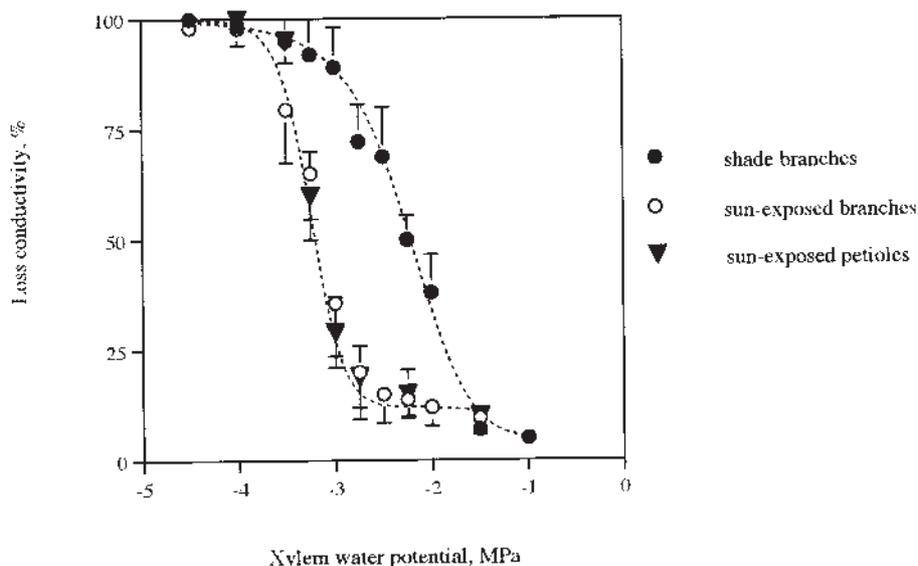


Figure 2. Percent loss of hydraulic conductivity as a function of the xylem water potential in one-year-old twigs of *Fagus sylvatica* harvested on sun-exposed branches of the top of the canopy, or in shaded branches from the base of the crown ($n = 15$).

No significant differences were observed between internodes and petioles of sun-exposed branches.

3.4. Stomatal behavior during water stress

Control trees showed a strong gradient of g_s and Ψ within the crown (figure 3). Sun-exposed branches exhibited higher g_s values and more negative Ψ values than intermediate and shade branches. Throughout the experiment, control trees remained constant Ψ and g_s values with small variations due to differences in mean air temperature (data not shown). From day 218 to 222, we did not observe significant differences between control and stressed trees.

The time course of stomatal conductance and leaf water potential during tree dehydration is shown on figure 3a at three levels in the crown. During water stress, one to two hours after the first cuts, we observed a decrease of stomatal conductance (g_s). Stomatal conductance was reduced in the shade branches while leaf water potential did not drop to very negative values (-3.3 MPa). In the middle of the crown, g_s decreased drastically one day after the cuts, but stabilized at one third of its initial value. The sun branches kept the highest g_s values, with a slower decrease. The second cut induced a strong effect and severely limited the water flux. As a result, Ψ dropped down to critical values (-4 MPa) in the whole

tree. Stomatal conductance reached values close to zero the last day.

We can observe in figure 3b the evolution of the difference between Ψ_{xylem} and Ψ_{leaf} when water potential decreased. When the leaves did not transpire (in the morning when Ψ was close to the predawn water potential, and during drought when stomata were closed), Ψ_{leaf} was close to Ψ_{xylem} . Using figure 3b we can link up figure 3a and figure 4 which use Ψ_{leaf} and Ψ_{xylem} respectively. When Ψ_{leaf} dropped to almost -2.5 MPa, stomata closed and the values of Ψ_{leaf} and Ψ_{xylem} converged.

In figure 4, we plotted the pattern of PLC and g_s versus Ψ_{xylem} . The set points for stomatal closure and for cavitation induction were close in the shaded and sun-exposed twigs. A strong limitation of g_s occurred for light and shade branches when Ψ was close to Ψ_{cav} both. Reduction was more drastic for sun than shade branches.

3.5. Xylem anatomy

Sun-exposed and shade branches presented significant differences in mean vessel diameter, with wider vessels in sun-exposed twigs (table II). We noticed significant differences between short and long twigs for light and shade branches (i.e. long twigs had wider vessels). These differences in conduit diameter were correlated with an increase in vessel density. Long

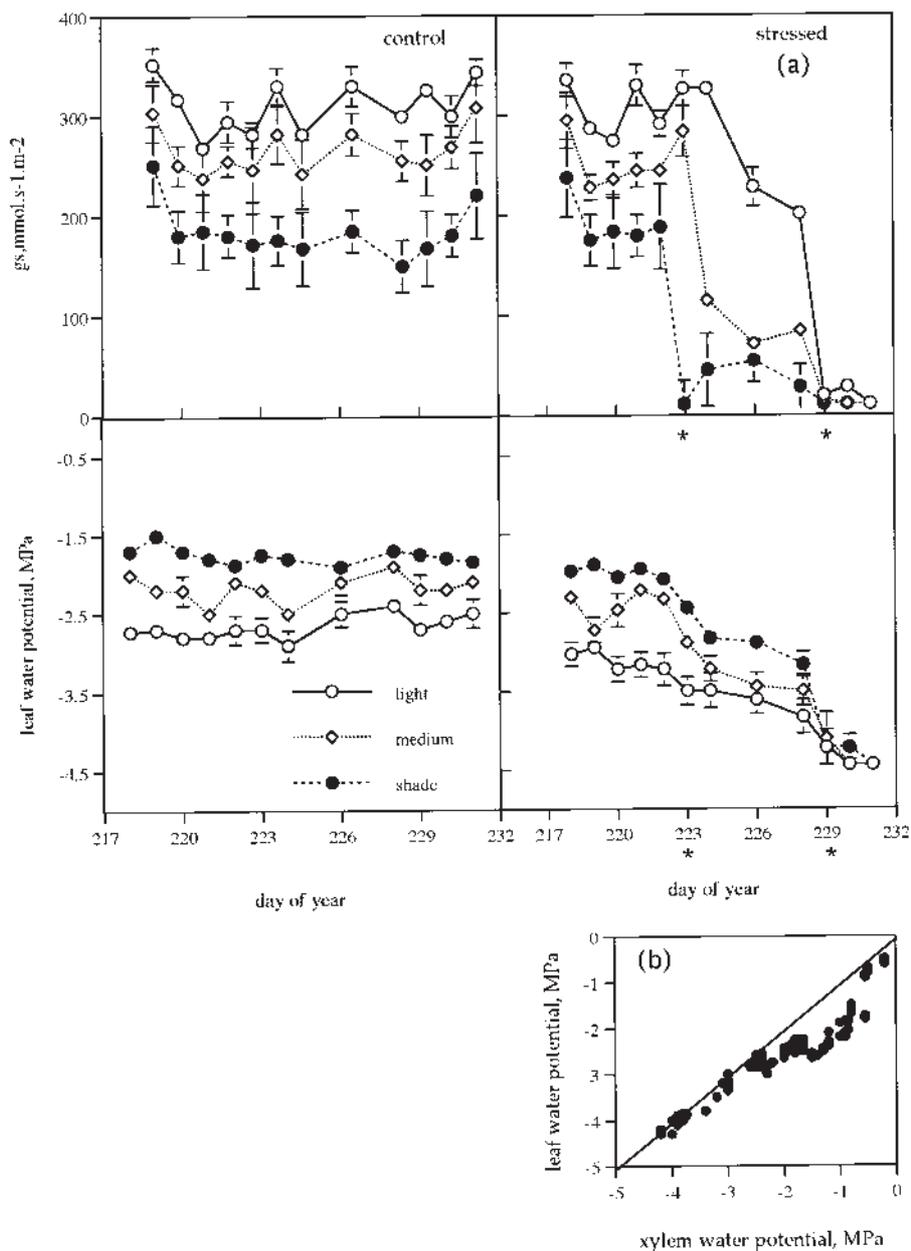


Figure 3. Time course of stomatal conductance (g_s) and leaf water potential at three levels in the crown of *Fagus sylvatica* during water stress (a). The stars indicate the cuts in the trunk. (b) Leaf water potential versus xylem water potential. ($n = 6 \times 3$ for g_s measurements and $n = 6$ for water potential measurements). Stars indicate days when cuttings were made.

sun-exposed twigs presented the greater vessel density. We could not observe significant density differences between short twigs in relation to irradiance.

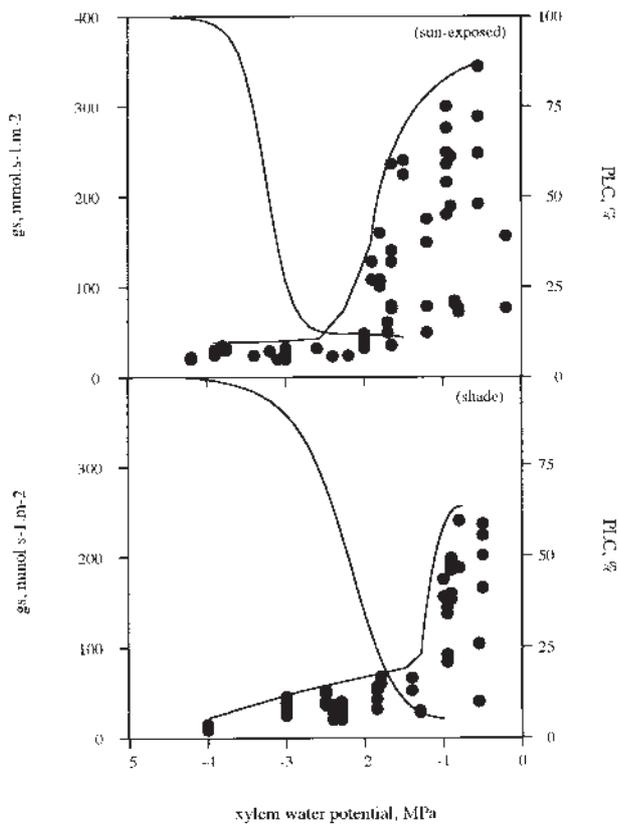
4. DISCUSSION

We found a large within crown gradient of hydraulic properties. Sun-exposed branches presented higher LSC

than shade branches (figure 1). This gradient was linked to microclimate acclimation (irradiance, figure 1) and vulnerability gradient. Difference in vulnerability is quite high between sun-exposed and shade branches (almost 0.8 MPa). Studies on potted saplings exposed to different irradiances presented a similar vulnerability gradient between sun-exposed saplings and shaded ones ([5], unpublished data).

Table II. mean vessel diameter and vessel density of twigs grown under different light regimes. (Data having a letter in common are not significantly different: $p = 0.01$).

	Mean vessel diameter (μm)	Vessel density (vessel/ mm^2)
Long twig (sun)	30.11 ± 4.15 a	1350 ± 35 a
Short twig (sun)	26.19 ± 4.73 b	730 ± 34 c
Long twig (shade)	24.06 ± 2.58 b	946 ± 39 b
Short twig (shade)	21.69 ± 1.89 c	698 ± 30 c

**Figure 4.** Evolution of stomatal conductance (g_s) during xylem water potential decreasing. Dark line replaces PLC development (see figure 2).

When water stress increased, our measurements indicated that stomata closed before excessive embolism occurred (figure 4). Sperry and Pockman [19] suggested that stomata were responding to a threshold leaf water

potential co-occurring with the upper end of the cavitation range. In our case, g_s was decreased before Ψ reached Ψ_{cav} (figure 4). The direct response of stomata to changes of humidity (VPD , Ψ) is well documented [11, 21]. Such a control loop is advantageous because it allows an early limitation of water loss.

Hydraulic conductance in the soil and at the soil root interface is reduced by soil water depletion [16]. If there is no efficient stomatal limitation of water losses, water potential drops to critical values and significant embolism develop. When Ψ drops below a threshold value (Ψ_{cav}) depending of the porosity of the bordered pit membranes, embolism increases rapidly [3, 18, 21]. It is usually shown for trees that during sunny days Ψ values reached very close to critical values inducing embolism. Stomatal regulation allows the trees to maintain Ψ above Ψ_{cav} [4, 14].

Water stress induced by cuts develops more rapidly than natural one. This has to be taken into account for the interpretation of the results.

There are three hydraulic mechanisms that limit the development of embolism; (1) decrease of the vulnerability to cavitation (increase xylem safety by limiting the pit pore membrane size), (2) increase xylem efficiency (higher LSC) resulting in less negative water potential; (3) hydraulic segmentation which confines embolism development to the peripheral parts of the tree (petioles) and maintains xylem integrity in the shoots.

In beech, we showed large differences in water stress responses with different embolism development depending on the position in the crown: sun branches had a higher resistance to water stress than the shade ones and they maintained g_s at negative Ψ values very close to Ψ_{cav} . These physiological differences result in hydraulic differences between the two kind of branches. Cochard et al. [5] reported strong differences in vulnerability to cavitation for adult trees and potted saplings acclimated to

various light conditions. The higher the irradiance, the lower was the vulnerability. In our experiment, we observed similar results with a lower vulnerability for the sun branches (*figure 2*). This difference increased with higher *LSC* values. Therefore, beech sun-exposed branches present an efficient acclimation to limit embolism development. This acclimation is efficient both under good water supply conditions (during high climatic water demand and high irradiance, *table I*) and during water stress when xylem tensions increase drastically following the limitation of the soil water supply. Acclimation of sun branches allows the tree to maintain sufficient stomatal conductance to maintain gas exchange at very negative Ψ values (*figure 3*).

The differences in vulnerability to embolism between shade branches and sun branches could not be explained by anatomical differences (*table II*). According to a comparative study among ring-porous, diffuse-porous and conifer species, conduit volume does not correlate with vulnerability to embolism caused by water stress [20]. It seems that size of pores in the cell wall is the most important anatomical feature regarding drought-induced embolism [20, 31]. However pit pore diameter is difficult to measure and it is difficult to achieve a sufficient statistical distribution [6]. It seems therefore that pore size is adapted to the water tensions induced during stem ontogeny. Sun branches submitted to higher tensions than shaded ones during previous years and growth phases adapt pore size during their ontogenesis.

Sun branches are more water efficient and less vulnerable to xylem embolism than the shaded ones. This difference can compensate a higher position in the tree [30]. A higher position with a higher climatic water demand needs an efficient water transport to sustain water losses. Microclimat analysis within the crown (*table I*) show big differences between light and shade conditions with a very low *VPD* in the shade that induces low transpiration. Therefore, sun-exposed branches are able to sustain a high climatic water demand and are able to resist to water deficit by maintaining xylem integrity with a low vulnerability and an efficient stomatal response.

Vulnerability curves made on petioles (*figure 2*) did not reveal significant differences to the shoot measurements. Thus no significant hydraulic segmentation was observed in beech. Hydraulic segmentation does not achieve a gradient of vulnerability. At the end of the experiment, when leaves were drying, shoots were totally embolised. Tyree et al. [27] showed for walnut a higher vulnerability of petioles than of stems. This can efficiently prevent any embolism of shoots by shedding its

leaves. Cochard et al. [4] showed that for *Populus* embolism developed concurrently in the petioles and the internodes, as there is no efficient hydraulic segmentation.

During water stress, when Ψ decreases, branches of a tree show different Ψ values depending on their position in the crown. Shade branches dropped to Ψ_{cav} values less negative than sun branches. They require an earlier stomatal regulation than the light ones. When we compare the evolution of *gs* values of sun-exposed and shaded branches for increasing stress, we notice that shade branches closed the stomata faster than sun-exposed branches. Whereas sun branches (and medium branches) keep higher *gs* values at more negative Ψ values. When we compare *gs* evolution and embolism development (*figure 4*), *gs* values decreased drastically for Ψ values close to the values of Ψ_{cav} for the two kind of branches. Shade and sun branches presented an early stomatal regulation during drying and stomatal closure prevented Ψ from dropping below the point of xylem dysfunction. Previous observations made during early water stress (data not shown) shown less negative Ψ values in the lower parts of beech trees. This pattern of *gs* response to water stress within the trees allow the stomatal closure throughout the crown and avoid water losses in the lower parts.

In conclusion, embolism remained low in *Fagus*, (less than 20% at the end of summer) even though water potentials often approached Ψ_{cav} . Stomatal control of xylem embolism [10] is particularly important in trees that can not reverse embolism during growing season. Stomatal response must occur early and sufficiently fast to protect xylem from dysfunction.

Acknowledgements: D.L. was supported by a grant of the french ministry for higher education and research. This study was partly supported by an ONF-INRA contract. We are grateful to E. Dreyer, O. Brendel and R. Pittis for helpful reviews of the manuscript. The authors want to acknowledge valuable suggestions from anonymous reviewers.

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