



What Science
Can Tell Us

Water for Forests and People in the Mediterranean Region

– A Challenging Balance

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How Plant Species Cope with Water Stress

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A lack of water poses stressful conditions for plants. Here we will discuss adaptations to the deficit of water in the soil. Sufficient water in the soil is necessary for plant survival, as maintaining the water flux from roots to leaves insures sufficient cell turgor for growth, nutrient turnover and stomatal opening to allow gas exchange.

Plants have developed various strategies, at different time scales, to cope with reduced water availability in the soil: phenological adjustments, water status control, morphological and anatomical features which may vary between and within species.

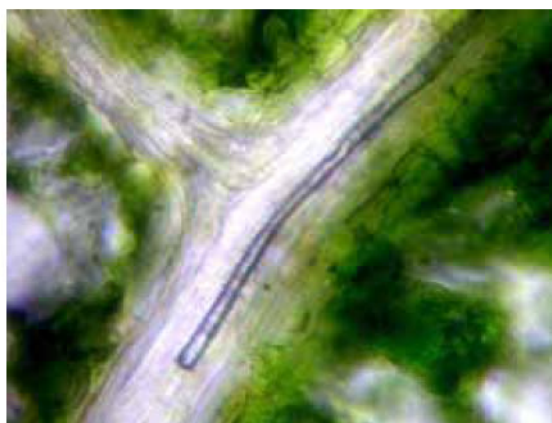
Herbaceous plants can **escape** periods with reduced water availability during the annual cycle by completing the growth / flowering / seed production cycle entirely before the onset of a drought period. Perennial and woody plants, such as forest trees, cannot completely escape drought periods; however, the adjustment of budburst, leaf development and drought induced leaf shedding can limit the impact of drought on the growth cycle, as has been shown for different deciduous and evergreen Mediterranean oak species.

Drought resistance in forest trees is thus mainly a question of survival and competition within an ecosystem; in forestry, however, it is also a question of maintaining growth. Drought resistance strategies can be grouped into **avoidance** and **tolerance** mechanisms, where drought tolerance mechanisms can be divided into **dehydration avoidance** and **dehydration tolerance**.

Maintaining sufficient hydration of tissues is one strategy with which to **avoid** drought stress, and can be measured through the water potential of tissues. Stomatal closure with the onset of drought will conserve water in the plant (measured as water potential) and thus protect it; however, productivity decreases as less carbon can enter the plant.

Another strategy is to **tolerate** the decreasing water potential of the tissue where stomata are kept open and productivity does not decrease. This is achieved by plants either through increasing **dehydration tolerance** by osmotic adjustment in the cells, anatomical properties of the water conducting elements (e.g. loss of conductivity) allowing a higher tension on the water column; or by increasing **dehydration avoidance**, for example by reducing total leaf surface, stomatal density, increasing leaf thickness, leaf cuticular and sclerophylly of leaves as well as increasing below ground mass fraction (root/shoot ratio) and rooting depth.

Figure 37. An air bubble trapped in a xylem vessel of a tree leaf vein. During water stress, the tension in the xylem sap increases and cavitation can occur. This provokes the entry of air in the xylem conduits which ruptures the water supply to the leaves and may eventually lead to plant death by desiccation. Mediterranean tree species are much more resistant to cavitation than other species, which partly explains why they can better cope with intense water stresses. Photo by H. Couhard.



While some of these strategies require time to develop, especially morphological and anatomical adjustments, other strategies involve rapid responses. Some of the most rapid responses of plants to acclimate to a soil water deficit are stomatal closure and osmotic adjustments. This is followed by **morphological adjustments** such as increased root growth and for continuous growing plants changes in stem and leaf morphology. The exploration of available soil moisture is especially important for Mediterranean plants and important differences between species exist. For example, it was shown that *Quercus ilex* had a deeper root system compared to *Q. suber* and that *Q. ilex* maintained root growth during a drought compared to *Q. cerris* and *Q. frainetto*. Significant differences in root biomasses were reported for four different Mediterranean pine species with different degrees of drought tolerance. However, differences do not only exist among different species – they also exist within a given species where genetic variation results in a diversity of responses. For example, significant differences have been shown for the biomass allocation to the roots compared to the shoots among *Pinus pinaster* families and among *Cedrus libani* provenances, where provenances from the dryer sites had larger root systems.

In the following, we will clarify two particularly interesting traits: species differences in embolism in water conduits during drought stress and the diversity of water use efficiency within species.

Under pronounced water stress, an **embolism in the conducting vessels** – preventing the sap to ascent from soil to leaves – may occur and lead to tree and branch dessication and mortality. Thresholds of xylem critical pressure related to embolism are highly variable between species – Mediterranean species being among the most drought resistant.

As indicated above, sap in the xylem conduits is under large negative pressure (=tension). Water is physically metastable under this condition, and may change to a more stable gaseous phase by **cavitation**. Cavitation, in turn, provokes an **embolism**, i.e. it breaks the integrity of the water columns in the xylem pipes (Figure 37) and thus impairs the mechanisms that permit sap to ascent from the soil to the leaves. The physiological consequences of cavitation are of great significance because it may eventually lead to shoot or tree mortality by desiccation. This explains why much effort over the past three decades has been devoted to the characterisation and understanding of cavi-

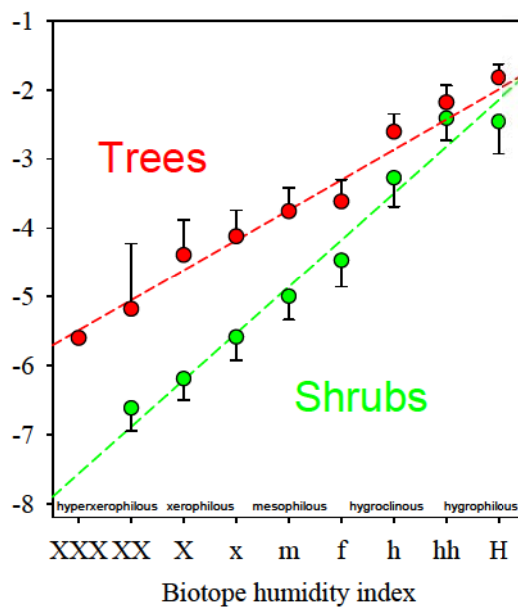


Figure 38. Correlation between the xylem vulnerability to cavitation of nearly one hundred woody species of the French flora and the humidity index of their habitat. Species cavitation resistance is estimated by the xylem pressure provoking 50% of cavitation (P_{50} , MPa). The biotope humidity index is from Rameau et al. (1989, 1993, 2008). Species from dry habitats are clearly more resistant to cavitation. In a same habitat, shrubs are more resistant to cavitation than trees, probably reflecting a more shallow root system in the former species.

tation in trees. These studies clearly show that cavitation only develops when the xylem pressure drops below a critical value P_{cav} . P_{cav} is probably one of the most variable physiological parameters across tree species.

The most vulnerable species (like *Salix* or *Populus*) have P_{cav} values as high as -1.5 MPa. In contrast, the most cavitation resistant species (like *Cupressus* or *Callitris*) have P_{cav} values below -10 MPa. Such a large range has profound implications on species water relations and their responses to water stress. The xylem conduits of species with high P_{cav} are intrinsically unable to support high water stress levels. Therefore, these species have to close their stomata early during a drought to avoid deleterious embolisms from developing and are thus **drought avoiding**. In contrast, species with low P_{cav} can tolerate the presence of more intense water stress and tend to be more **drought tolerant**. In both cases, a remarkable coordination between xylem and stomatal functions can be observed: stomata close to control xylem pressure, allowing to keep its values slightly above P_{cav} .

The high drought resistance of Mediterranean tree species comes at the cost of high wood densities and low growth rates.

The behaviour of many Mediterranean species is quite surprising at first sight. As a rule, they are very resistant to cavitation (Figure 38) and tend to display the most negative P_{cav} values measured so far. Nevertheless, the behaviour of their stomata does not differ much from the behaviour of species with higher P_{cav} values. In other words, stomata close well before xylem pressures reach the critical P_{cav} values. They are both avoidant in terms of water loss and tolerant in terms of xylem function. As a result, the hydraulic safety margin of Mediterranean species is higher than in more temperate species. This strategy largely explains why Mediterranean species are highly drought resistant. However, there are costs associated with this behaviour. First, stomata can remain open only during a

Box 8. Investigations on drought adaptation related traits: some results

Traits related to drought adaptation were studied in the provenance or population trials of most of the major Mediterranean forest tree species (e.g. *Pinus halepensis*, *Pinus brutia*, *Pinus pinaster*, *Pinus nigra*, *Pinus canariensis*, *Pinus pinea*, *Juglans regia*, *Castanea sativa*, *Quercus suber*, *Quercus coccifera*, *Quercus ilex*, *Cedrus libani*) and concerned survival; growth; the biomass of different compartments; wood anatomy related to water conducting elements; water use efficiency; stomatal conductance and density; CO₂ assimilation; plant water status; leaf osmotic adjustment; leaf anatomy; antioxidant status; hydraulic conductivity and loss of conductivity. Sometimes, trait measurements for one environmental condition are not sufficient to characterise population differences, although when a plasticity index is calculated for different environments, then differences might be determined. This was the case for *Pinus halepensis*, where saplings from a Garrigue site showed significantly higher plasticity compared to a rock site; this, however, was not the case for *Quercus coccifera*.

Genetic variation was also studied using neutral genetic markers: for *Castanea sativa*, a study detected a geographical pattern that was linked to rainfall; for *Pinus pinaster*, *P. nigra* and *P. uncinata*, intra-population genetic diversity was linked to summer precipitation.

short part of the “growing” season, i.e. when water is available. This may imply that these species must maximise their carbon gain during this period, which comes at the cost of poor water use efficiency. The second drawback is that the construction cost of xylem conduits with low P_{cav} is very high. This is because conduit walls must be mechanically reinforced to cope with the high xylem tensions, requiring even more carbon resources.

Adaptive traits for drought increase the chance of survival under soil water deficit. Their variations between and within species (among populations) allow the selection of better-suited seed sources for plantation.

All these traits discussed above can be called “adaptive” for drought if they increase the chance for survival under soil water deficit conditions. Differences in adaptive traits between species are one cause for observed species distributions, for example along gradients from mesic to more xeric environments. However, also within species, diversity can exist for a given trait, resulting from differences in the genetic background. This genetic diversity provides the basis for adaptation of populations (plants within a common environment) to their local environmental conditions. The genetic background of each individual is called its genotype. Adaptation is a process that will change the composition of different genotypes within a population through natural selection over generations, thus creating differences among populations. Observing trees grown from seeds from different populations in one or several common environments (e.g. provenance trials) is a means to detect such differences and thus populations that are better adapted to certain environments than to others. This can result in direct recommendations for seed source classification and planting strategies.

Diversity has been shown within different Mediterranean plant species in their capacity to accumulate biomass through photosynthesis for a given amount of water used, referred to as **Water Use Efficiency (WUE)**. This opens the way to potential applications in breeding and silviculture.

Box 9. A genetic approach to Water Use Efficiency (WUE)

Only few studies have further dissected this diversity for WUE in Mediterranean forest trees. This can be done with controlled crosses, to either estimate heritability or to dissect the observed variability within a full-sib family into Mendelian inherited components, i.e. Quantitative Trait Loci (QTL) detection. The first QTL suggesting a genetic determinism for WUE in Mediterranean forest tree species was found for *Pinus pinaster*. Another study detected 17 QTL for WUE in *Castanea sativa*, explaining a low to moderate proportion of the total phenotypic variance. QTLs were distributed throughout the whole genome. However, when comparing these QTL to QTL for WUE in *Quercus robur*, for which an oligogenic control was shown with few major QTL; however, no QTL co-localised between the two species. Although genetic maps also exist for families of *Pinus halepensis* and *Juglans regia*, no QTL detection studies have been published to date. For *Pinus pinaster*, QTL have also been detected for growth and wood properties. The QTL detection studies cited above are either based on optimal conditions or natural plantations with no published results to date on QTL detection under drought conditions. Such QTL are a starting point to characterize both functional and gene candidates. Genes related to drought stress can then be used for population genetic studies, elucidating patterns of natural selection and adaptation, which represent the major resource for a durable, adaptive silviculture.

Water use efficiency (WUE), the ratio of accumulated biomass for a given amount of water used, can be estimated for large numbers of samples by measuring the carbon isotope composition (^{13}C) of plant material (leaves, wood, wood extracted cellulose). Differences among populations in WUE have been found for *Pinus halepensis*, *Pinus pinaster*, *Juglans regia*, *Castanea sativa*, *Quercus ilex* and *Cedrus libani*. These population differences across many species suggest that WUE is a trait which has been selected in specific environments and is thus probably important for fitness and survival. However, WUE is not necessarily a trait directly linked to drought stress resistance, but needs to be interpreted within specific environmental situations. Classical examples are found for *Pinus pinaster* and *Castanea sativa* where trees from *a priori* dryer provenances showed lower water use efficiency. WUE is a composite trait whose full understanding requires deeper exploration, in particular through genetic studies (see Box 9).

Recommended reading

- Baquedano, F. J., Valladares, F. and Castillo, F.J. 2008. Phenotypic plasticity blurs ecotypic divergence in the response of *Quercus coccifera* and *Pinus halepensis* to water stress. *European Journal of Forest Research* 127: 495–506.
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