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Hydraulic architecture of trees: main concepts and results

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Abstract – Since about twenty years, hydraulic architecture (h.a.) is, doubtless, the major trend in the domain of plants (and especially trees) water relations. This review encompasses the main concepts and results concerning the hydraulic of architecture of trees. After a short paragraph about the definition of the h.a., the qualitative and quantitative characteristics of the h.a. are presented. This is an occasion to discuss the pipe model from the h.a. point of view. The second part starts with the central concept of embolism and give a review of important experimental results and questions concerning summer and winter embolism. The last part deals with the coupling between hydraulic and stomatal conductances. It discusses the theoretical and experimental relationships between transpiration and leaf water potential during a progressive soil drought, the increase of soil-root resistance and its consequences in term of xylem vulnerability, the factors controlling the daily maximum transpiration and how stomates can prevent “run away embolism”. In conclusion different kinds of unsolved questions of h.a., which can be a matter of future investigations, are presented in addition with a classification of trees behaviour under drought conditions. To end, an appendix recalls the notions of water potential, pressure and tension.

hydraulic architecture / cohesion-tension theory / summer embolism / winter embolism / drought resistance

Résumé – Architecture hydraulique des arbres : concepts principaux et résultats. Sans aucun doute, depuis une vingtaine d’années, l’architecture hydraulique (a.h.) est devenue une approche majeure dans le domaine des relations plantes-eau (et particulièrement pour les arbres). Cette revue présente les principaux concepts et résultats concernant l’a.h. Après un bref paragraphe sur la définition de l’a.h., les caractéristiques qualitatives et quantitatives définissant l’a.h. sont passées en revue. À cette occasion le « pipe model » est discuté du point de vue de l’a.h. La seconde partie commence avec le concept central d’embolie et continue avec une présentation des principaux résultats et questions touchant l’embolie estivale et l’embolie hivernale. La dernière partie analyse le « couplage » entre les conductances hydraulique et stomatique. Il y est discuté des relations théoriques et expérimentales entre la transpiration et le potentiel hydrique foliaire durant la mise en place d’une sécheresse progressive du sol, de l’augmentation de la résistance sol-racines et de ses conséquences en terme de vulnérabilité du xylème, des facteurs contrôlant la transpiration maximale journalière et de quelle manière les stomates peuvent prévenir l’emballement de l’embolie. La conclusion fait état de différentes questions non résolues, qui pourraient faire l’objet de recherches futures et esquisse une classification du comportement des arbres vis-à-vis de la sécheresse. Pour finir, un appendice rappelle les notions de potentiel hydrique, de pression et de tension.

architecture hydraulique / théorie de la cohésion-tension / embolie estivale / embolie hivernale / résistance à la sécheresse

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1. INTRODUCTION

During the last decades a new approach of plant and, especially, tree water relations has developed. It is well structured around two main axes: the cohesion-tension theory [37, 38, 92] of the ascent of sap which deals with the physics of the sap movement, and the electrical analogy used for modeling water transport within the tree and in the soil-plant water continuum, using resistances, capacitances, water potentials, flow. Presentation of the cohesion-tension theory and its current controversies have been presented in many recent papers [26, 33, 82, 113, 135]. The use of an electrical analogy for describing the water transfer through the soil-plant water system is rather old: the idea probably comes from Gradmann [47], but really begins with the article “Water transport as a catenary process” by Van den Honert [143]. It was the main formalism used to deal with water transport in the soil-plant-atmosphere continuum from that date until the 1980’s, before the hydraulic architecture approach takes over.

It is important to remember that after a period of intense work and debate (from the end of the 19th century to ca. the first half of the 20th), research on the cohesion-tension theory was abandoned with focus instead put on Ohm’s law analogy [32]. The resurrection of studies concerning this theory is mainly the result of some pioneers like J.A. Milburn, M.H. Zimmermann and M.T. Tyree.

Hydraulic architecture (h.a.) has made a big improvement in our knowledge by taking into account these two approaches and linking them in a way which allows a much more realistic and comprehensive vision of tree water relationships. Although several papers have been devoted to h.a. [23, 89, 127, 137], we think that there is still a place for a comprehensive and updated introduction intended, as a handbook for frequent reference, to scientists, technicians who are working on tree functioning from one way or another, and students learning tree physiology, but without being specialized in plant water relations. Therefore, to facilitate the understanding, many illustrations have been included in the text where explanations of the figures could be given at greater length than in the legend.

2. CHARACTERIZATION OF THE HYDRAULIC ARCHITECTURE (H.A.)

2.1. What is the hydraulic architecture?

The h.a. can be considered as a quite well defined region within the vast domain of tree water relations. The expression “hydraulic architecture” was coined by Zimmermann probably in 1977/78, after the first congress on “The architecture of Trees” organized in 1976 in Petersham (MA, USA) by Hallé, Tomlinson and Oldeman, during which he probably got the idea. However, surprisingly, his article of 1978 and, especially, his remarkable book “Xylem Structure and The Ascent

of sap” (1983), whose chapter 4 is entitled “Hydraulic Architecture”, does not contain any definition of this new expression.

Since that time several definitions have been proposed:

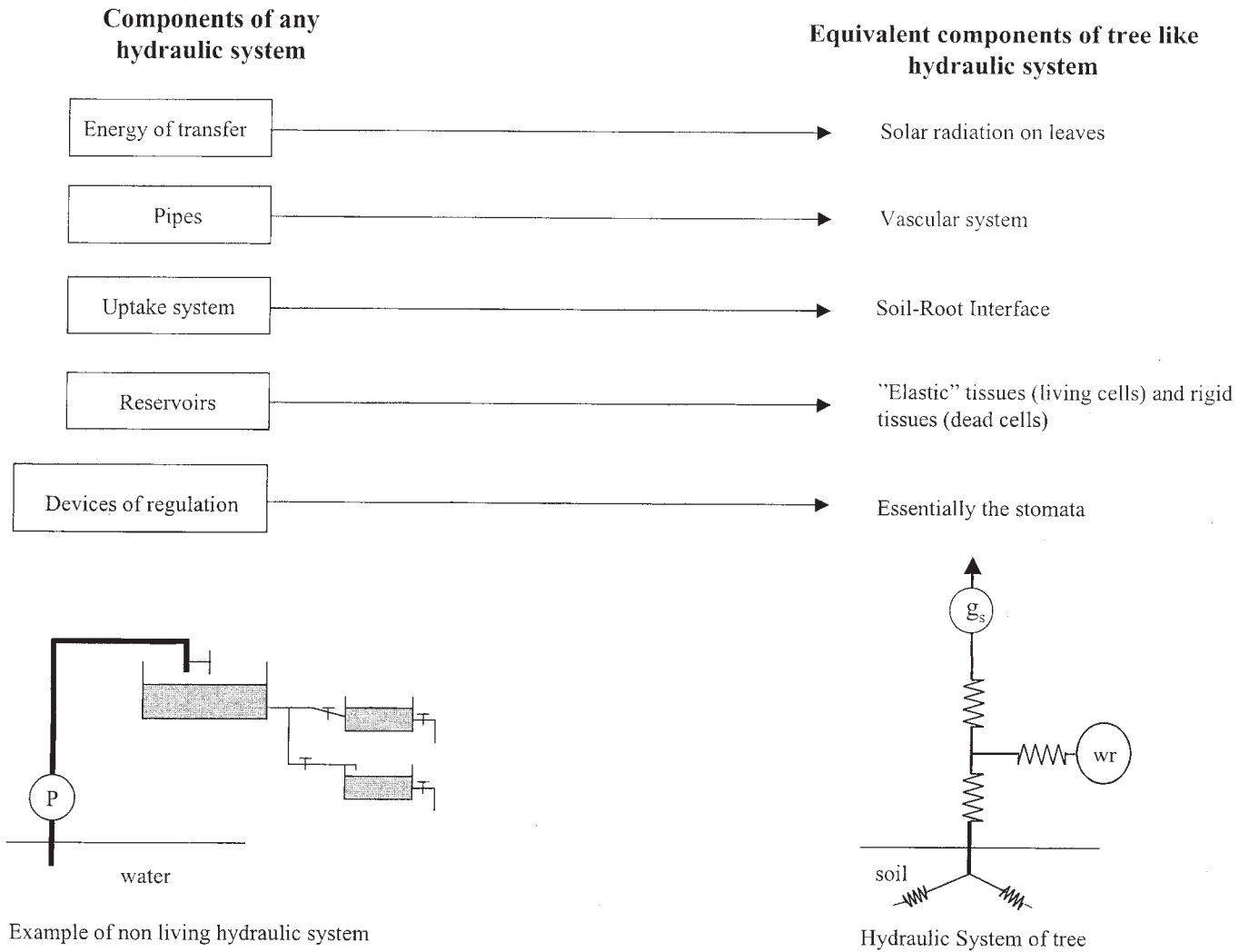
- “h.a. describes the relationship of the hydraulic conductance of the xylem in various parts of a tree and the amount of leaves it must supply” [125];
- “h.a. governs frictional resistance and flow capacity of plant organs” [89];
- “h.a. is the structure of the water conducting system” [127];
- “h.a., that is how hydraulic design of trees influences the movement of water from roots to leaves” (Tyree, 1992, unpublished talk);
- “the set of hydraulic characteristics of the conducting tissue of a plant which qualify and quantify the sap flux from roots to leaves” (Cochard, 1994, unpublished talk).

The soil-root interface can be considered either as a boundary conditions of the plant’s hydraulic architecture or as a part of this hydraulic system. As we will see in Section 4, it plays an important role in the tree’s water use, in any case.

In fact, h.a. has two different meanings:

- (a) A special approach to the functioning of a tree as a hydraulic system. A tree can be considered as a kind of hydraulic system (*figure 1*). Any such system (dam, irrigation system for crops or houses, human blood vascular system, etc.) is composed of the same basic elements: a driving force, pipes, reservoirs, regulating systems. For trees (and for plants in general) the driving “force” is, most of the time, the transpiration which, as the cohesion-tension theory states, pulls water from the soil to the leaves, creates and maintains a variable gradient of water potential throughout the plant. The energy requirement for transpiration is mainly solar radiation. Thus, when transpiration occurs, the water movement is a passive process along a very complex network of very fine capillaries (vessels and tracheids), which form the xylem conducting system. This conducting (or vascular) system has two kinds of properties: qualitative and quantitative properties.
- (b) The result of this approach in terms of maps of the different hydraulic parameters and other measured characteristics, which define the peculiar h.a. of a given tree. It is of course impossible to build such a complete hydraulic map for a large tree; only parts of this map are usually drawn which give some general or species-dependent characteristics of the h.a.

Examples of relevant questions which can be answered through a study of h.a. are: “How do trees without apical control ensure that all branches have more or less equal access to water regardless of their distance from the ground? In times of drought how do trees program which branches are sacrificed first? [127]. What determines the highest level of refilling after embolism? Can we explain some of the differences in life history or phenology of trees or even herbaceous plants (e.g. drought deciduousness) in terms of differences in



▲ **Figure 1.** Tree as a hydraulic system; P = pump; g_s = stomatal conductance; wr = water reservoir.

hydraulic architecture? Does hydraulic constraints limit tree height or tree growth?

2.2. Qualitative characteristics of the hydraulic architecture

The hydraulic architecture of a tree shows three general qualitative properties: integration, compartmentation and redundancy.

Integration (*figure 2, right*) means that in most cases (for exceptions see for example [145], the vascular system of a tree seems to form a unique network in which any root is more or less directly connected with any branch and not with a single one. In other words, the vascular system of a tree forms a single, integrated network. Let us represent the tree vascular system by a graph, each leaf and each fine root being

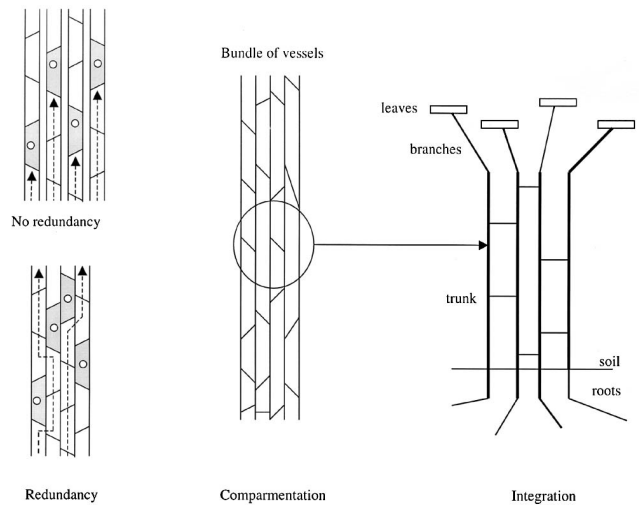


Figure 2. Illustration of the three main qualitative characteristics of the hydraulic architecture of a tree: integration, compartmentation and redundancy.

a different summit. To say that the vascular system forms a unique network means that there is always at least one path between any given summit (between any given root and any given leaf). It is of course impossible to check such an assumption with a large tree. Nevertheless the main idea to keep in mind is the fact that within a tree many possible anatomical pathways, with different resistances, can be used to connect one shoot and one root. It means that water is allowed to flow not only vertically along the large number of parallel pathways formed by files of conducting elements, but also laterally by the pit membrane of these elements which provide countless transversal ways between them. Among the different observations supporting this conclusion, two can be quoted: the dye injection experiments and the split-roots experiments. Roach's work [97] deals with tree injection, i.e. when a liquid is introduced into a plant through a cut or a hole in one of its organs. As Roach said: "The development of plant injection was mainly the indirect result of the attempts of plant physiologists to elucidate the cause of the ascent of sap in trees". Unfortunately the work of Roach is not aimed at tracing the path followed by the transpiration stream. Nevertheless and even if we should be aware of the fact that dyes and water pathways can differ, Roach's work gave extremely interesting and curious information about the connections between different parts of a tree from the leaf level to the whole tree level. As an illustration, here are some quotations from his article:

- "In working with young leaflets, such as those of tomato, a half leaflet is the smallest practical injection unit" (p. 177);
- "If a leaf-stalk injection be carried out on a spur carrying a fruit either the whole fruit or only a single sector of it may be permeated, according to the position of the injected leaf-stalk in regard to the fruit" (p. 183);
- "Experience with apple and other trees has shown that the cut shoot immersed in the liquid must be at least as large as the one to be permeated, otherwise permeation will not be complete" (p. 197);
- "The lower the hole is placed on the branch the greater is the amount of liquid which enters other parts of the tree" (p. 202);
- "There is not a root corresponding to each chief branch and the roots seem to divide quite independently of the division into branches" (p. 207).

The results of Roach are difficult to interpret because they are very dependent on the experimental conditions (time of the year, transpiration and soil water conditions, etc.) on the one hand and the species (distribution of the easiest pathways between a given point, injection point, and the rest of the tree) on the other hand. In split-root experiments [5, 45, 62] part of the roots of a plant is in a dry soil compartment, the rest being in a well-watered soil. Under these conditions, which in fact, reproduce what happens for the root system of a tree in a dry-

ing soil, the whole shoot and not just part of it, is supplied with water.

Compartmentation (*figure 2*, middle) is almost the opposite property of the vascular system. It simply follows from the fact that the conducting system is built up to hundreds of thousands or millions or even more elementary elements, tracheids and vessels. Each element is a unit of conduction, in communication with other elements by very special structures, the pits, which play a major role in protecting the conducting system from entrance of air (see Section 3.4.). There are two main types of conduits: tracheids and vessels. Even if some tracheids can be quite long (5–10 mm), those of most of our present-day conifers do not exceed 1 or 2 mm. By contrast, vessels, especially in ring porous trees like oaks, can reach several meters, and may even, be as long as the plant (John Sperry, personal communication). However in most cases (there are notable exceptions, like oak species), these conduits are very short in comparison with the total length of the vascular system going from roots to leaves. It forms a kind of small compartment. When air enters the vascular system it invades an element. Such a property is the necessary property complementary to integration because it allows the conducting system to work under a double constraint: to be continuous for water, and discontinuous for air. In fact, conduit length affects water transport in two opposing ways [29, 154]. Increased length reduces the number of wall crossings, therefore increasing the hydraulic conductance of the vascular pathway. However, a countering effect arises, when cavitation occurs, from the fact that a pathway composed of long conduits will suffer a greater total conductance loss for an equivalent pressure gradient. Another aspect that can be linked up with compartmentation is the "hydraulic segmentation" idea of Zimmermann [154] which can be defined "as any structural feature of a plant that confines cavitation to small, distal, expendable organs in favor of larger organs representing years of growth and carbohydrates investment" [127].

Redundancy (*figure 2*, left) has two meanings in the present context. First of all, it says that in any axis (trunk, branch, twig, petiole), at a given level, several xylem elements are present, like several pipes in parallel. Therefore if one element of a given track is blocked, water can pass along another parallel track. This is very well illustrated by saw cutting experiments [70]. The second meaning has been pointed out by Tyree et al. [133]. It takes into account an additional anatomical fact: in general a track of conducting elements is not alone but is in close lateral contact with other track of vessels or tracheids. In this case redundancy can be defined (in quantitative terms) as the percentage of wall surface in common. Such a design where conduits are not only connected end to end but also through their side walls, shows pathway redundancy. *Figure 2* (left) clearly indicates that in this case the same embolism (open circles) does not stop the pathway for water movement. Redundancy is higher in conifers than in vessel-bearing trees.

2.3. Quantitative characteristics of hydraulic architecture

Quantitative characteristics concern the two main elements of the conducting system, namely the resistances and the reservoirs. Several expressions deal with the resistances or the inverse, the conductances. In fact, two main types of quantities are used: conductances (*k*), where flow rate is expressed per pressure difference, and conductivities (*K*), where flow rate is expressed per pressure gradient. When either a conductivity or a conductance is expressed per area of some part of the flow path, the *k* and *K* can be provided with a suffix (ex.: “s” for xylem area, “l” for leaf area, “p” for whole plant leaf area, “r” for root area, “g” for ground area, etc.).

The hydraulic conductance *k* (kg s⁻¹ MPa⁻¹) is obtained by the measured flow rate of water (usually with some % of KCl or other substance that prevent the presence of bacteria or other microorganisms which tend to block the pits) divided by the pressure difference inducing the flow. Hydraulic conductance is then the reciprocal of resistance. The water can be forced through isolated stem, root or leaf segment by applied pressures, by gravity feed, or drawn by vacuum with similar results, as long as the pressure drop along the plant segment is known. Hydraulic conductance refers to the conductance for the entire plant part under consideration [43].

The hydraulic conductivity *K_h* (kg s⁻¹ MPa⁻¹ m) is the most commonly measured parameter. *K_h* is the ratio between water flux (*F*, kg s⁻¹) through an excised branch segment and the pressure gradient (d*P*/d*x*, MPa m⁻¹) causing the flow (figure 4). The larger *K_h*, the smaller its inverse, the resistance *R*. *K_h* can also be considered as the coefficient of the Hagen-Poiseuille law which gives the flow (m³ s⁻¹) through a capillary of radius *r* due to a pressure gradient Δ*P*/Δ*x* along the pipe:

$$\text{Flow} = dV/dt = (\rho r^4 / 8 \eta) / (\Delta P / \Delta x) = K_h (\Delta P / \Delta x)$$

with *V* = volume of water; ρ = the density of water; η = coefficient of viscosity of water (kg m⁻¹ s⁻¹) and *t* = time.

Viscosity depends upon solute content (for example, a concentrated sugar solution is quite viscous and slows down the flow considerably). In general, the solute concentration of xylem sap is negligible and does not measurably influence viscosity. Viscosity is also temperature-dependant [1, 25]. It is important to note that flow rate, d*V*/d*t*, is proportional to the fourth power of the capillary diameter. This means that a slight increase in vessel or tracheid diameter causes a considerable increase in conductivity. As an example [154] lets us suppose we have three vessels. Their relative diameters are 1, 2 and 4 (for example 40, 80 and 160 μm). Under comparable conditions, the flow in the first capillary being 1, will be 16 in the second and 256 in the third. This tells us that if we want to compare conductivities in different woody axes, we should not compare their respective transverse-sectional vessel area, vessel density or any such measure. We must compare the sums of the fourth powers of their inside vessel diameters (or radii). As a consequence, small vessels carry an insignificant amount of water in comparison with large ones. In the

previous example, the smallest capillary would carry 0.4%, the middle one 5.9% and the large one 93.8% of the water.

When many capillaries of different diameters, *d_i*, are present in parallel, like the vessels in the transverse section of a branch, the Poiseuille-Hagen law is written as follows:

$$\text{Flow} = K_h \Delta P / \Delta x \text{ with } K_h = (\pi \rho / 128 \eta) \sum_{i=1}^n (d_i^4).$$

The principle of measurement of the hydraulic conductivity *K_h* proceeds from the above equation. The branch segment is submitted to a small water pressure difference Δ*P* which induces a flux. This flux is measured with a suitable device like, for example, a recording balance. Knowing the flux, Δ*P*, and the length *L* of the sample, *K_h* can be calculated. It should be remembered that, although the principle of this method is very simple, its application requires many precautions [107].

According to the Hagen-Poiseuille law, *K_h* should increase if the number *n* of conduits per unit-branch cross-section or the average conduit diameter increases. However it is important to realize that when measuring *K_h* of a branch, one does not refer either to the diameter of the conducting elements or to their number. Therefore, saying that *K_h* can be viewed as the coefficient of the Hagen-Poiseuille law does not imply that *K_h* is proportional to *r* to the fourth power. There is no simple and stable relation between the total cross section of a branch and the composite conducting surface of the tracheids or vessels, which change along the branch. Regression curves of *K_h* versus branch diameter are shown in figure 3 [16]. They lead to a relation between *K_h* and *S* as: *K_h* = *S*^α with 1 < α < 2.

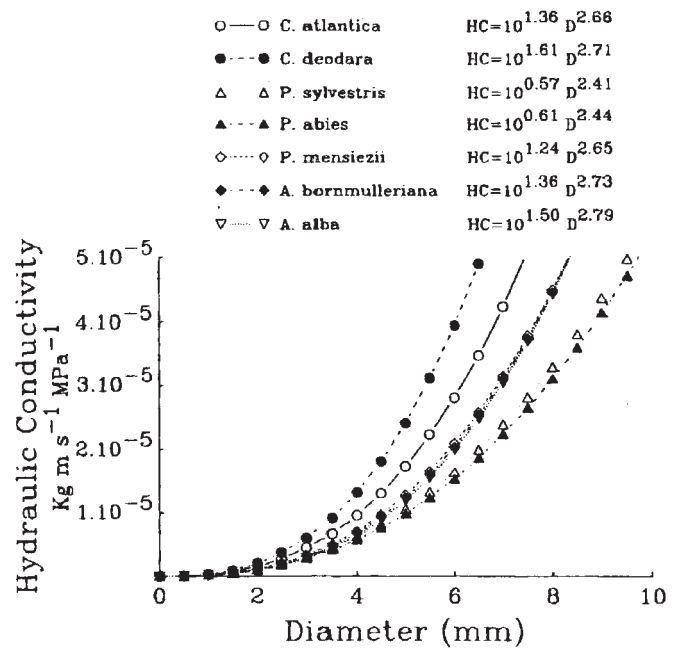


Figure 3. Example of regression between the hydraulic conductivity *K_h* and the diameter of the different tree species. Note that all coefficients of regression are > 2, meaning that *K_h* is more than proportional to the branch section (from [16]).

Whole plant leaf specific conductance k_p ($\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-2}$) can be calculated by dividing the measured flow rate of water through the stem by the pressure difference and the total leaf surface of the tree. It is a useful parameter because it allows calculation of the soil-to-leaf average pressure drop for a given rate of water.

Recently, published results [144, 156], have shown an effect of ionic composition on hydraulic conductance. This effect seems to be small (10%) in most of the experimented plants species and dose-dependent, but it can be significant in other plants, depending on the ion concentration, pH, and non-polar solvent. In addition, concerning the significance of

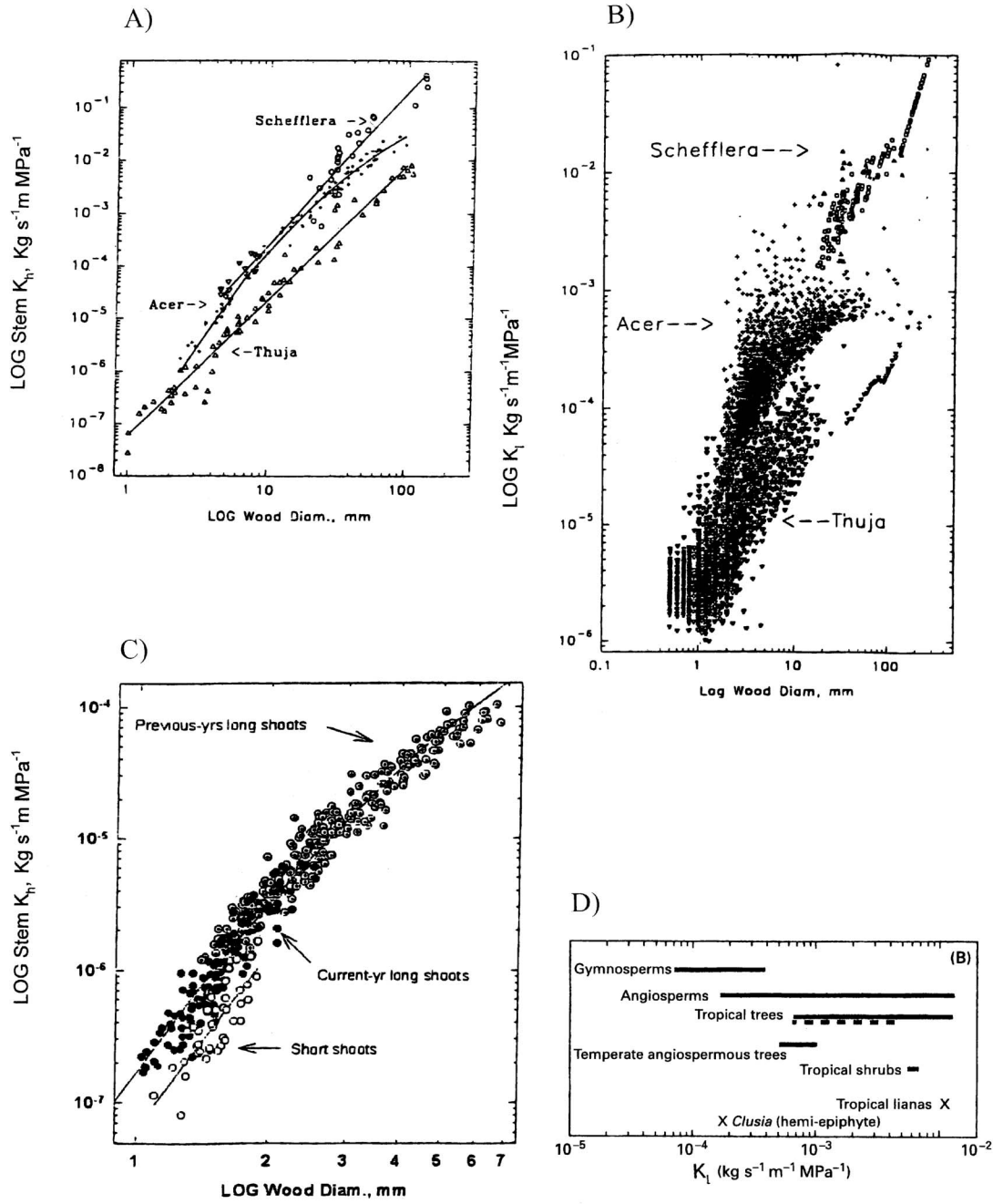


Figure 4. Examples of results of the hydraulic conductivity K_h , and leaf specific conductivity K_l . **A:** Log-log relation between K_h (ordinate) and stem diameter (excluding bark, abscissa) per unit stem length for *Thuja*, Δ ; *Acer*, \circ ; *Schefflera*, ∇ (from [128]). **B:** Same log-log relation for the same species, but for leaf specific conductivity K_l (from [128]). **C:** Log-log relation between K_h (ordinate) and stem diameter (excluding bark, abscissa) for three types of shoots of *Fagus sylvestris* (from Cochard, unpublished data). **D:** Ranges of K_l by phylogeny or growth form, read from the bottom axis. Dashed line indicates *Ficus* spp; "x" indicates a range too short to be represented (from [90]).

these results in relation to the paradigm of the xylem as a system of inert pipes, they also suggest that measurements of conductance should be made with standard solutions, in term of ionic concentration at least.

Hydraulic resistance R_h , and hydraulic specific resistance R_{hs} . Definition of these two quantities derives from the basic Ohm's equation: $\text{flux} = \Delta\Psi/R_h$. Therefore the units of hydraulic resistances will depend on those expressing the flux (assuming $\Delta\Psi$ is in MPa). For flux expressed in kg s^{-1} , R_h will be in $\text{MPa kg}^{-1} \text{s}$ and for flux expressed as a density of flux (the corresponding surface referring to either the sap wood or the leaf surface), then R_{hs} will be in $\text{MPa kg}^{-1} \text{s m}^2$ (see *figure 15C* as an example where kg is replaced by dm^3).

The specific conductivity K_s which is given by $K_s = K_h/S$ ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$), where S is the sapwood cross-section and K_h the hydraulic conductivity expressed in $\text{kg s}^{-1} \text{m MPa}^{-1}$. It is a measure of the "porosity" of the branch segment. As there are many ways to determine this cross-section it is important to specify which one is used, otherwise differences in K_s cannot be directly compared. Besides, according to its definition, K_s is proportional to the section of conducting wood of a branch: it means that the Poiseuille-Hagen law is no more valid at the branch level, since along the branch the composition of wood (distribution and number of conducting elements of different diameter) will vary.

The leaf specific conductivity K_l ($\text{kg s}^{-1} \text{m MPa}^{-1}$) is obtained when K_h is divided by the leaf area distal to the branch segment (A_l , m^2). This is a useful measure of how a branch supplies water to the leaves it bears. Its main use is to calculate the pressure gradients along an axis. Let us suppose that we know the average transpiration flux density (T , $\text{kg s}^{-1} \text{m}^{-2}$) from the leaves supplied by the branch segment and that there is no capacitance effect (no change in the water content), then the pressure gradient in the branch segment (dP/dx) is equals to T/K_l . So the higher the K_l , the lower the dP/dx needed to supply the leaves of this axis with water. This conclusion involves two constraints: transpiration per leaf surface is the same, capacitance effects are negligible. A water potential gradient $\Delta\Psi/\Delta x$ is therefore defined for a given rate of transpiration.

The Hubert value HV. Among the different approaches which have been worked out to get a better understanding of the building of this vascular system, Huber [56] made several measures of the following ratio, named by Zimmermann [154], the "Huber Value" (HV) defined as the sapwood cross-section (or the branch cross-section) divided by the leaf area (or sometimes the leaf dry weight) distal to the branch. It is easy to see that $K_l = \text{HV} \times k_s$.

Two main series of results (expressed as the ratio of the total cross section, in mm^2 , of the xylem at a given level, over the total fresh weight of leaves above that level, in g), have been obtained by Huber:

- inside a tree this HV is not constant: sun leaves have larger HV than shade leaves as the apical shoot in comparison with the lateral branches;

- between species adapted to various climates, large differences also exist: Dicots and Conifers from temperate climates of the north hemisphere have HV values around $0.5 \text{ mm}^2 \text{ g}^{-1}$. For species living in humid or shaded sites, HV values are lower: 0.2 for underground story herbs, 0.02 for Nymphaea. On the contrary, plants from dry and sunny countries have HV of 5.9 in average. It is interesting to note that succulents, which have solved the problem of water supply by storage, show very low HV, around 0.10. We will see hereunder that this approach is close to the pipe model proposed by Shinozaki.

As quoted by Zimmermann [154] this parameter is not very useful for two main reasons. Firstly, the true conducting surface of a trunk or branch is a variable portion of the whole section, which should be determined. Secondly and more important (see above the discussion of the Poiseuille law), the flux of a capillary is proportional to the fourth power of the radius. In other words, through the same cross section of wood and with the same gradient of water potential, $d\Psi/dx$, small to very large fluxes can run depending on the distribution of the section of the vessel elements. This is why Zimmermann [153] has proposed the use of the K_l .

Water-storage capacity. There is considerable evidence that trees undergo seasonal and diurnal fluctuations in water content. These fluctuations can be viewed as water going into and out of storage. Water-storage capacity can be defined in different ways [43]. The relationship between water content and water potential is known as the (hydraulic) capacitance, C_w , of a plant tissue; it is the mass of water ΔM_w , that can be extracted per MPa (or bar) change in water potential ($\Delta\Psi$) of the tissue: $C_w = \Delta M_w/\Delta\Psi$ (kg MPa^{-1}). It is also customary to define C_w for a branch as C_w per unit tissue volume ($\text{kg MPa}^{-1} \text{m}^{-3}$) or for leaves, per unit area ($\text{kg MPa}^{-1} \text{m}^{-2}$). In general these capacitances are difficult to measure, especially because they are not constant but vary with the water potential. Another expression is the water-storage capacity (WSC), which is the quantity of water that can be lost without irreversible wilting. Theoretically, $\text{WSC} = V(1 - \theta)$, where WSC is the storage capacity (e.g. in kg), V is the weight of water when the tissue is at full turgidity and θ is the critical relative water content leading to irreversible wilting (dimensionless number less than 1). There are practical problems in applying the above equation [43].

According to Zimmermann [154] there are three mechanisms involved in water storage in a tree: capillarity, cavitation and elasticity of the tissues. Cavitation and capillarity effects are the most poorly understood of these. Elasticity of tissue is certainly, for most species, the prevailing mechanism of water storage. Living cells of different parts of the tree have high water content and "elastic" walls. They act as minute water reservoirs having a given capacitance in a

series-parallel network arrangement. When cells rehydrate, they swell, when they dehydrate, they shrink. The ecophysiological significance of the storage capacity of trees is that it may influence the ability of the tree to continue photosynthesis and, even growth, despite temporary drought conditions.

Some results involving the previous definitions will now be given. *Figure 4A* [128] shows some examples of K_h data, and *figure 4B* [128] the relationship between the logarithm of K_h and the logarithm of the diameter of the stem for three species. The relation is approximately linear. More important, when the diameter changes by two orders of magnitude (1 to 100), K_h varies by six orders of magnitude. As a consequence, K_h will change along a branch. The figure also shows large differences between the K_h of branches belonging to different species. For example the smallest leaf-bearing branches of *Schefflera* had K_h close to those of *Acer* branches of the same diameter. However, K_h of larger branches (20 to 30 mm in diameter) were 3 to 10 times larger in *Schefflera* than in *Acer*. *Thuja* has K_h s 10 to 20 times smaller than the other two species for branches of the same diameter [128]. *Figure 4C* shows with *Fagus sylvatica* another interesting result which demonstrates that there are links between the “botanical” architecture as developed by the French School of Montpellier [11, 54] and the hydraulic architecture. The curves express the same type of correlation between the logarithm of K_h and the logarithm of the diameter for one year shoots. The upper curve summarizes data from long shoots, the lower curve data from short shoots. It is clear that for a given diameter, K_h

of the short shoots tends to be less than K_h of long shoots. It seems therefore that the conditions undergone by a branch during its development can have hydraulic implications [22]. Similarly considerable differences between the whole plant hydraulic conductance of two co-occurring neotropical rain-forest understory shrub species of the genus *Piper* have been found [39bis]. These results reflect the conditions where both species are encountered: *P. trigonum* occurs in very wet microsites, whereas, in contrast, *P. cordulatum* is the most abundant in seasonally dry microsites.

Results dealing with root hydraulic conductances are quite rare. An interesting comparison between shoot and root hydraulic conductances in seedling of some tropical tree species shows that, at this stage, shoot and root conductances (and leaf area) all increased exponentially with time [136]. Concerning the roots also, uncertainty appears to exist in the scarce literature regarding the effects of mycorrhizal fungi (ecto and endo-) on the host root hydraulic conductance. So far most studies have been performed in very young seedlings (two to ten months). A recent comparison [83bis] between 2-year-old seedlings of *Quercus ilex* inoculated and non-inoculated with *Tuber malanosporum* Vitt. showed that root conductance of the inoculated seedlings is 1.27 time greater than those of the non-inoculated seedling. This result has been obtained when the root conductance is scaled by leaf area; in contrast this root hydraulic conductance is lower if reported per unit root area. This example illustrates how important it is to get a correct comprehension of the units used to express the results before trying to explain them.

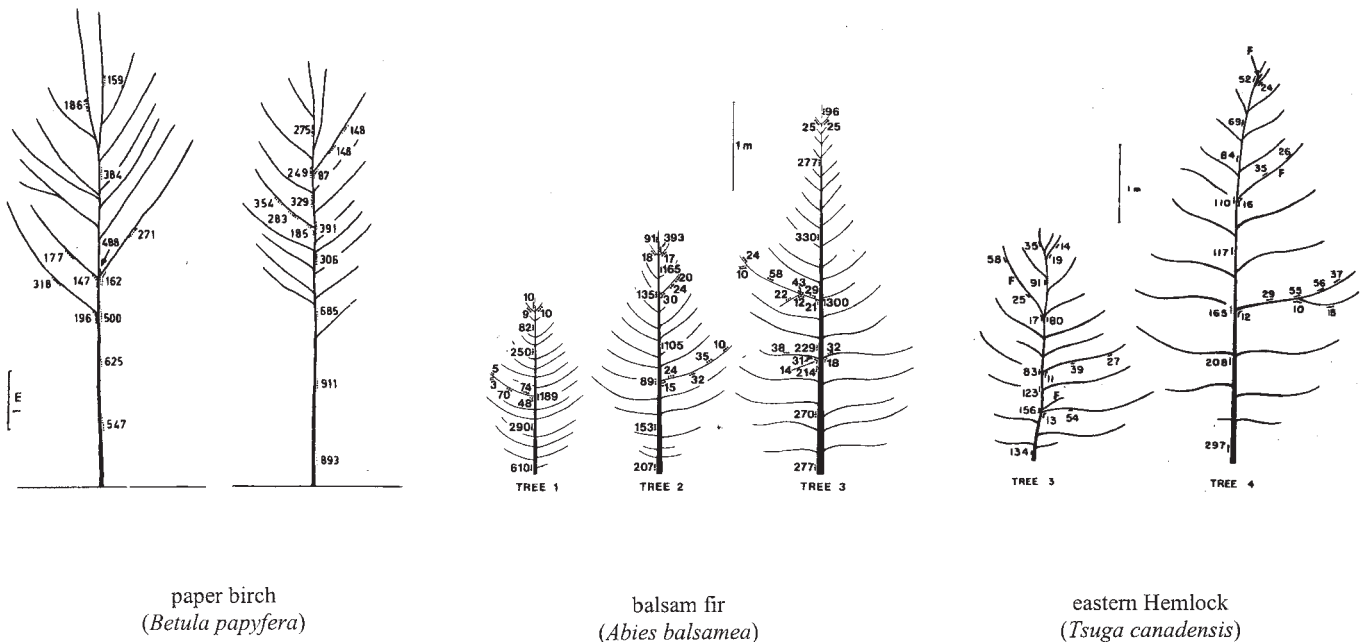


Figure 5. Examples of leaf specific conductivity maps. From left to right: paper birch, *Betula papyfera*, in microliters per hour, per gram fresh weight of leaves supplied under conditions of gravity gradient, 10.3 kPa m^{-1} (from [153]); balsam fir, *Abies balsamea*, same units except per gram of dry weight (from [40]); eastern hemlock, 19-year-old trees, *Tsuga canadensis*, same units as for balsam fir (from [41]).

According to its definition, the leaf specific conductivity (K_l) depends firstly on the factors controlling the value of K_h and secondly on the factors that make the leaf surface variable. Therefore it is not surprising that, in *figure 5B*, the variability of K_l is greater than that of K_h . As mentioned above, the principal value of K_l is to allow dP/dx , (an estimate of the water potential gradient $\Delta\Psi/\Delta x$, or more precisely, the pressure gradient component of the water potential, see Appendix) along a branch bearing a given foliar area to be calculated. *Figure 4D* summarizes ranges of values of K_l . Hydraulic parameters are now available for many tropical and temperate species [12, 90, 138]. K_l values ranged over more than two orders of magnitude, from a low of 1.1 (in *Clusia*) to 171 (in *Bauhinia*) $\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$. The conifers had low K_l (values in the range of 1–2) because they have very narrow conduits and diffuse porous trees had about double these values. Not surprisingly, the highest values were in lianas, which “need” wide vessels to promote efficient transport to compensate for narrow stems. Nevertheless, as pointed out by Patiño et al. [90], it is still difficult to be definitive in generalizing interspecific patterns in terms of hydraulic parameters with a data base of only some tens taxa.

Pipe model and hydraulic architecture. The “pipe model theory of plant form” [102, 103] views the plant as an assemblage of “unit pipes”, each of which supports a unit of leaves. It said that “the amount of leaves existing in and above a certain horizontal stratum in the plant community is directly proportional to the amount of the stems and branches existing in that horizon” [102]. According to the authors, this statement applies at different scales from a simple branch, to an isolated tree and a plant community. Many experimental results support this hypothesis and show that the cross-sectional sapwood area at height h and the foliage biomass above h , are related through constant ratio. However results also indicate that the ratio may be different for stem and branches and that the transport roots obey a similar relationship [43, 72]. Several models of tree growth use the pipe model [71, 72, 84, 91, 141, 142].

In fact the pipe model of Shinozaki can be viewed as a new formulation of one of the Pressler law which said, more than one century ago, that “the area increment of any part of the stem is proportional to the foliage capacity in the upper part of the tree, and therefore, is nearly equal in all parts of the stem, which are free from branches” [10]. From what as been saying above, the pipe model assumption is also very close to the Huber value. As pointed out by Deleuze [36], pipe model, Huber value and allometric relations between leaf surface and stem area are closely related. Nevertheless allometric relations are static and descriptive in nature, like the Huber value, whereas the pipe model theory supposes a conservative relation between structure and functioning.

The pipe model has been useful in predicting canopy leaf mass or leaf area from stem cross section, and is of some value in modeling tree growth, resource allocation and biomechanics [127]. However this model is of little value in

understanding tree as hydraulic systems. First it is submitted to the same criticism as the Huber value. As K_l shows, the stem cross section allocated per unit leaf area and the vessel diameter in the stems vary widely within the crown of many trees. Second, it does not consider the varying lengths of transport pathways to different leaves on a tree. This is well explained with the example given by Tyree and Ewers [127]: “Imagine a unit pipe of mass, u , supporting leaf area, s . If the transport distance, h , were doubled with the same leaf area supplied, four unit pipes would be required to maintain the same hydraulic conductance k . If the leaf area were doubled as the transport distance doubled, eight unit pipes would be necessary to equally supply the leaves with water”. Underlying explanation is as follows: if neither the pipe units characteristics nor the difference of water potential between soil and leaves change, doubling the distance will then divide the gradient of water potential by two, from $\Delta P/\Delta x$ to $\Delta P/2\Delta x$. To keep the same flux through the system, it is necessary to double the cross area of flux, i.e. to associate two pipe units, doubling then the resistance of the pathway:

$$\text{Flux} = K_h \Delta P/\Delta x = K_h \Delta P/2\Delta x + K_h \Delta P/2\Delta x.$$

As pointed out by the same authors, trees minimize this massive build up of unit pipes, as they age, in two ways. First those that lack secondary growth (e.g. palms) initially are oversupplied with xylem and should attain considerable height before water transport limits. Those with secondary growth, normally produce wider and longer vessels or tracheids at their lower part as they age, which more or less compensate for the increasing distance of transport. As stressed by Jarvis [58] this is also a way trees use to keep the range of water potential of their leaves approximately constant as they grow in height.

Keeping in mind the previous remarks, attempts to build a general and realistic model for the hydrodynamics of plant seem far from being successful. For example, the one published by [147], although based on valuable concepts (allometry laws, theory of resource distribution through a branching network, etc.), contains also several oversimplified assumptions (branching network is supposed to be volume filling, leaf and petiole size are invariant, network of identical tubes of equal length within a segment, constancy of the leaf area distal to a branch, no water capacitance effects, no variable hydraulic conductance, ..., and no indications concerning the boundary conditions in soil and air, etc.), which, in our opinion, ruin the benefit of the use of these concepts. As outlined by Comstock and Sperry [29]: “to model the hydraulic behavior of plants accurately it is necessary to know the conduit length distribution in the water flux pathway associated with species-specific xylem anatomy”. Besides, such models have a more problematic defect: they are almost impossible to validate. We think that without a close cooperation between theoreticians and experimenters such general approaches will not have the impact they otherwise could have.

2.4. Examples of synthetic data on hydraulic architecture: hydraulic maps

The first step in building the h.a. of a tree is to measure the hydraulic quantities of different axes and to draw a map, called hydraulic map [137], of their values for different axes. Introduction of the “high pressure flow meter” [132] enabled direct and rapid estimates of the hydraulic resistance of the different elements of the tree structure. Nevertheless few such maps have been published. *Figure 5* gives three examples of leaf specific conductivity maps [40, 41, 153]. Several conclusions can be drawn from these data: (i) an important variability of K_1 exists between different branches of the same tree and differences within the same individual can be greater than between species: for *Betula* from 911 to 87; for *Abies* from 3 to 610; for *Tsuga*, from 10 to 297; (ii) K_1 varies along a branch but irregularly. Reasons for that are unclear. It is expected that K_1 diminishes with branch diameter but its dependence to the leaf area distribution along the branch can obliterate this trend; (iii) K_1 decreases with the order of axe: it

is greater in the trunk than in the other branches, and lower at the junctions. In *Tsuga*, the smallest diameter stems have K_1 s 30 to 300 times smaller than the largest boles. This means that the pressure gradients, dP/dx , needed to maintain water flux to transpiring leaves distal to the smallest stem segments, will be 30–300 times steeper than the corresponding gradients at the base of the boles [127], being larger in the main branch than in a secondary branch. Zimmermann [154], spoke about a “bottleneck”. This is a general result: hydraulic constrictions at branch junctions are frequently found especially at unequal junctions, i.e. where a small branch arises from a large branch. The basal proximal segment (in the main branch) is more conductive than the junction itself, usually by a factor of 1.1–1.5 [130].

Another example of synthetic data on hydraulic architecture is the negative xylem pressure profile, i.e., the variations of the pressure component of xylem water potential, with height. One speaks also in terms of tension or pressure profiles (see Appendix for the meaning of these different and

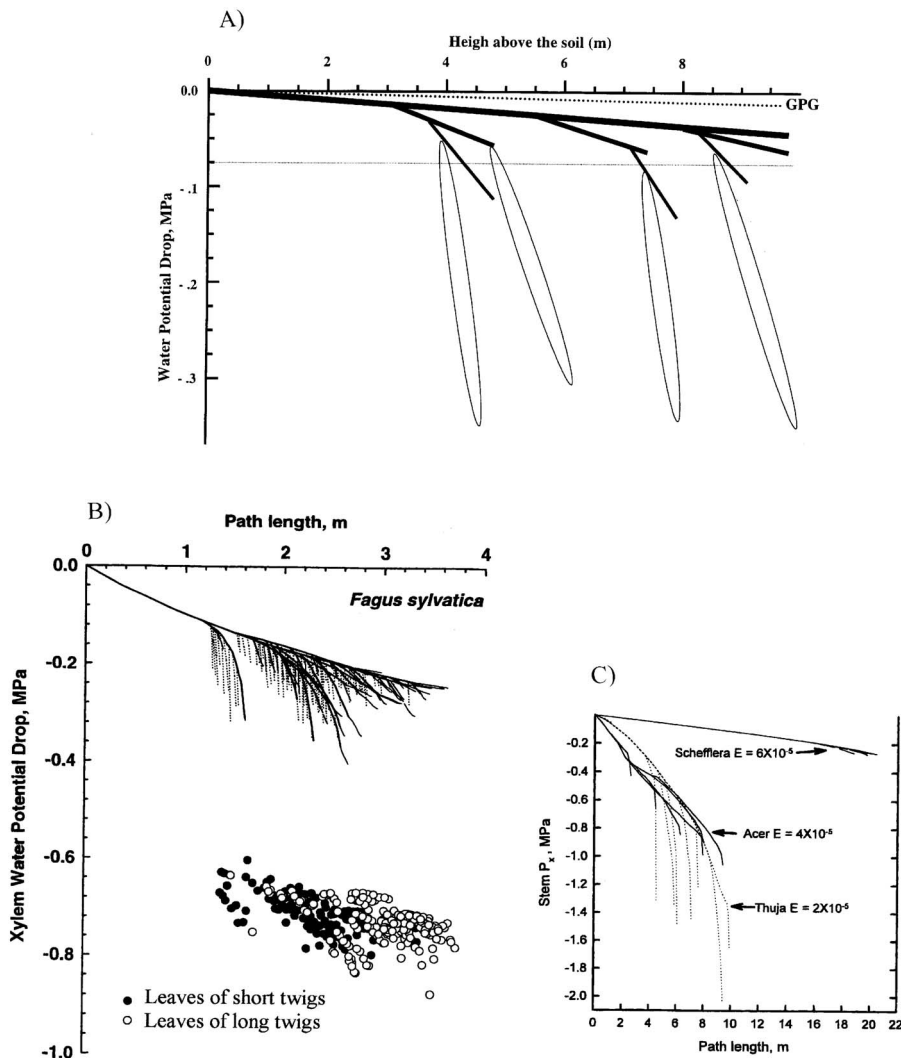


Figure 6. Examples of xylem negative pressure profiles or (gradient) in trees. **A:** Theoretical profile, showing that most of the gradient of tension is in the leaves; the dotted horizontal line stress the fact that the same tension (here 0.075 MPa) can be found at different elevations. GPG line is the tension profile of a stable water column, or gravitational potential gradient. **B:** Example of such gradient of tension in beech, *Fagus sylvatica* (from Cochard, unpublished results). **C:** Other examples of tension gradients for three different species. $E =$ evaporative flux density $\text{kg}^{-1} \text{s}^{-1} \text{m}^{-2}$ (from [128]).

related expressions). These profiles give the value of the xylem sap negative pressure (sap tension) at a given height. *Figure 6A* represents a theoretical example of such xylem pressure profiles supposing that the xylem pressure in the trunk, at the soil level, is zero. It can be seen that the higher the order of an axis, the steeper is the xylem pressure gradient. For the tree species studied so far, another general fact, emphasized in the drawing, is that the main hydraulic resistance of the trunk-leaf pathway is within the leaf or at least in the petiole-leaf unit [4, 131, 132]. Further research is needed to determine whether or not this fact is a consequence of the resistance of the extra-vascular sap pathway in the leaf. From the functional point of view, if this characteristic hold for all the leaves of a crown, it means that leaves located at the top of the crown will not be disfavored by the longer pathway sap follows to reach them.

Having in mind these theoretical trends of the negative xylem pressure profiles in trees, it is now profitable to look at some measured profiles as presented in *figure 6B* and *C*. The case of *Fagus sylvatica*, illustrates the general fact mentioned above: whereas the water potential values for different orders of branches are between -0.08 and -0.37 MPa, those of leaves are between -0.60 and -0.9 MPa. In *Thuja occidentalis* and *Acer saccharum*, the difference in xylem pressure disappears for the trunk, but not for the branches. It can also be seen that the negative pressure gradients in *Schefflera morototoni* barely exceed that required to lift water against the gravitational potential gradient (GPG) or hydrostatic slope to be more simple, (*figure 6A*). *Schefflera morototoni* is an interesting extreme with K_{1s} about ten times greater than those of *Acer saccharum* stems of similar diameter.

Leaf hydraulic resistances have now been measured for a number of tree species but for very few herbaceous species [76]. As said above, most of the resistance in the above ground part of a tree is located within the leaf blade. For example the leaf resistance expressed as a percentage of the total resistance between trunk and leaves is 80 to 90% for *Quercus* [132] around 80% for *Juglans regia* [131] less than 50% for *Acer saccharum* [150]. Measurements of leaf resistance in young apical and old basal branches of a *Fraxinus* tree have yielded contrasting results [22]. Most of the resistance was indeed located in the leaf blade in the apical shoots, but for older shoots, the resistance was mainly in the axis. This was attributed to the higher node density in older shoots.

Two consequences can be drawn from distribution of resistances in shoots. Firstly, many trees can be compared from the h.a. point of view, to “brooms”: many minor shoots with their leaves, forming a set of very high resistances in a parallel arrangement, plugged into a trunk of low resistance. *Thuja* is a good example of such a “broom” hydraulic architecture: the gradient of xylem pressure is much smaller in the trunk (roughly 0.02 MPa m^{-1}) than in the branches, at least ten times larger. Secondly the main factor of variation of the xylem pressure is neither the height, as still often said, nor the

length of the pathway from the roots to the leaf. This can be seen in the *figure 6A* (horizontal dotted line): the same value of xylem pressure is found at several different elevations. What determines the gradient of xylem pressure, dP/dx is the hydraulic resistance (inverse of K_h) of the water pathway between the trunk and the leaves. *Figure 7*, from [124], clearly shows this main feature from a model of the h.a. of *Thuja*: there is no good correlation between the water potential of minor shoots (< 0.8 mm diameter) and the total path length from soil to shoots (above left diagram) or the vertical height of the shoot (above, right diagram). In contrast, the lower diagrams show close correlation between this water potential and the sum of the leaf specific resistance defined as $\sum R_i A_{li}$ where R is the segment resistance and A_{li} is the total leaf area fed by the segment and the summation is over all segments along the pathway. If all leaves have the same transpiration T and steady state conditions apply, then the drop in Ψ along the hydraulic path should equal $T \sum R_i A_{li}$. The lower left diagram shows the correlation for all segments < 0.5 cm diameter. The improved correlation (lower right diagram) demonstrates that most of the hydraulic resistance is encountered in the minor branches. The curvature in the correlation is a consequence of capacitance effects.

An interesting modeling approach has been developed [39] which combines locally measured root hydraulic conductances (from literature), with data on the root architecture (topological and geometrical aspects). For a given distribution of soil water potentials and either a given flux or water potential at the collar, water fluxes along the roots, as well as

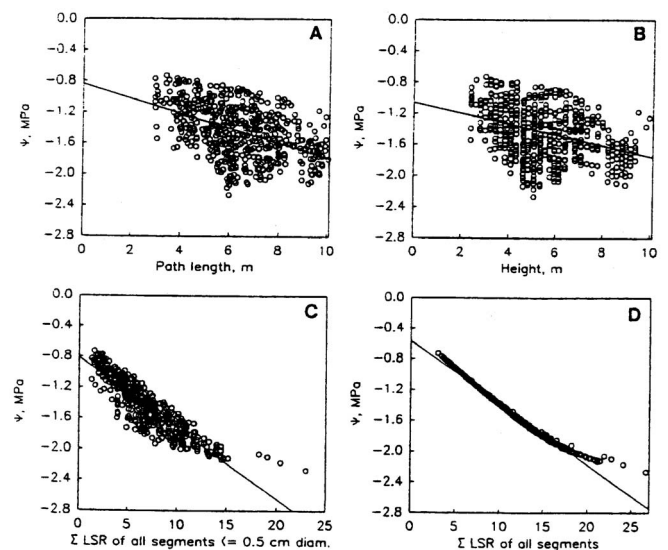


Figure 7. Plots of water potential of minor shoots (< 0.8 mm in diameter) of *Tsuga canadensis* versus the total path length from soil to shoot (upper left), versus height (upper right), versus sum of the leaf resistance (lower left) of all branches having a diameter < 0.5 cm, and versus the sum of leaf specific resistance of all the branches (lower right). Σ LSR are $kg^{-1} m^2 s$ MPa. (from [123]).

the xylem water potentials, can be calculated everywhere in the root system. As expected, water potential distribution along the root system is very dependent of the type of branching (adventitious or taproot for example) and the distribution of the elementary root conductances.

3. VULNERABILITY AND SEASONAL EMBOLISM

As stated by the cohesion-tension theory [118, 135] water ascends plants in a metastable state of tension, i.e., at negative pressures. The most crucial consequence of this state of tension in the xylem sap is the occurrence of cavitation [19, 81, 106, 139]. Cavitation is the abrupt change from liquid water under tension to water vapor. As water is withdrawn from the cavitated conduit, vapor expands to fill the entire lumen. Within hours or less, air diffuses in and the pressure rises to atmospheric [66, 125]. The conduit then becomes “embolized” (air-blocked). The replacement of water vapor by air is the key point that makes embolism serious since air cannot be dissolved spontaneously in water as can water vapor.

It is now clear that drought can induce cavitation and xylem embolism. This is not the only cause (see Section 3.5) but during summer, this is, by far, the main factor. Therefore, resistance to cavitation is perhaps the most important parameter determining the drought resistance of a tree. A vulnerability curve (VC) is a measure of that “resistance” in particular stem, branch or petiole. It is a relation between the tension of the sap in the xylem conduits and the corresponding degree of embolism as estimated by acoustic detection [79, 96, 100, 126] or, much more frequently, by a hydraulic method [107].

3.1. The vulnerability curves (VC)

Figure 8A gives an example of one recent method to determine a vulnerability curve in field (Xyl'em Instrutec Licensed INRA). The principle is simple. A segment of branch collected from the tree under study is first rehydrated to reach complete hydration (full turgidity). Then it is submitted, by means of a collar pressure chamber, to successive increasing steps of air (or nitrogen) pressures. These pressures are positive pressures, above the value of xylem pressure corresponding to full turgidity, which is zero by definition (see Appendix). As a result, mesophyll cells begin to squeeze, thus pushing water from these cells to the xylem vessels and to the protruding end of the branch, where it is collected. The plant sample is now slightly dehydrated. Repeating such small increase of pressure with time will lead to a regular dehydration of the sample and to more and more negative values of its water potential (an intuitive image of this process is the progressive squeezing of a sponge full of water). At each chosen step, the level of embolism is estimated by the measured conductivity K_h expressed as a percentage of the maximum K_h obtained after removal of embolism [17, 107].

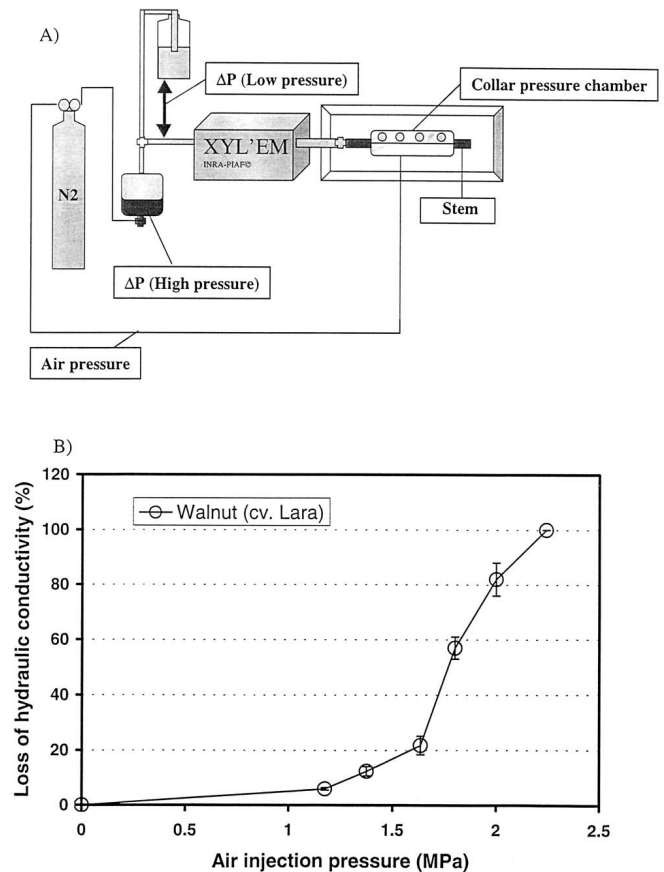


Figure 8. A: Diagram of the apparatus (injection method, one of the possible methods) used to build a vulnerability curve. B: Example of a vulnerability curve, for a branch of walnut tree, *Juglans regia* (from Ameglio, unpublished result).

In other words a VC, specific to a given axis, is a relation between water potential and the corresponding loss of hydraulic conductivity (figure 8B). It therefore requires a technique similar to that necessary for the measurement of the hydraulic conductivity.

3.2. Examples of vulnerability curves

Figure 9A and B presents some examples of VCs obtained for different trees belonging to Angiosperms and Gymnosperms [127]. As can be seen there are very large differences of vulnerability between species. Among the least vulnerable taxa are *Juniperus virginiana*, a widely distributed conifer capable of growing on both mesic and xeric sites and *Rhizophora mangle*, a mangrove growing in saline coastal marshes but whose roots exclude salts from the xylem sap. For these species the water potential for just 20% loss of conductivity occurs at -5 to -6 MPa which are very low values. Presently the less vulnerable species have been found in very dry areas. *Ceanothus megacarpus*, growing in the California chaparral, can resist negative pressures lower than -10 MPa.

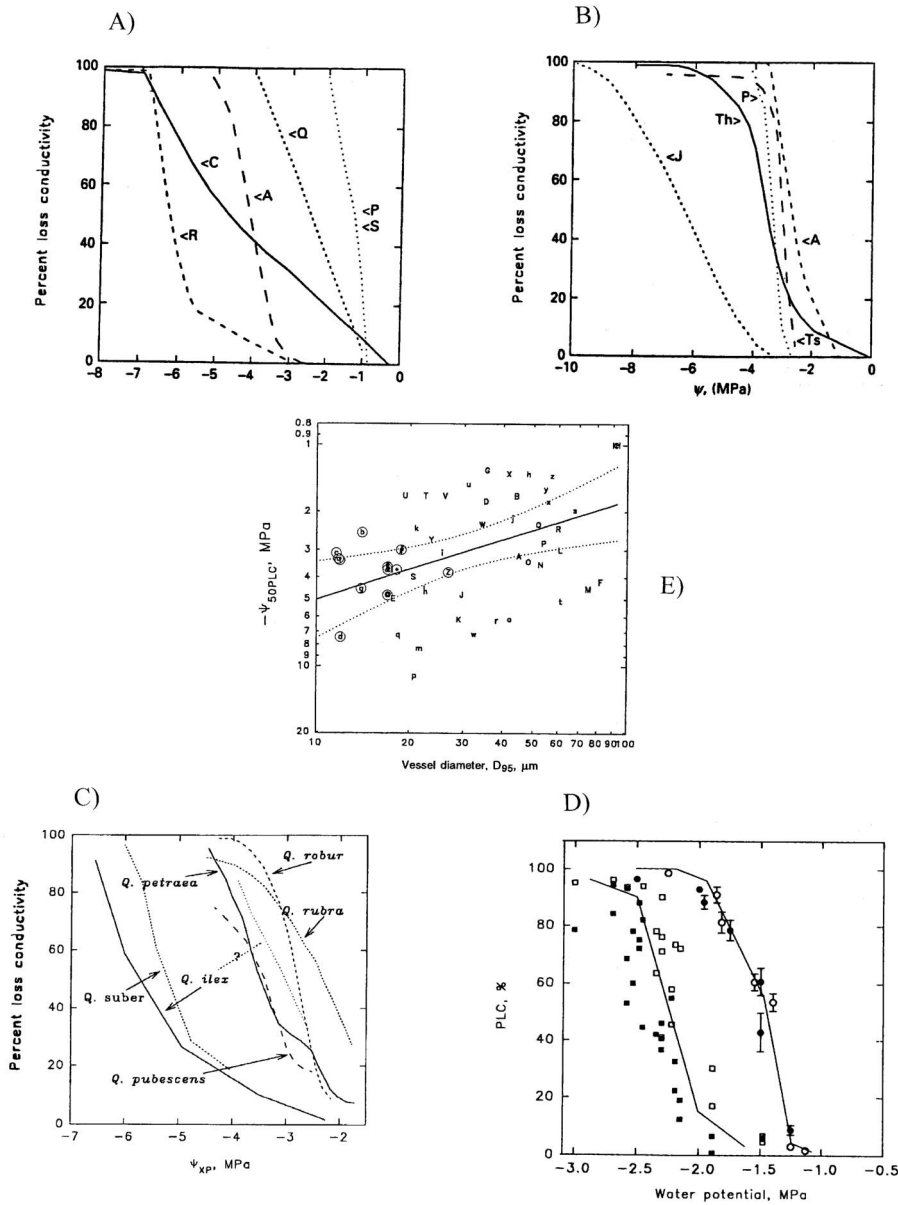


Figure 9. Examples of vulnerability curves. **A:** Intergeneric examples. Angiosperms. R: *Rhizophora mangle*; A: *Acer saccharum*; C: *Cassipourea elliptica*; Q: *Quercus rubra*; P: *Populus deltoides*; S: *Schefflera morototoni* (from [127]). **B:** Intergeneric examples. Gymnosperms. J: *Juniperus virginiana*; Th: *Thuja occidentalis*; Ts: *Tsuga canadensis*; A: *Abies balsamea*; P: *Picea rubens* (from [127]). **C:** Intrageneric example. *Quercus* (from [134]). **D:** Vulnerability curve of different axes of the same walnut tree, *Juglans regia*, showing a rare example of vulnerability segmentation (from [131]). **E:** Log-log plot of xylem tension causing 50% loss hydraulic conductivity (Ψ_{50PLC}) and mean diameter of the vessels that account for 95% of the hydraulic conductance (D_{95}). Each symbol is a different species. The solid line is the linear regression of the log-transformed data. The dotted lines are the 99% confidence interval for the regression (from [133]).

According to Pockman and Sperry [95], *Juniperus monosperma* did not begin to cavitate until pressures below -10 MPa and *Larrea tridentata* was completely embolized at a pressure of -14 MPa or even less. For *Ambrosia dumosa* growing at Organ Pipe Cactus National Monument (Arizona), this threshold is around -12 MPa [78]. At the other extreme of vulnerability are *Populus deltoides* Bartr. ex Marsh and *Schefflera morototoni* which lose 50% of their hydraulic conductivity at -1.5 MPa. *Populus deltoides* is a temperate mesic species which grows preferentially where water tables are high, and *Schefflera morototoni* is an evergreen species which grows in rain forests and is an early colonizer of gaps [137].

Some vulnerability curves for roots have been published [5, 67, 111], which show that the root xylem in woody plants is generally more vulnerable to cavitation than shoots of the same individuals (see references in [95]). Because of their great susceptibility to cavitation, small roots have been called the “Achilles’ heel” for water transport within the plant [51]. In this way, embolism may be confined to replaceable roots rather than the stem [95].

An implicit consequence of these VCs is that no strong correlation exists between the diameter of the xylem elements and their vulnerability to summer embolism, as was assumed around the eighties. This has been clearly shown by numerous experimental results, summarized in figure 9E

[133]: the log-log plot of xylem tension causing 50% loss of hydraulic conductivity (Y axis) and mean diameter the vessels that account for 95% of the hydraulic conductance (X axis) as a weak correlation (regression accounts for only 21% of the variation). This statistically significant relation is insufficient to be of predictive value of vulnerability. *Figure 9C* illustrates the VCs of different species among the genus *Quercus*. The differences of vulnerability are about as large as between the diverse species of Angiosperms represented *figure 9A*. There is a striking correlation between vulnerability curves and general perception of drought tolerance from the silvicultural literature: the arid-zone species (*Q. ilex* and *Q. suber*) are less vulnerable than mesic-zones species (*Q. robur* and *Q. petraea*). It is worth noting that even 100 percent loss of conductivity of branches may be nonlethal for *Quercus* species. While most branches died at a soil water potential of -5 MPa, resprouting can occur from roots and some axial buds [134]. Eventually, *figure 9D* gives the only known example, so far, of what is called “vulnerability segmentation”. The idea comes from Zimmermann [154] who spoke of “hydraulic segmentation” as we have seen before. Zimmermann argued that hydraulic segmentation is vital in arborescent monocotyledons, such as palm trees. A palm tree, once formed, can never add new vascular tissue, as dicotyledonous and coniferous trees do. In palms there appears to be substantial hydraulic constriction at the level of the leaf junction [104]. Zimmermann said that this is an essential feature of palm hydraulic architecture to confine embolism to leaves during drought. Leaves are renewable parts, but if the stem is embolized, then the tree may never recover. Tyree and Ewers [127] extended Zimmermann’s hypothesis to include “vulnerability segmentation”. This exists when the vulnerability of leaves, petioles or minor branches is greater than that of larger branches and the bole. *Figure 9D* shows such a case for walnut: the VC of stems and petioles gave an order of vulnerabilities of the components of the tree: petioles > current-year shoots > one year-old shoots [131]. When petioles reached 90% loss of hydraulic conductivity, the leaf water potential Ψ was approximately -1.9 MPa; at the same Ψ , the stems had lost only about 15% of their maximum hydraulic conductivity. This is in contrast to several *Quercus*, *Fraxinus* or *Populus* species where there is no difference in the VC of stems and petioles [18, 20, 22]. This study on walnut is the first case showing that drought-induced leaf shedding is preceded by cavitation in petioles before cavitation in stems, due to vulnerability segmentation. However, it is not definitively known that cavitation causes leaf abscission or what the underlying processes are. In the same way more work has to be done to confirm whether or not a causal link exists between the vulnerability to cavitation and branch dieback [98]. The great susceptibility of the small roots to embolism can also be considered as another expression of the vulnerability segmentation.

There is now ample evidence from the literature that VCs vary considerably between species or between organs in a

same species. More recent studies have furthermore suggested that VCs can also vary for a same organ according to environmental growth conditions. For instance, shade-grown branches of *Fagus sylvatica* are more vulnerable than sun-exposed branches [24]. Vulnerability to cavitation is probably an important parameter to consider in order to understand tree phenotypic plasticity.

3.3. Summer embolism

During summer, trees undergo drought if the soil dries. Such conditions lead to a decrease of the soil water potential and to a large increase of the hydraulic resistance at the soil-root interface (see Section 4.2). The water potential of leaves will decrease and the xylem sap negative pressure will also decrease. Therefore cavitation and its consequence, embolism will develop and the hydraulic conductivity of the distal parts of tree will decrease. *Figure 10A* shows, for 30-year-old trees of four oak species [18], the seasonal change in percentage loss of hydraulic conductivity due to embolism in petioles (above) and twigs (below). The open symbols relate to control (irrigated) trees and closed symbols to water stressed trees. It can be seen that there is always, throughout the year, some degree of embolism, even in the well-watered trees. This residual embolism probably comes from vessels with not very well-formed walls or which have been wounded during bad weather or disease.

Another conclusion from these data is that embolism develops during the drought period; but several months of drought are necessary to induce a significant degree of embolism. In fact, efficient mechanisms of defense develop (see below). These results also clearly showed that there is no recovery of embolism after drought has ended. Yang and Tyree [149] presented a model of hydraulic conductivity recovery well confirmed by experimental data. Embolism may dissolve in plant if Ψ_x becomes positive or close to positive for adequate time periods. Embolisms disappear by dissolution of air into the sap surrounding the air bubbles. For air to dissolve from a bubble into liquid sap, the gas in the bubble has to be at a pressure in excess of atmospheric pressure [137]. P_g being the pressure of gas in the bubble and P_l the pressure in the liquid surrounding the bubble ($P_l = \Psi_x$) if the difference $P_g - P_l$ is less than the capillary pressure (originating from the surface tension τ), then the gas will dissolve. If this quantity is greater no dissolution will appear. For instance, let us consider an air bubble trapped in a of $60 \mu\text{m}$ vessel diameter. The capillary pressure caused by the surface tension is then equals to ca. $+5$ kPa (see Jurin’s equation on this page). Therefore, the xylem pressure must be higher (less negative) than -5 kPa for the bubble to dissolve. Practically, this signifies that, in a non transpiring and well-watered tree, passive embolism can only occur in the root system and up to 50 cm in the trunk. To dissolve embolism higher in the tree, an active mechanism is required, i.e. a positive root pressure.

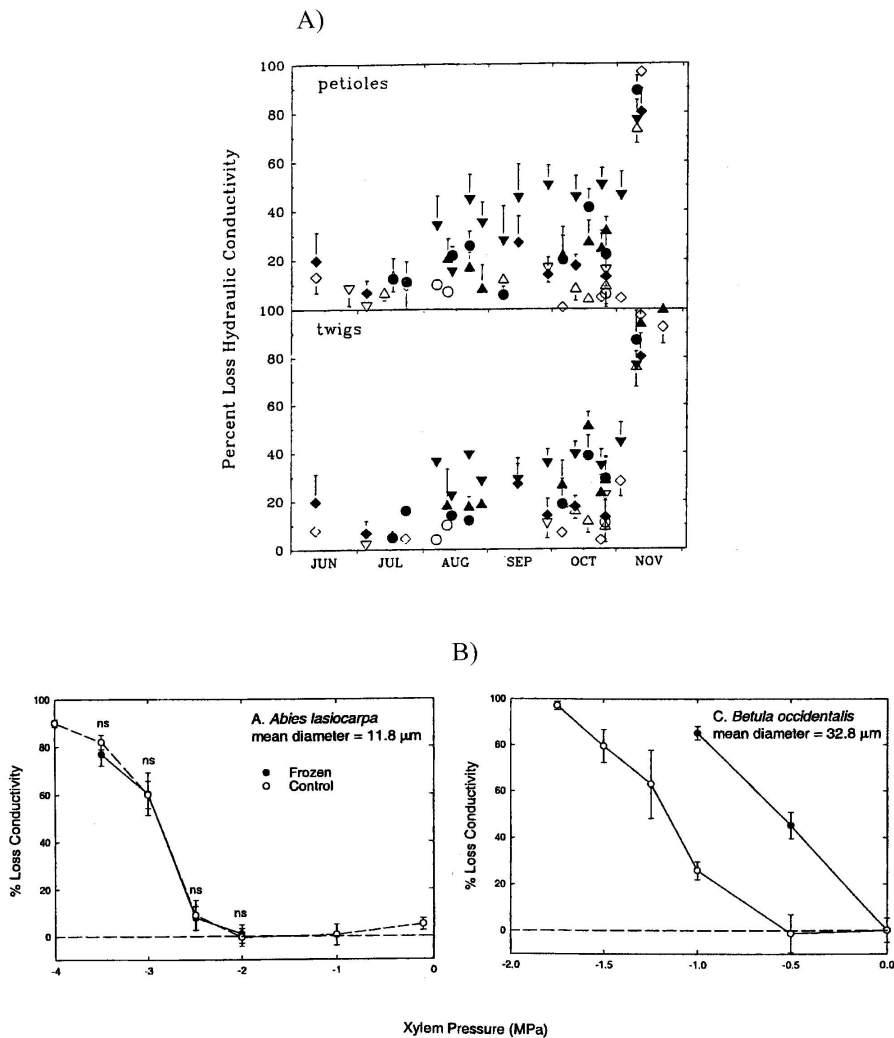


Figure 10. A: Seasonal evolution of xylem embolism in petioles (upper) and one-year old twigs (lower) for both control (open symbols) and water stressed (solid symbols) trees expressed in % from completely hydrated twig or petiole specimens. ∇ *Quercus robur*; \blacktriangle *Quercus rubra*; \bullet *Quercus petraea*; \blacktriangle *Quercus pubescens* (from [18]). **B:** Vulnerability curves for frozen (solid symbols) and control (open symbols) stems versus xylem pressure for a coniferous (left) and a diffuse-porous deciduous tree (see Section 3.5). Results indicate increasing vulnerability to cavitation by freezing with increasing conduit diameter: freezing causes no additional loss of conductivity relative to water stress controls in *Abies* contrary to what happens in *Betula* (from [35]).

However, one must be careful in generalizing, at least for the results and explanations dealing with recovery of embolism. For a long time it was clear that no recovery of embolism can occur during drought. Some theoretical explanations [93] and, especially, recent results [55, 155] suggest that refilling may be more common than previously thought, and that it might occur under negative pressure. More work is needed to get a clear view on this question.

Last but not least, as soon as negative air temperatures occur at the beginning of November, embolism reaches a maximum (hundred percent of loss of hydraulic conductivity). This important result, which has been confirmed by laboratory experiments [15] indicates that another type of embolism, induced by negative air temperatures, can occur in trees. It also shows that the vascular tissue of *Quercus* is extremely affected by this freezing-induced embolism (see Section 3.5).

3.4. How to explain the drought-induced embolism? The air-seeding explanation

While there are many potential causes of xylem cavitation [92, 133], the experimental evidence strongly favors the “air-seeding” explanation [31, 106, 113, 154]. This states that cavitation occurs when air outside a water-filled conduit is aspirated into this xylem element through pores of the pits in the walls (figure 11A). These pores will retain an air-sap meniscus until the difference of pressure between outside and inside (i.e., xylem pressure, P_x) across the meniscus, exceeds the capillary forces holding it in place. Outside means either atmosphere, P_a , or an adjacent air-filled conduit, where the pressure is near atmospheric pressure. As Jurin’s law (or the capillary equation) states these forces are a function of the pore diameter d , the surface tension of water, τ , and the contact angle between water and the pore wall material (α). The critical pressure difference ΔP_{crit} required to force air through a circular wetted pore can be predicted by this law:

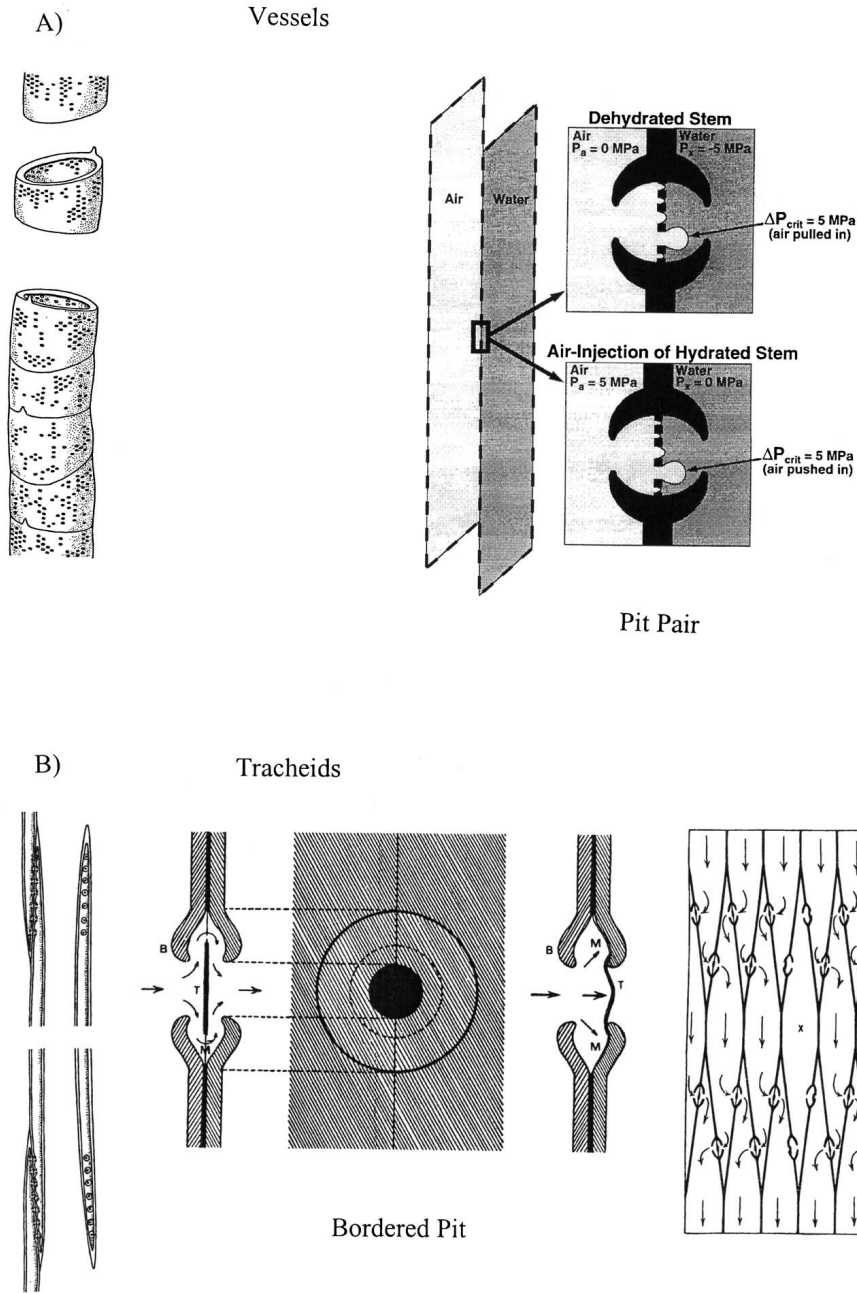


Figure 11. Cavitation in tracheids and vessels. **A** Left: part of a vessel of oak, large-porous wood (diameter ca. 200–400 μm , length until some meters) showing vessel elements and pits grouped in small dispersed areas. Right: illustration of the air-seeding explanation. Two adjacent xylem vessels are shown, one being embolized (air filled) the second functional (with sap). Far Right: enlarged view of the intervessel pit structure. The air-seeding explanation states that xylem cavitation in a “dehydrated stem” is initiated by air pulled through the pit membrane pores. This occurs when the air pressure (P_a usually near zero) minus the xylem pressure (P_x , usually negative) across the air-water meniscus at the pore creates a pressure difference (ΔP_{crit}) sufficient to displace the meniscus. In the example shown, the ΔP_{crit} of 5 MPa is reached when $P_x = -5$ MPa. A corollary of this explanation is that by injection of air in a “hydrated stem”, where xylem pressure is atmospheric (0 MPa), ΔP_{crit} can be achieved by raising the air pressure (to + 5 MPa in this example) (from [113]). **B** Left: spindle-shaped tracheids (diameter of some μm or tens of μm , length of some mm) showing small bordered pits. Centre: enlarged views of a bordered pit of a coniferous tracheid; left of centre: pit in section, arrows indicating the path of water from one tracheid to the next; centre: surface view of the same pit; right of centre: section showing the valve-like action of the torus. T = torus; M = pit membrane; B = pit border. Far Right: tangential section of coniferous wood. The tracheid in the center (marked x) is embolized. Water flows around it. The negative pressure in the xylem has pulled the pit membranes away from the embolized dead cell to seal it off (from [133]).

$$\Delta P_{\text{crit}} = (4\tau \cos\alpha) / d$$

with ΔP in Pa, τ in N m^{-1} , d in m; for water in glass capillaries as well as in the xylem elements of plants $\cos\alpha = 1$; $\Delta P_{\text{crit}} = P_a - P_x$.

From this equation it is clear that the bigger the pore, the smaller ΔP_{crit} becomes. Taking P_a as a constant, the largest pore between two adjacent conduits will then determine the less negative xylem pressure, P_x which provokes cavitation. An approximation of Jurin's law rewritten in a simplified manner and thus made directly useful for biologists is [154]:

Pore diameter (in μm) \times pressure difference (in atm or bars) ≈ 3 .

For example, if the biggest pore is 0.2 or 0.1 mm in diameter, then the minimum stable P_x will be, approximately, -15 or -30 atm, respectively.

Figure 11A illustrates this for a typical inter-vessel pit membrane. The diagram shows two adjacent vessels, one filled with air, the other with sap. As water stress increases, P_x becomes more negative and ΔP increases and eventually reaches the critical value where air is pulled into the conducting element through the pit membrane pore and "seeds" cavitation. As supposed by the air-seeding explanation, only the magnitude of ΔP is the triggering factor. Therefore the same result can be achieved either by water stress, as in natural conditions, or by injecting air within a hydrated stem, as in experimental conditions [17].

The air-seeding explanation has been supported by many different experiments [113] and can now be considered as the correct explanation of drought-induced embolism. Its most important consequence is the fact that the vulnerability to embolism is directly determined by the diameter of the pit pores and not by the diameter of the conduits. This could be a useful indication for estimating a priori the degree of safety of a conducting system in regard to vulnerability. However, difficulties still remain as to which is the correct pore diameter to take into account. Most of the time, pit pore diameters are measured using electron microscopy techniques, under relaxed conditions. However under natural conditions, as the pit membrane is subjected to large pressure differences prior to air seeding, it is strongly suspected to be stretched (Sperry, personal communication). Therefore, the exact diameter of the pores can be very different in the relaxed state vs the stretched state, depending on the mechanical properties of the pit membrane.

In conifers where a torus is present in the pit of tracheids (figure 11B, T), the situation is different. When a tracheid embolizes, the pit membrane is deflected against the pit chamber wall and the torus covers the pit aperture (figure 11B, right). However, this sealing action of the torus is not perfect and air is apparently still able to pass through this torus-blocked pit wall. The problem is to find which way air uses. In the species studied by Sperry and Tyree [109], *Abies Balsamea* (L.) Mill., *Picea rubens* Sarg. and *Juniperus virginiana* (L.), when air enters, it probably does not happen

through the torus which appears to be without pores and forms a tight seal over the aperture. Air should then pass through the deflected pit membrane. Besides, the porosity of the pit membrane that supports the torus (the margo, M) is too large to prevent air entering at P greater than 0.1 MPa in most cases. It therefore could not account for the observed embolism-inducing pressures, which are much less negative. The conclusion of the authors is that the air-seeding pressure is not directly a function of pore size but of membrane flexibility, because the seeding may occur when the torus is displaced from its normal sealing position over the pit aperture. In other words, it can be supposed that the displacement of the pit membrane reduces the size of its pores.

3.5. Winter embolism

During winter, freeze-thaw events can induce embolism and reduce the hydraulic conductivity of temperate woody plants [15, 110]. The seasonal development of embolism in the xylem conduits of *Quercus petraea* showed a sharp and total loss of conductivity following the first fall frost (figure 10A). Similar observations have been made on *Fraxinus excelsior* [22], another ring porous species. Temperate ring porous species thus seem highly vulnerable to frost-induced embolism. The situation is different for diffuse porous and conifer species. For diffuse porous trees, such as *Acer* [108] or *Fagus* [50], the increase in embolism is more gradual and reaches high degrees only after repeated periods of frost. Conifers exhibit another extreme situation because they do not seem to suffer at all from winter embolism. It has been argued that freezing-induced embolism can limit the growth, survival, and geographic distribution of plant species [64, 94, 110, 134]. These studies suggest a link between xylem anatomy and the vulnerability to frost: the larger the conduit, the higher the vulnerability [42]. This link has clearly been established in a systematic study of the degree of late winter embolism in the xylem of many hard and softwood species [133, 146]. A positive relationship was found between the specific hydraulic conductivity (which is primarily a function of conduit size) and the degree of embolism (figure 12). This is in opposition with what has been shown in figure 9E.

Davis et al. [35], carried out a technique which enabled them to consolidate more precisely this result. They showed that plants with mean conduit diameter above 30/40 μm are extremely sensitive to cavitation by freezing, even for a modest xylem pressure (say -0.5 MPa). Therefore, besides their specific vulnerability to summer embolism, species having large conduits will have an additional sensitivity to winter cavitation: under the same water stress conditions (as determined by xylem water potential) they will have more chance to be embolised during period of below zero temperature than during period of mild temperatures. This is well illustrated (figure 10B): *Betula occidentalis* having mean diameter conduits much larger than *Abies lasiocarpa* is therefore much more susceptible to freezing-induced cavitation.

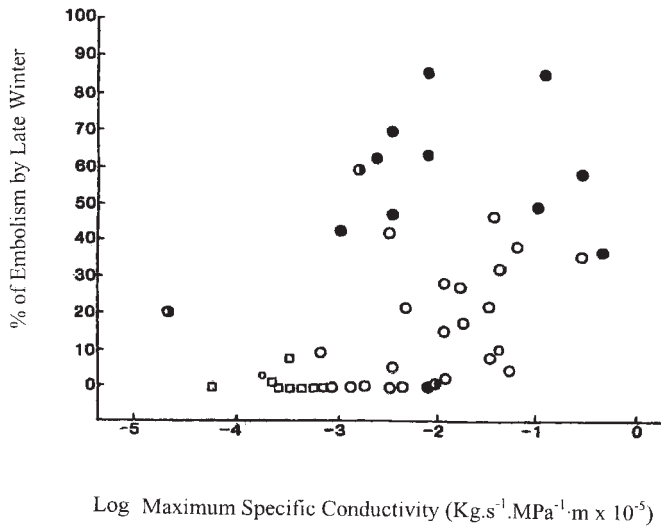


Figure 12. Interspecific vulnerability to frost-induced embolism. The degree of xylem embolism was measured at the end of the winter for a large number of conifers (open squares) diffuse-porous (open circles) and ring-porous species (closed circles). This degree of embolism is expressed as a function of the xylem specific hydraulic conductivity which primarily correlates with conduit sizes: the larger the conduits, the higher the conductivity, the higher the embolism at late winter time. See also *figure 10* (from [146]).

3.6. The “frost-thaw” explanation

Why should larger conduits be more prone to winter embolism? Our current explanation is based on a frost-thaw mechanism. When sap temperature drops a few degrees below 0°C , ice forms which creates air bubbles (air is almost not soluble in ice). It is assumed that during the thawing, when xylem tensions exceed a critical value, air bubbles are progressively released to the liquid phase and air-water menisci are created (*figure 13*).

As it can be deduced from the above discussion (*figure 13*), for a bubble of air to be stable, neither increasing or decreasing in size, the pressure difference, $P_g - P_l$, between the gas and the liquid phases must be equal to $4\tau/d$ (see capillary equation above). Or we can say if $P_l < (P_g - 4\tau/d)$ the bubble will expand to fill the whole conduit. The larger the initial size of the bubble, i.e., the larger the diameter of the conduit, then the closer can be P_l to P_g , i.e. the smaller the tension in the liquid to produce indefinite expansion and therefore gas filling of the conduit. Larger conduits are more vulnerable probably because bubbles are initially larger. The initial size of the bubbles can explain differences between species but cannot explain alone all the observations. In *Fagus sylvatica* for instance it has been recently observed [65] that young terminal shoots were more vulnerable than larger xylem segments which contradicts the conduit size-vulnerability relationship. Under controlled conditions, it was established that the terminal shoots were freezing and thawing before the

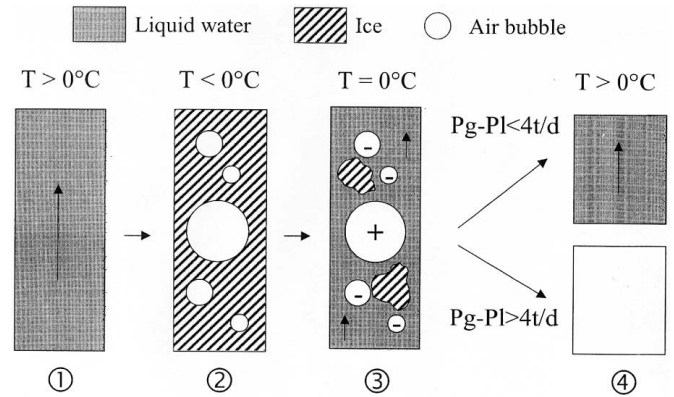


Figure 13. Mechanism of frost-induced embolism. The breakdown of water columns in xylem conduits following a frost-thaw event is probably due to the expansion of air bubbles formed during sap freezing. Tensions developed in the xylem at thawing are large enough to prevent the collapse of the largest bubbles caused by their surface tension. When temperatures decrease below 0°C , the liquid column of sap freezes and ice forms (2). Gas being much less soluble in ice than in the liquid sap, bubbles of different sizes appear (2). When temperatures increase above 0°C , ice sap thaws (3). Depending on their initial size and on the xylem tension at thawing, bubbles will either collapse (the smaller ones) or, in the contrary expand (the larger ones) (4). P_g = gas pressure of the bubbles; P_l = xylem sap pressure; t = surface tension of the sap; d = conduit diameter; T = temperature.

remainder of the branch. This suggests that on freezing, water was expelled from the apex (due to ice expansion). On thawing, this water deficit will induce high hydrostatic tensions. In beech, the development of hydrostatic tensions might determine the formation of embolism more than the sizes of air bubbles alone.

Recently Cochard et al. [26] have argued that vessel embolism occurs during the freezing phase in cryo-scanning electron microscopy observations. However the volume of air present in the vessels appears to be much greater than can be accounted for by the volume of air dissolved in the sap. This result suggests that we are far from having a clear understanding of the underlying physics governing the processes that occurs during frost-thaw cycles.

If trees experience high loss of hydraulic conductivity during winter, how can they cope with this situation when sap flow is reactivated in spring? Several authors [3, 50, 105, 108, 112] have suggested that positive pressures in the xylem, during spring in particular, can have important implication for dissolution of freezing-induced embolism in temperate woody plants. Zhu et al. [151] found that in *Betula alleghaniensis* Britt., freezing damage to roots resulted in lower spring root pressures, less recovery from winter embolism, and higher shoot dieback.

Although most authors have considered positive pressures in the xylem to be important for dissolving embolism [3, 50, 55, 105, 129, 139], mechanisms of winter pressure formation

remain poorly understood. The most studied plants in this regard are species of *Acer*, for which there are several hundred papers dealing with the flow of maple sap [60, 74, 80, 88, 122]. It is clear that in *Acer*, winter xylem pressures are derived from the stem and not the root. The sap exudation from the stumps of felled trees at that time of year is negligible whereas copious exudation occurs from excised shoots [73, 119]. Proposed mechanisms in *Acer* can be categorized into either “physical models” or “vitalistic models”. According to physical models, the winter pressures are due strictly to freeze-thaw events [87, 122]. In contrast, according to vitalistic models, activities of living cells in the xylem are required for pressure buildup [59, 73, 74, 148]. It is known that at low, non-freezing temperatures, starch in stem parenchyma cells is broken down into sugars, especially sucrose [75]. Although sucrose appears to play a role in the pressure build-up in *Acer* stems, the buildup of sucrose is apoplastic and the osmotic role of sucrose in the formation of stem pressures has been questioned [30, 60]. It has also been suggested that the living parenchyma cells are crucial for gas production, leading to temperature dependent changes in gas pressure in the air spaces within the wood fibres [101].

As in *Acer*, walnut trees (*Juglans regia* L.) have been observed to display positive pressures in the xylem sap during the winter, autumn and spring. Autumn and spring xylem pressures appeared to be of root origin and were positively correlated with soil temperature [44]. Winter stem pressure was associated with low temperatures and with high sugar concentrations in the xylem sap [2, 7]. A simple osmotic model could account for the modest positive winter pressures at low, non-freezing temperatures, but not for the synergistic effects of freeze/thaw cycles.

Many other species lack such high pressurization periods (*Quercus*, *Fraxinus*, *Castanea*, Conifers, etc.). Therefore, conduits embolised during winter time remain permanently non-functional and may eventually become plugged by tyloses [15]. New functional vessels are then produced before leaf expansion and will insure most of the sap supply to the leaves during the growing season [49]. Species not suffering from winter damages or capable of reactivating their xylem conduits can, on contrary, rely on their sapwood to supply the new leaves with water. For these species the new ring growth is delayed and occurs only after full leaf expansion. Tree phenology in spring may thus correlate with their xylem history. However, as mentioned above, recent results show that active (?) refilling can also take place in the presence of high xylem tension; however the mechanism underlying this process has not yet been identified [55, 139, 156].

A detailed example of study concerning the mechanisms of xylem recovery from winter embolism can be found [27]. In mature beech trees, hydraulic conductivity in the terminal branches decreased progressively during winter. Two periods of recovery have been identified. The first occurred early in the spring before bud break and during the period of positive xylem pressure measured at the base of the tree trunk. Active

refilling of the embolized vessels caused the recovery. The second recovery of hydraulic conductivity occurred after bud break when the cambial activity resumes, producing new functional conduits. Therefore two mechanisms whose effects can vary according to climatic conditions and species, can explain shoot hydraulic recovery of broadleaf trees in the spring. *Figure 14* presents a schematic representation of the progression and recovery of embolism for a current beech year shoot (formed in year n). In (1) a cross section of the current-year shoot is shown in late summer of year n , when cambial activity has ceased and when all xylem vessels are still filled with water: no embolism, hydraulic conductivity equal to its maximum value, e.g. when the shoot is fully hydrated, $K_w = K_{wn}$, and PCL (% loss of conductivity) is equal to zero. For the year n , this maximum value is then K_{wn} . Following freeze-thaw events, some vessels become filled with air and PCL increases up to a more or less important value, α in late winter (2). Then two possibilities can take place. The first is that vessels do not refill before the onset of ring development. The reduction of PCL value α , will only be possible by the formation of new vessels and will be a function of the increase of the xylem surface A_{n+1} and $K_{(wn+1)}$ (K_w of the new ring). In this case K_w increases in comparison with its previous value, because the growth produces more new functional xylem than the remaining embolized vessels (5). The second possibility is when positive pressures can take place during early spring and refill some embolized vessels. The residual PLC, β , will therefore becomes less than α (3). Later on, the cambial reactivation will further decreases of PCL to a value $< \beta$ (4). Therefore the paths (2) \rightarrow (3) \rightarrow (4) and (2) \rightarrow (5) can be differentiated by comparing concurrent changes in PLC and K_w . The first with its refilling step (walnut, maple) should lead to a residual embolism lower than the second (oak, ash).

4. THE COUPLING BETWEEN HYDRAULIC AND STOMATAL CONDUCTANCES

Although the behavior of stomata in the presence of various stress (water, light, CO_2) is well established, the underlying mechanisms remain largely unknown. In the presence of soil water deficits for instance, stomata gradually close which reduces leaf water loss. The production of specific hormones (ABA) by roots has been proposed as a coupling factor between the stomatal aperture and the soil water deficit [120]. In this part we will describe an alternative coupling between stomatal behavior and hydraulic properties.

4.1. Theoretical and experimental relationships between transpiration and leaf water potential during a progressive soil drought

According to the Ohm's law analogy, there is a simple relationship, for steady state conditions, between leaf transpiration and the average leaf water potential:

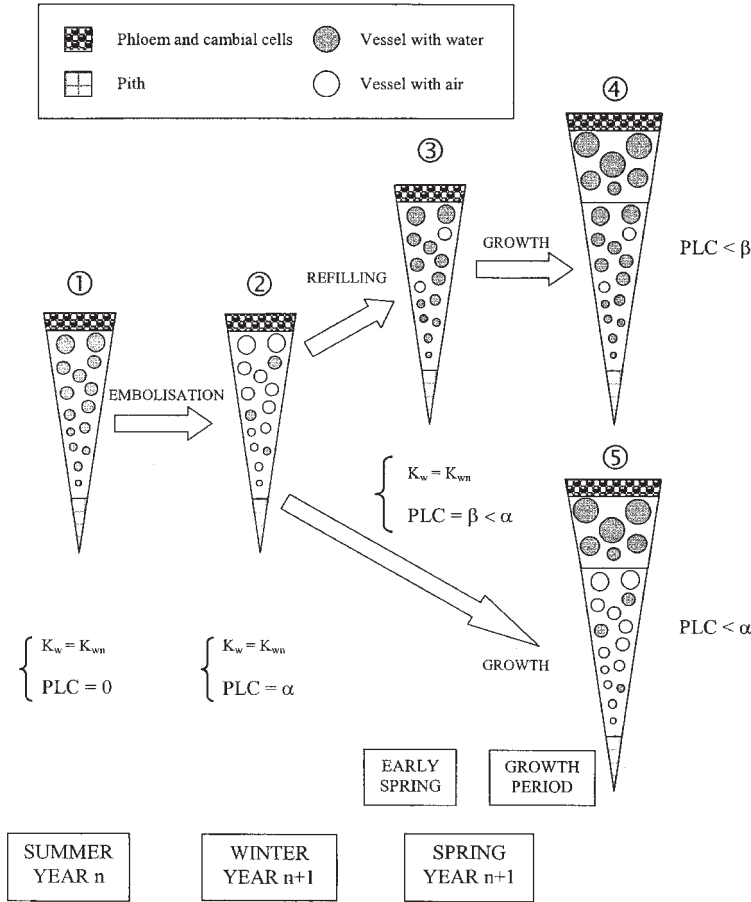


Figure 14. Schematic representation of progression and recovery of embolism for a current-year shoot (formed in year n) of beech. Two main phenomena contribute to this recovery: refilling of already build vessels and production of new vessels. More explanations in the text (from [27]).

$$\Psi_{leaf} = \Psi_{soil} - F \times R_{plant}$$

where Ψ_{leaf} and Ψ_{soil} are the leaf and soil water potentials (MPa), F the whole plant transpiration rate (mmol s^{-1}) and R_{plant} ($\text{mmol s}^{-1} \text{MPa}^{-1}$) a coefficient that we call the “whole plant hydraulic resistance” by analogy to an electrical circuit. R_{plant} includes all the hydraulic resistances along the sap pathway from the soil to the leaves. Experimental relationships between F and Ψ_{leaf} have been established for many species. The relationships are usually linear, but may also be curvilinear. The latter situation might be caused by non-steady state conditions or variable R_{plant} resistances. [69] followed the Ψ_{leaf} vs. F (sap flux density) relationships in a natural stand of *Picea abies* during a progressive soil drought (figure 15A). In control the relationships are close to linear, suggesting that R_{plant} was independent of the transpiration rate. However, R_{plant} varied considerably during the development of drought as indicated by the increase of slope. This result is important because it demonstrates that considerable changes in the plant hydraulic system can occur during a water shortage. The leaf water potential is therefore a poor estimate of the plant capacity to extract water from the soil.

When derived from the F vs. Ψ_{leaf} relationships, R_{plant} integrates soil, vascular and non vascular plant resistances. The question is then to know which resistance increases the most during a drought period?

4.2. The increase in soil-root resistance

Further observations during the previous study suggested that the increase in R_{plant} is most likely located at the soil-root interface or in the bulk soil itself. For instance, Lu [68] followed the changes in branch resistance R_{branch} . Contrary to R_{plant} , R_{branch} was nearly constant all through the drought period (figure 15C). The increase in R_{plant} could not be ascribed to cavitation events in the branch systems. Furthermore, the decrease in R_{plant} was reversed after soil rehydration. Because loss of conductivity due to cavitation is irreversible in conifers, it was therefore unlikely that the change in R_{plant} was located in the xylem system. In *Picea*, most of the drought-induced variation in R_{plant} was therefore due to a reversible extra-vascular phenomenon. However, if the impact of xylem cavitation was only minimal in this study, this was probably the result of an active stomatal regulation. This is illustrated

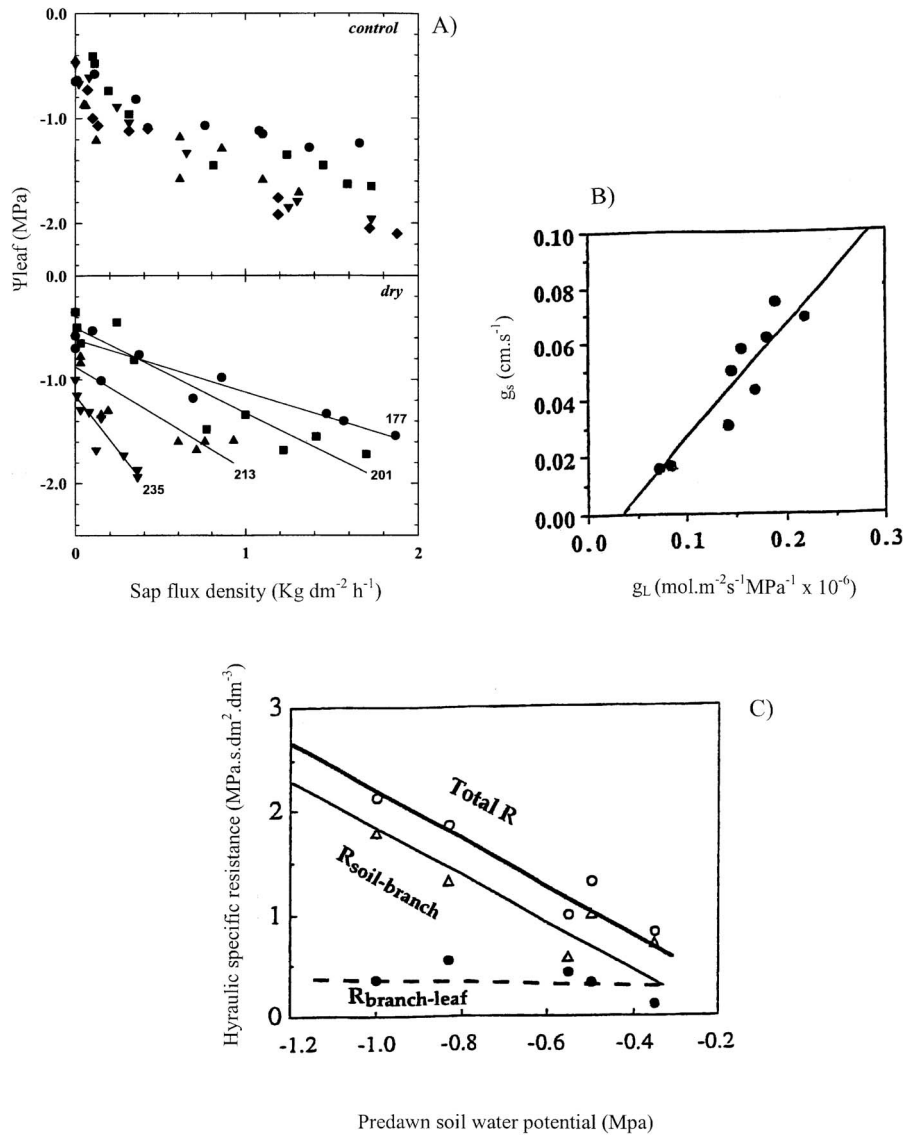


Figure 15. A: Tree transpiration (x axis) versus leaf water potential (y axis) in *Picea abies* for well-watered plant (control) and increasing soil drought (dry, numbers refer to days of the year). The relationships were rather linear, but were clearly modified by water stress: the whole plant hydraulic resistance, which is represented by the slope of the relationships, was increased during drought (from [69]). **B:** Changes in whole plant hydraulic resistance during drought. Total hydraulic resistances derived from the slopes in A, are expressed as a function of predawn (soil) leaf water potentials. Total resistance is calculated from the following expression $\Delta\Psi(\text{soil-leaf}) = F/R_{\text{total}}$ where F is the transpiration per sap wood surface; R_{total} was divided into two components: soil to branch and branch to leaf. The increase in total R with drought was located in the soil-branch pathway and very likely in the soil-root compartment (from [69]). **C:** Coupling between total hydraulic conductance g_L and stomatal conductance g_s . Midday stomatal conductances were linearly related to whole plant hydraulic conductances in the *Picea* experiment (from [68]). The decrease in hydraulic conductance during drought caused a stomatal closure and hence a reduction of transpiration.

in figure 15B, where the midday leaf stomatal conductance (g_s) is expressed as a function of the whole plant hydraulic conductance ($g_L = 1/R_{\text{plant}}$). A decrease in g_s during the drought development was coupled with a decrease in g_L . The result of this stomatal regulation is visible in figure 15: the maximum transpiration rate was reduced with increasing soil drought, and, consequently, the drop in Ψ_{leaf} was minimized. Various physiological reasons could explain why the plant tended to

minimize the drop of Ψ_{leaf} during a water shortage (to prevent loss of cell turgor for instance). Another possible reason might involve a protection against xylem cavitation.

4.3. The consequence of xylem vulnerability

When the xylem water potential (Ψ_{xylem}) drops below a threshold value (Ψ_{cav}) then cavitation occurs. It has been

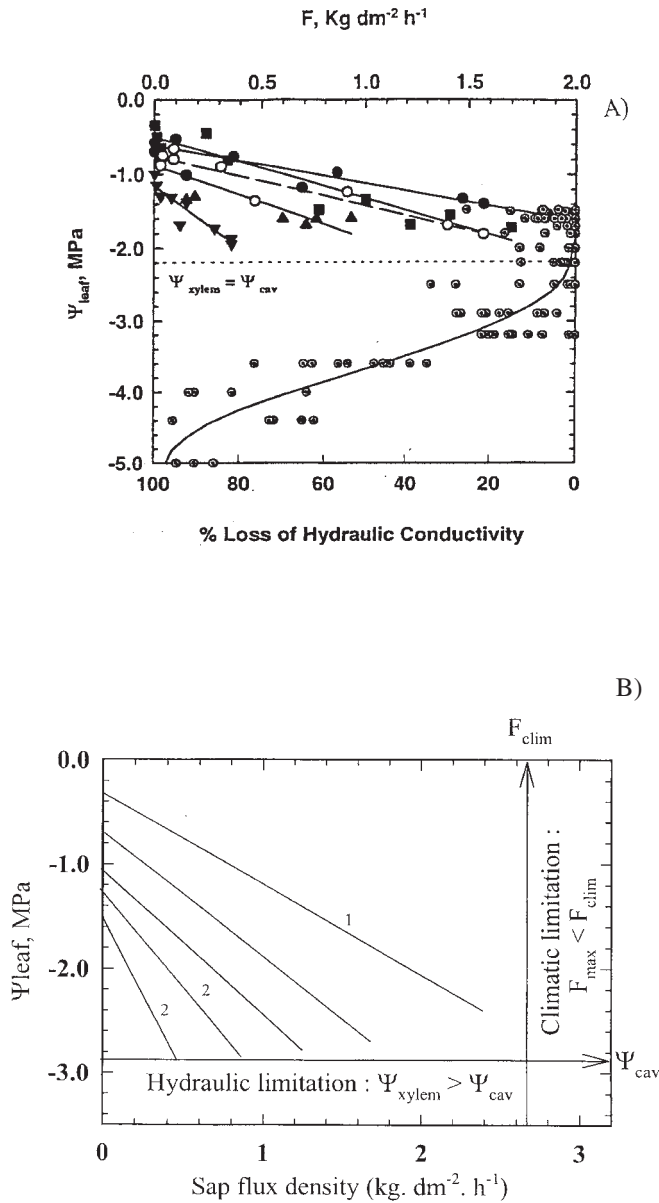


Figure 16. A: Consequences of xylem vulnerability on tree water relations. The vulnerability curve of *Picea abies* (Ψ_{leaf} vs. percent loss of conductivity) shows a steep increase of embolism for water potentials lower than $\Psi_{cav} = -2.2$ MPa (horizontal line). For well watered trees Ψ_{leaf} was close to -2 MPa but always remained above Ψ_{cav} during water stress because of a coupling between maximum transpiration rates (F , lower x axis) and whole plant hydraulic conductance (from [69], modified). **B:** Factor controlling maximum water loss. Flux/Potential relationships help in understanding daily maximum transpiration rates in *Quercus*. For well watered trees (line 1), F_{max} is probably limited by climatic conditions such as light level, air vapor pressure deficit or CO_2 concentration. However, for water-stressed trees (lines 2), whole hydraulic resistances increased (steeper slopes) causing Ψ_{xylem} to reach values close to Ψ_{cav} . The xylem vulnerability set an hydraulic limitation to oak water relations (from [20], modified).

previously demonstrated that Ψ_{cav} is determined only by ultra-anatomical properties of wall pits (figure 11). The onset of cavitation is then given by the simple physical law shown in Section 3.4. For any conduit, if Ψ_{xylem} becomes lower (more negative) than its specific Ψ_{cav} value then cavitation must occur. Therefore, Ψ_{cav} puts a functional limitation to the xylem physiology. The question now is: how close is Ψ_{cav} to the Ψ_{xylem} values experienced during a drought period?

Figure 16A compares the time-course of midday Ψ_{leaf} values with the vulnerability curve established on the xylem of the same species, *Picea abies*. It is first important to note that because of large extra-vascular leaf resistances [133, 137], Ψ_{leaf} is significantly lower than Ψ_{xylem} . However when stomatal, soil and soil-root resistances are increasing during drought periods, Ψ_{leaf} and Ψ_{xylem} agree more closely [22]. Therefore, when the soil drought was maximal, Ψ_{xylem} was very close to Ψ_{cav} (within a few bars). In *Picea*, the control of leaf water loss by an active stomatal closure prevented Ψ_{xylem} from reaching damaging values, and thus contributed to the maintenance of xylem integrity. The consequence of xylem vulnerability is thus to put an effective functional limitation to the maximum transpiration rate of a plant.

4.4. Factors controlling the daily maximum water loss

From the previous results it is now possible to see what are the main controlling factors of the daily maximum water loss (F_{max}). The maximum transpiration rate depends in the first instance on ambient climatic conditions (mainly light, vpd and $[\text{CO}_2]$). For each day there is a climatic maximum water loss F_{clim} and F_{max} can never exceed F_{clim} . According to what has been discussed in the previous paragraph, we can also define a maximum water loss (F_{cav}) based on the hypothesis that $\Psi_{xylem} > \Psi_{cav}$ to maintain the xylem integrity. Combining with equation of Section 4.1, we have:

$$\Psi_{xylem} > \Psi_{cav} = \Psi_{soil} - F_{cav} \times R_{soil-xylem}$$

or

$$F_{max} < F_{cav} = (\Psi_{soil} - \Psi_{cav}) / R_{soil-xylem}$$

where $R_{soil-xylem}$ is the hydraulic resistance to the sap pathway from the soil to any xylem segment.

To illustrate the relationships between F_{clim} and F_{cav} , a diagram (figure 16B), summarizes a data set very similar to the previous *Picea* experiment (figure 16A) but for a *Quercus* species [20]. When R_{plant} (and $R_{soil-xylem}$) is low (high soil humidity) then F_{clim} is lower than the theoretical F_{cav} . F_{max} is then limited only by external climatic conditions, F_{clim} . However, when R_{plant} increases because of soil drought, F_{cav} becomes lower than F_{clim} and an internal hydraulic limitation appears. The factors controlling F_{max} are thus both internal and external to the plant. The fact that *Quercus* and *Picea* (and probably most species) are operating close to the point of xylem dysfunction and that R_{plant} is soon and drastically increased by drought implies that these trees are rapidly facing an internal

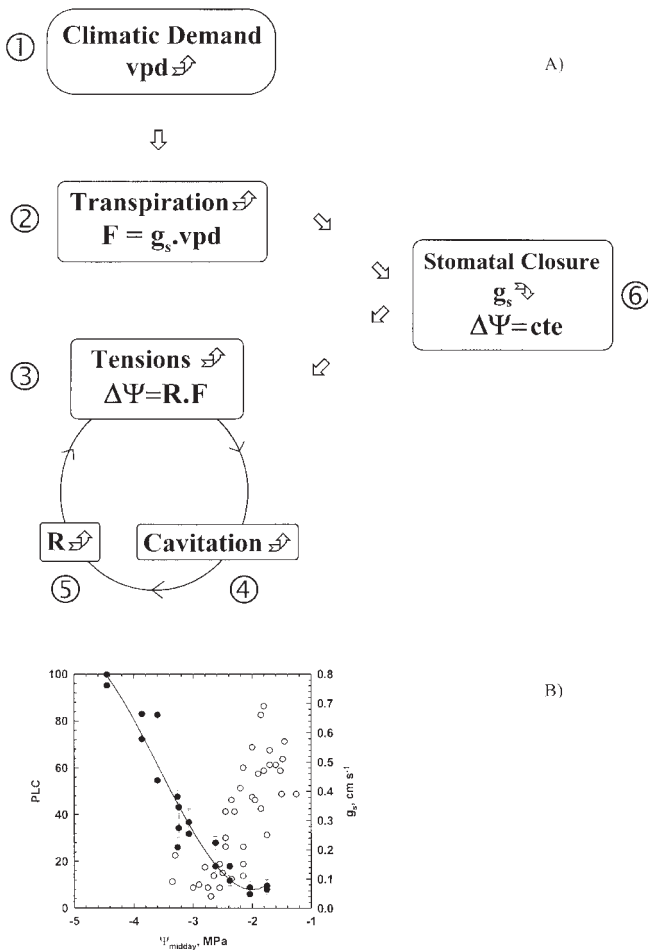


Figure 17. A: The embolism cycle: the higher the transpiration, the lower the Ψ_{xylem} , the higher the risk of cavitation; for most plant species, this “vicious” or run-away embolism circle is stopped by an active stomatal closure stomatal. **B:** This is the case for *Quercus petraea*: stomata (open symbols) are completely closed before xylem embolism develops (closed symbols). More explanations in the text (from [20]).

hydraulic limitation which induces a stomatal closure preventing a “runaway embolism” [125].

4.5. Stomatal closure can prevent “runaway embolism”

When the blockage of xylem conduits through embolism leads to reduced hydraulic conductance an increase of tension is required in the remaining vessels to maintain the same water flow to leaves; then more embolism and tension will be generated in a vicious circle called “runaway” or “catastrophic embolism”. The cycle stops only when the xylem is fully embolised unless stomatal closure reduces the transpiration and hence the drop in Ψ_{xylem} . Figure 17A illustrates the process. High climatic demand (large air vapor deficit,

vpd, ①) causes high transpiration rates F ($F = g_s \times \text{vpd}$, where g_s is the stomatal conductance, ②) which may induce xylem water potential ($\Delta\Psi = R \times F$, where R is the plant hydraulic resistance, ③) lower than the cavitation threshold. Cavitation of the conducting elements ④ is followed by embolism causing loss of hydraulic conductivity ⑤, lowering furthermore the water potential ③ then causing more cavitation ④. This is the “runaway embolism circle”. It is supposed that for most plant species, this circle is stopped by an active stomatal closure ⑥ that reduces transpiration and keeps xylem potential above the cavitation threshold. Figure 17B shows the case for *Quercus petraea* [20]: stomata are completely closed (open symbols) before xylem embolism develops (closed symbols).

Stomatal closure appears then as a key mechanism in the protection against lethal xylem dysfunction’s. Experimental evidence for this concept is difficult to obtain because stomata close efficiently, which stops the cycle. Runaway embolism is therefore a kind of “limiting concept” deduced from models of the dynamics of water flow and xylem blockage [61, 124]. Sperry et al. [114] extended this concept by including the entire soil-leaf continuum and the combined effects of hydraulic failure (for a critical value of Ψ) which can happen at the soil-root contact (rhizosphere) or within the vascular system. In particular, they showed two important features. When the root-to-leaf area ratio is low, the soil has a coarse texture, and the involved plant species is resistant to cavitation, then the weak point is at the soil-root contact. In contrast, when the root to leaf ratio is higher, the soil has a fine texture and the species is vulnerable to cavitation, then the weak point is the vascular pathway. It is worth noting, however, that in this model, the radial resistance of roots is not taken into account. Hacke et al. [52] argued that because this model gives “a reasonable fit to the seasonal pattern of transpiration and water potential data, ..., by implication [it] suggests that changes in hydraulic conductance caused by processes not modeled, such as changes in radial conductance of roots, ..., were less important to the overall continuum conductance than changes modeled in soil and xylem”. However, compensation effects of processes not taken into account in this model could lead to the same conclusion. In other words, this model as useful as it may be, does not necessarily prove that the radial resistance could not play an important role in particular situations. For example, it has been shown in desert plants that the radial resistance increases considerably during soil drying, as soon as the soil water potential starts to be lower than the root water potential [86]. This increase of the radial resistance (probably involving aquaporins, [77]) prevents root dehydration. Furthermore, it is important to remember that the few results reporting comparison between radial and total root resistance (see review article [117]), all concluded that the radial is larger than the longitudinal resistance. As a consequence, embolism in the root xylem should be quite important before affecting the global root resistance. In the present state of our knowledge, general conclusions regarding the respective importance of

radial and longitudinal root resistance are premature. Large differences probably exist according to types and age of roots, species and environmental conditions.

Cochard et al. [21], studied the water relations of a *Populus* hybrid (*trichocarpa* × *koreana*) known to lack efficient stomatal closure in the presence of soil water stress. It was actually found that only stomata in mature leaves were unresponsive to water stress. Stomata from young expanding leaves were still responsive but lost their aperture control when aging. Soon after water withdrawal, high degrees of embolism appeared in mature leaf petioles and shoot internodes, but embolism steadily declined toward shoot apices. In other words, the better the control of stomatal aperture, the lower the degree of embolism. Where stomata were not capable of reducing leaf water loss, embolism occurred and leaves eventually fell. The “safety margin” for stomata seems very narrow because maximum loss of conductivity were noticed for leaves deviating of about 30% from the optimal complete closure. A similar result has been found on *Betula occidentalis* [111].

This point has been studied within different species by Sperry [115], who gives an estimate of the safety margin by comparing the xylem water potential Ψ_{CT} , at 100% loss of conductivity with the actual minimum xylem water potential Ψ_{min} experienced by 73 species. There is a significant correlation between Ψ_{CT} and Ψ_{min} . Plants that are more drought resistant are also more resistant to cavitation. The safety margin, based on the difference $\Psi_{min} - \Psi_{CT}$ ranges from 1 to 0.5 MPa. As pointed out by Sperry: “These and other observations suggest that much of the stomatal closure observed during drought is a result of the amplifying effects of declining of the liquid hydraulic conductance from soil to leaf rather than a strictly proportional response to drying soil”. Results [28] with walnut trees submitted to water stress suggest that stomata were not responding to changes in Ψ_{soil} , root or shoot resistance per se, but rather to their impact on the rachis or leaf water potential. It can be concluded from all the published results that if a kind of coupling does exist between hydraulic and stomatal conductances to preserve the possibility of water flow from the soil to the leaves, the exact mechanism by which this coupling is regulated is still a matter of discussion. As pointed out by Comstock [29bis], “major questions remain unanswered on how water stress signals perceived at root and leaf locations are integrated at the guard cell to control stomatal behavior”.

5. CONCLUSIONS

The hydraulic architecture approach is certainly the major new trend in tree water relations, which has emerged in the last decade. It brings together three different and so far very often completely separated ways of studying plant water relations. The first is the very classical and well-established Van den Honert approach (the use of the electrical analogy to deal

with water transfer through the soil-plant-atmosphere continuum). The second is the application of the recently revisited and very much improved cohesion-tension theory. The last is quantitative anatomy of vessels and tree branching considerations [130, 133]. Although this approach is still very young it has already renewed many aspects of the way we look at tree water relations. It has already given new and valuable answers to old questions concerning the significance of ring and diffuse porosity [57]. It can be predicted without risk that in the near future this approach will continue to develop.

However, much more work should be done on species-specific xylem anatomy and especially on the changes with time in the more or less integrated network of connections between the roots and branches of the same tree. Recent works of André [8, 9] and Fujii and Hanato [46] have revealed many important new anatomical features of the xylem anatomy and showed how much our knowledge in this domain can be improved by appropriate techniques.

Likewise, Hacke et al. [53], have given evidence for an interesting quantitative anatomical feature. They showed a correlation between wood density and cavitation resistance: the more drought-tolerant the plant, the more negative the xylem pressure can become without cavitation, and the greater the wood density. It seems therefore that wood density is not only related to support of the plant against gravity, wind, snow, etc., but also to support the xylem pipeline against the collapsing by large negative pressure.

Concerning cavitation and drought-induced embolism, we have now well founded explanations. Nevertheless many questions need additional work. For example, does the presence of other substances within the sap (ions, inorganic acids, hormones, etc.), the variations of pH or other physical-chemical characteristics have an effect on cavitation? If, without doubt, cavitation in most of the cases, is closely linked to pit pore's size (“air seeding” explanation) is it the only way cavitation can occur? Which quantitative anatomical features will be necessary to model a vulnerability curve? The determining factors of the propagation of cavitation within a branch are also still very poorly known, just like those that determine and control of pit pore size and pit pore distribution. If genetics play, more or less directly, a part in the determination of this size it is also probable that either internal (physiological status at the time when vessels form, mechanical properties of the pit membrane) and external (climatic, etc.) conditions may be also important.

From the point of view of ecophysiological considerations, h.a. concepts are used in two different domains: drought resistance and freezing-induced xylem dysfunction. For drought resistance, there are increasing evidence that plant ability to lose water from leaves is also associated with its ability to supply leaves with water. Under these conditions, the specific relationships between the plant hydraulic conductivity and the tension resulting from cavitation leads, ipso facto, to the limits on the range of tension over which gas

exchange can occur and makes clear the fact that large differences in drought tolerance between species correlate with these hydraulic limits. Besides, taking into account the variation of conductance in the two “bottlenecks” of the soil-plant continuum (soil-root zone and vascular pathway) has led to new suggestions for explanations concerning the possible linked evolution between root-shoot ratios and cavitation resistance in response to soil type and water availability: “Plants should be hydraulically compatible with their soil” [114]. This statement also expands the discussion on stomatal regulation. The process (chemical or/and hydraulic signal, ..., or something else) which allows the coupling between stomatal conductance and hydraulic conductance can be compared to a safety bell: although always present, it is the determining factor of stomatal regulation only when events in soil and climate threaten the functioning of the conducting system. Beside, as we know, many other factors influence the stomatal conductance. The problem is nevertheless to understand how these different kind of regulations work together. From this drought adaptation point of view, the already collected results (Cochard, unpublished) concerning the stomatal and hydraulic conductances relationships, suggest a first schematic classification of the tree species into three major groups (figure 18). Species from the first, and apparently most important group, at least among the experienced species, control loss of their hydraulic conductivity by stomatal closure: the value of Ψ_{xylem} which provokes 10% loss of hydraulic conductivity also lead to a 90% of stomatal closure. Beside two other “strategies” seem to occur. One is formed by species (PP: *Prunus persica*) which maximizes stomatal conductance: for the Ψ_{xylem} which lead to 10% loss of conductivity their stomatal closure is much less than 90%. The other (CA: *Cupressus arizonica*) has the opposite behavior: it minimizes the loss hydraulic conductivity by closing its stomata at a Ψ_{xylem} much higher than the one required to provoke 10% loss of hydraulic conductivity.

The second closed direction in which h.a. concepts are used and very useful is freezing-induced xylem dysfunction. In this regard, it is a reasonable temptation to say that there is a functional connection between the dominance of conifers within the very cold areas and the fact that, bearing very narrow tracheids, they are enable to resist to freeze-induced embolism, in opposition with broadleaf trees. Therefore as for drought resistance it seems that another anatomical feature is a key point to understand the resistance of trees to frost.

Progress in h.a. are also possible in a quite different direction: the partition of water fluxes between the different parts of a tree under given conditions of transpiration. Until now h.a. has given a mapping of the different hydraulic capabilities of the conducting system. It is like having the quantitative description of the hydraulic resistances of the tubing from an irrigation system: this does not give you the distribution of actual flows within the different parts of the system, which depends on the water headings (equivalent to the water poten-

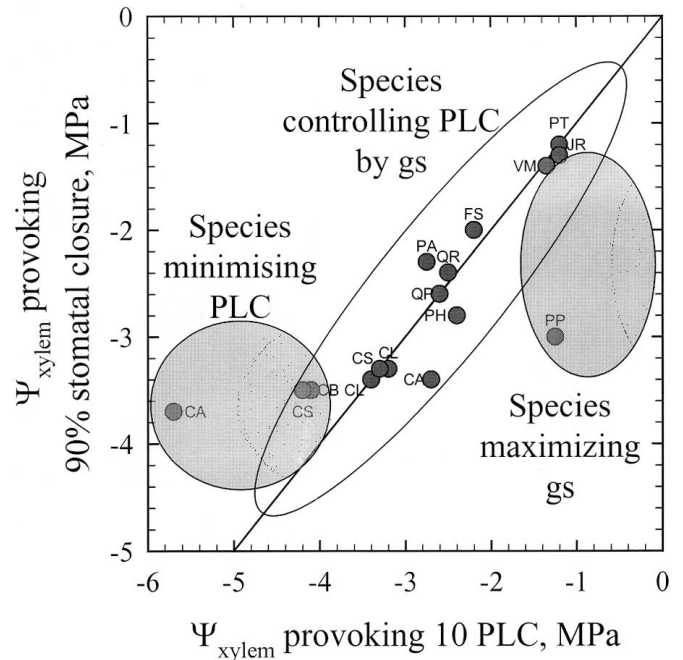


Figure 18. Hydraulic architecture of tree and drought. Three main groups can be distinguished. In the first, most important, trees control extension of embolism by stomatal closure. In the second, trees favour a large stomatal conductance g_s ; in the last they seem to close their stomata before a significant degree of embolism can occur. (from Cochard, unpublished collected results): PT = *Populus trichocarpa*, [21]; JR = *Juglans regia*, (Cochard and Améglio, unpublished); VM = *Vaccinium corymbosum*, [6]; FS = *Fagus sylvatica*, [24]; PP = *Prunus persica*, [4]; PH = *Pinus halepensis*, (Froux and Huc, unpublished); QR = *Quercus robur*; QP = *Quercus petraea*, [20]; PA = *Picea abies*, [69]; CL = *Cedrus libani*, (Ladjal and Huc, unpublished); CA = *Cedrus atlantica*, (Froux and Huc, unpublished); CS = *Cupressus sempervirens*, (Froux and Huc, unpublished); CB = *Cedrus brevifolia*, (Ladjal and Huc, unpublished); CA = *Cupressus arizonica*, (Froux and Huc, unpublished).

tial differences) across the system. In order to have a better understanding of the water functioning of a tree we now need to get a spatial mapping of the real fluxes which flow within the various parts of a tree under given boundary conditions. As said in Section 2.2, this field has been opened, among others, by Roach [97]. To our knowledge, since that date, few attempts have been made to determine the patterns of water movement in trees, by using dyes as Roach did [145, 152] or methods allowing the quantification of flow along a branch or a root, or a sector of a trunk [48, 83, 140]. In other words we have still a very elementary knowledge of the distribution of absorption among the roots, how the water flux from any one root spreads out within the growth rings, thus reaching not only a single branch but a large part of the crown [154], how the distribution of fluxes along a tree is affected by pruning practices or by the decay of a major root, how the patterns of water movement within a tree change with soil drying and

climatic conditions. A significant progress on that field will be realized by improving our knowledge about the anatomical connections between the root system and the shoot. Another most promising direction of research is the one where hydraulic architecture and “botanical architecture” meets as said, thirteen years ago by Zimmermann: “It will be of considerable interest to link hydraulic architecture types to the morphological tree-classification of Hallé Oldeman and Tomlinson [54], although one must realize that the morphology is an expression of all functional adaptations, not only the hydraulic one. It will also be of considerable interest to study developmental events such as the change of hydraulic properties of a lateral as it assumes the function of the main stem in sympodial branching, etc.” [154]. We can formulate other questions: how does the hydraulic conductance of axes change with aging? Do the reiterated complexes have specific hydraulic characteristics? If the crown of an old tree is a true colony of individuals of various size, does this mean that these individuals present also some hydraulic specificity? There is a vast, open and promising field of research. Among different questions, this direction of research will probably help to solve the present debate on how hydraulics limits tree height and growth [13, 99].

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APPENDIX: WATER POTENTIAL, PRESSURE, TENSION

Either in the text or in the figures of this introduction, several different expressions have been used concerning the state of water in trees: water potential, xylem water potential, tension or pressure profiles. For the reader in a hurry it can be said that these different terms are, in the present context, more or less equivalent. For the reader not familiar with the water-plant terminology, and who wants to understand a little more, the following explanation should be of some help.

There are different possible definitions of the water status in a plant. Two types are in major use. The first is based on the mass of water present (ex.: the water content), the second on the energetic status of water. Water potential is a measure of the latter. Water potential Ψ is an intensive (i.e., a quantity which is not dependent of the amount of water present on the plant sample, unlike the water content which is an extensive variable) thermodynamic variable. It is derived from the classical chemical potential μ , which represents “the work involved in moving one mole (18 g) of water from a pool of pure water at atmospheric pressure, at the same temperature as the system under consideration, and at the zero level, to some arbitrary point in a system” [85]. It determines, under certain conditions, the water movements between the soil and the roots, or two different parts of the same plant, or the leaves and the atmosphere for example. The water potential, Ψ , of the water present within a system containing water (soil, plant tissue, wood, fruit, seed, paper, etc.), is given by the following expression:

$$\Psi = (\mu_w - \mu_w^0)/V_w = P + \Pi + \rho_w \times g \times h$$

where Ψ is the water potential in bars, or megaPascals, MPa. (1 bar \approx 1 atmosphere; 1 MPa = 10 bars); μ_w^0 is the chemical potential of water in the standard status (i.e., pure water at atmospheric pressure and same temperature as the system being considered); μ_w is the chemical potential of the water in the plant; V_w is the molar volume of water (18 cm³ per mole). P is the hydrostatic pressure (or hydrostatic potential, or pressure potential), Π the osmotic potential (osmotic potential = – osmotic pressure). The third term is a gravitational term, which accounts for the vertical position above a standard level. As work must be performed to raise an object in the gravitational field of the earth, the vertical position affects the chemical and thus the water potentials. If water moves 10 m vertically upward in a tree, the gravitational term changes: its contribution to the water potential is 0.1 MPa. In other words, in a standing hydrostatic 10 meter high column of water the difference of water potential, only due to the difference of elevation, is 0.1 MPa. Therefore this is a lower limit (named gravitational potential gradient in figure 7A) for tension gradients within a tree and *Schefflera morototoni* (figure 8) provides an example of an extremely efficient conducting system.

According to the above equation, Ψ is expressed as energy per unit of volume, i.e. as pressure. Therefore Ψ units are pressure units. A difference of Ψ between two locations in hydraulic continuity indicates that water is not in equilibrium, so there will be a tendency for water to move from the place where Ψ is high to a place where Ψ is lower.

When the water content of a tissue sample is maximal, this state is called that of full turgidity; the corresponding water potential is zero. All other water status situations, with lower water content in the tissue, correspond to negative values of Ψ . In plants, most of the time, Ψ is negative. Under these conditions water will flow from negative to more negative Ψ .

In the equation above and for a cell, P is the pressure (greater than atmospheric pressure) exerted by the cell wall within the cell. It is a positive term. However for a conducting element, P is a tension (a subatmospheric or more generally, a negative pressure). Therefore for a vessel or a tracheid, P is negative! Π is the osmotic potential of the cell sap; with the convention of sign used in the above equation (+ Π) it is negative.

Let us give an example of the application of the above equation for a cell and for a conducting element. For a root or leaf cell not at full turgidity, P is positive (+7 bars) and Π more negative (–12 bars). The resulting Ψ is negative: $\Psi = 7 + (-12) = -5$ bars. If the cell is at full turgidity, $P = -\Pi$ and $\Psi = 0$. For a conducting element the tension can be, –10 bars for example. But the osmotic potential of the xylem sap is generally very close to zero, –0.5 bars for example. The resulting Ψ is also negative: $\Psi = -10 + (-0.5) = -10.5$ bars. As can be seen for the vascular elements, Ψ and P are very close. Therefore one can often confuse both terms and approximate the total water potential of the xylem sap by its tension.

Concerning “tension” we point out the problem of sign. Most people in the literature refer to tension as a positive number, e.g. a xylem tension of +1.5 MPa equals a pressure (or water potential) of –1.5 MPa. So tension increases as water potential or pressure potential decreases. We therefore accept this conventional use of the word “tension” which is satisfying from the semantic point of view. Nevertheless we want to express our feeling that such a choice is at the same time confusing for non-specialists and not consistent from the physical point of view for the following reasons:

- The tension of the water in the xylem is really at a negative pressure; by contrast, the turgor pressure is really a positive pressure

exerted by the cell wall. The physical state of water at +5 bars (0.5 MPa) is different from the state at -5 bars. No cavitation and embolism will occur at positive pressure; they can appear in water under tension. Why is this important difference cancelled by considering the tension as a positive number, especially if, at the same time, it is recognized that tension is a negative pressure?

- This difference between positive pressure and tension (negative pressure) is basic for distinguishing the effects of root pressure and of transpiration on the xylem sap and for understanding the difference between phloem and xylem transport.

- As outlined above, since the osmotic pressure of the xylem sap is often very low, the water potential of the xylem can be approximated by its tension; it is confusing then to express this approximation as a positive value. Furthermore with this convention, we must also change the sign in front of P in the above equation: “-” if P is a tension, “+” if P is a turgor pressure!

From the understanding point of view, the simplest convention is the following. A negative water potential is called a tension (we will speak of a tension of -1 MPa); a positive water potential is called a pressure (we will speak of a root or stem pressure of 0.1 MPa).

Due to this, in this paper we have avoided use of the term “tension” except when no confusion was possible.

For additional information see more general reviews [14, 34, 116, 121] or treatises [63, 85].

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