WATER RELATIONS AND HYDRAULIC ARCHITECTURE OF PEACH TREES UNDER DROUGHT CONDITIONS

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Abstract

In this study we analyzed the vulnerability to embolism and the hydraulic architecture of peach trees. This species was particularly vulnerable to embolism. Vulnerability curves, established in the laboratory by introducing artificial embolism by application of positive pressure, showed that embolism significantly developed in stems when xylem water potentials felled below -1.5MPa and were fully embolised at -3.0MPa. Fifty percent loss of hydraulic conductivity was obtained when xylem water potentials became lower than -2.0MPa. At this point, the stomatal conductance was just reduced to 40 % of its maximal. In the field, under drought conditions, we measured significant degrees of embolism in stems, although stem embolism was limited by leaf fall. After irrigation, stem embolism was not repaired. We also analyzed the impact of new shoot formation on tree hydraulic architecture.

Résumé

Dans cette étude, nous avons analysé la vulnérabilité à l'embolie et l'architecture hydraulique de pêchers. Cette espèce y est particulièrement sensible. Les courbes de vulnérabilité, établies en laboratoire en introduisant un embolus artificiel par application de pressions positives, montre que l'embolie se développe significativement dans les tiges quand les potentiels hydriques du xylème tombent au dessous de -1,5MPa et l'embolie est totale à -3,0Mpa. Cinquante pourcent de perte de la conductivité hydrauliques sont obtenus quand les potentiels hydriques du xylème deviennent plus faibles que 2,0MPa. A ce moment, la conductance stomatale, est juste réduite à 40% de son maximum. Au champ, sous des conditions de sécheresse, nous avons mesuré des degrés significatifs d'embolie dans les tiges, quoiqu'ils en aient été limités par la chute des feuilles. Après irrigation, l'embolie des tiges n'est pas réparée. Nous avons analysé aussi l'impact de la formation de nouveaux rameaux sur l'architecture hydraulique de l'arbre.

1. Introduction

In plants, water moves from the soil to the leaves along a negative water potential gradient (Ψ, MPa) caused by frictional hydraulic resistances all through the sap pathway. Higher resistances result in lower water potentials for comparable transpiration rates. Low water potentials are well known to impair plant physiology because they can reduce growth rates, promote stomatal closure, and induce leaf turgor loss or xylem cavitation. In many plants, stem water potential, Ψ_x, regularly drops near the point of xylem dysfunction, $\Psi_{Cavitation}$, suggesting that cavitation is limiting (Tyree and Sperry, 1988 ; Sperry and Pockman, 1993) and this suggests that stomata may play an important role in controlling the development of xylem embolism. The first objective of this study was to analyze the role of stomata in controlling the development of xylem embolism.

In order to understand the water relations in peach crown it is thus important to consider hydraulic resistance measurements together with water fluxes and transpiration. However, it is only since the introduction of the High Pressure Flow Meter (Tyree *et al.*, 1993b) that direct and reliable estimates of whole plant hydraulic resistances are possible. The second objective of this study was to establish the hydraulic architecture of peach crowns, *i.e.*, to analyze the variation in hydraulic resistances within and between branches. In peach, buds can remain « dormant » on a trunk and develop only after several years. These shoots (sylleptic shoots) are usually more vigorous than older branches. We paid a special attention to these different types of branch to find out if high growth rate was correlated with some hydraulic parameters.

2. Materials and methods

Experiments were conducted in 1996 on 2-yr old Peach tree (cv O'Henry). Ten potted trees were transplanted to 50 dm^3 containers in 1995 in a soil consisting of 20 % clay soil, 40 % peat moss and 40 % light lava gravel. Five trees were subjected to drought. Control trees were irrigated daily. Midday leaf water potential, Ψ_{Min}, was measured with a pressure chamber and midday stomatal conductance with a Li-cor 1600 porometer on sun-exposed leaves. Percentage loss of hydraulic conductivity (%LHC) was measured on stems by the method described by Sperry *et al.*, (1987). The vulnerability curve (VC), (percentage loss of hydraulic conductivity versus the minimum water potential experienced by the stems) characterizes the effect of embolism on hydraulic conductivity. VC was obtained by introducing artificial embolism by application of positive pressure. The positive pressure needed to blow air through the largest water-filled pores is the same in magnitudes, but opposite in sign to, that needed to cause embolism during drought stress (Cochard *et al.*, 1992). Branch hydraulic resistance, R_{branch}, was measured as described by Tyree *et al.*, (1993) and Cochard *et al.*, (1997) with a high pressure flow meter (HPFM). In short, the technique consists in deriving R_{branch} from flow/pressure relationships. The HPFM is a capillary flow meter that measures the water flow (F, $mmol.s^{-1}$) entering a cut branch under high pressures (P, up to 0.5 MPa). Under such pressures the leaves are rapidly becoming water saturated, F becomes steady and water eventually drips out of the blades (P=0). Theoretically R_{branch} ($MPa.s.mmol^{-1}$) can then be computed as P/F. However, first results indicated that the P *vs.* F relationship had not a zero intercept. Consequently we measured F for two pressures, P1 and P2, and computed

R_{branch} as (P1-P2)/(F1-F2). Once R_{branch} was measured, we removed all the leaves and measured the remaining xylem resistance as above, the decrease in resistance being equal to R_{leaf}. The branch-to-trunk xylem resistance and the resistance of the branch trace into the trunk were also measured by connecting the remaining basal segment of the cut branch to the HPFM. This value was added to the previous R_{branch} and R_{xylem} resistances. Branch leaf area (LA) was measured at the end of the measurements in order to compute leaf area specific resistances (R^*_{branch} and R^*_{xylem}, MPa.s.mmol^{-1} m^2). All values were standardized to 20°C. The hydraulic resistances were measured for three representative trees. The trees were air cut at the base of their trunk and brought to the laboratory for analysis. A total of 59 branches were measured, representing respectively 97, 91 and 75% of the total leaf area for the different trees.

3. Results

Fig. 1 shows a VC and the percent LHC versus Ψ_{Min}. Embolism significantly developed in stems when Ψ_x dropped below -1.5 MPa and was total at -3.0 MPa. In the field, under drought conditions, we measured significant embolism in stems although stem embolism was limited by leaf fall. The percent LHC was lower than predicted by VC and this suggested that embolism in petioles was certainly more important than in stems. However this vulnerability segmentation was not sufficient to protect stems from embolism. Embolism in the petioles is certainly responsible for error in Ψ_{Min} determination. After rehydratation embolism was not repaired.

Fig. 2 shows the same VC and the relative conductance versus Ψ_{Min}. 50 % LHC was obtained when Ψ_x became lower than -2.0 MPa. At this point, the stomatal conductance was just reduced to 40 % of its maximal value. This fact can explain the significant embolism measured in the field (Fig. 1). Stomatal control plays a poor role in controlling the development of xylem embolism.

In Fig. 3, R^*_{branch} and R^*_{xylem} are expressed for the two types of branches as a function of the distance between the branch insertion on the trunk to the trunk apex. The branch hydraulic conductances were independent of the branch position in the crown. Significant differences were found between the two types of branches. R^*_{xylem} was slightly but significantly lower for one-year old shoots (0.058 std=0.016 MPa.s.m^2.mmol^{-1} *vs.* 0.081 std=0.027; p=0.0002); however R^*_{leaf} was unchanged (0.148 std=0.024 *vs.* 0.143 std=0.024; p=0.42). As a result the share of R leaf in R_{branch} was significantly higher in one year-old shoots (72.0% std=6.6) than in two year-old shoots (64.1% std=9.8, p=0.001). Because 2/3 of the above ground hydraulic resistance was located in the leaves the difference in whole branch resistances was small (0.206 std=0.028 *vs.* 0.224 std=0.027) but significant (p=0.017).

3. Discussion and conclusions

In peach trees, most of the aerial hydraulic resistance is located in the leaves. This seems to be a general feature for tree species studied so far (Tyree *et al.*, 1993a, 1993b). The reason is probably structural because the sap pathway into the leaf is eventually extra-vascular, *i.e.*, through cell membranes and along cell walls. However, we can find some adaptative traits in this structure.

First, if the highest resistance is within the leaf and all leaves exhibit comparable lc resistance, as for peach, then all the leaves in a crown will be equally supplied with wat Leaves located at the top of the crown are then not disfavored by the longer sap pathway

A second corollary of a high leaf resistance is that most of the water potential drop w be located in the extra-vascular sap pathway. The xylem water potential will then exhi higher (less negative) values, which will reduce the risk of cavitation. This is probab important for peach trees because the xylem is highly vulnerable and the stomatal cont rather poor (Fig. 2). In conjunction with high leaf capacitance, high leaf resistance w considerably buffer the effect of rapid variation of transpiration rates (due to wind or lig fluctuations) on the xylem water potential values. Under drought conditions, the situati is different because the xylem water potential value will be determined mainly by the s water potential and mostly by the below-ground drop in water potential (Cochard *et* 1996).

In peach crown, one year-old branches developed directly on the trunk (syllep shoots) exhibited significantly lower leaf specific xylem resistance than 2 year-c branches (proleptic shoots). This trait was independent of the branch position on th trunk. The difference was small (about 0.023 $MPa.s.m^2.mmol^{-1}$) which means that for average transpiration rate of 4 mmol s^{-1} this will represent a 0.1 MPa difference in xyle water potential. The higher resistance in older branches was probably caused by smal vessels and a higher node frequency. We do not know if this trend is accentuated branches are aging because the trees were too young, but this was the case in comparable study on ash trees (Cochard *et al.*, 1997). Higher xylem potential values c favor growth because the activity of meristem and cambium cells is rapidly impaired water deficit. The best possibility of growth in sylleptic shoots can explain why this tre can support high embolism vulnerability by new shoot growth after drought.

Further studies on the physiology of meristematic tissues in relation with the hydraul architecture are required before we can conclude about the impact of hydraulic resistanc on growth in trees.

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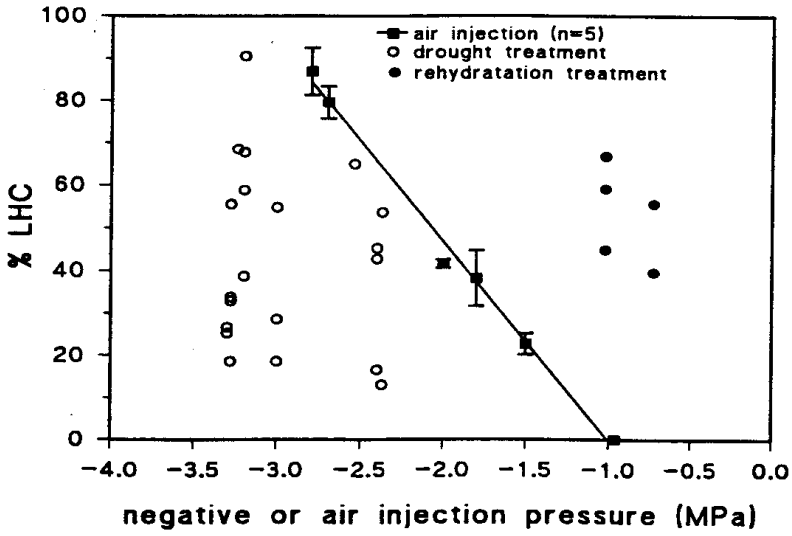

Figure 1 - Percent loss of hydraulic conductivity due to xylem embolism. The vulnerability curve was obtained by shoot pressurization in a pressure chamber. The natural level of embolism *vs* leaf water potential was measured during drought treatment and after rehydratation. Error bars represent standard error.

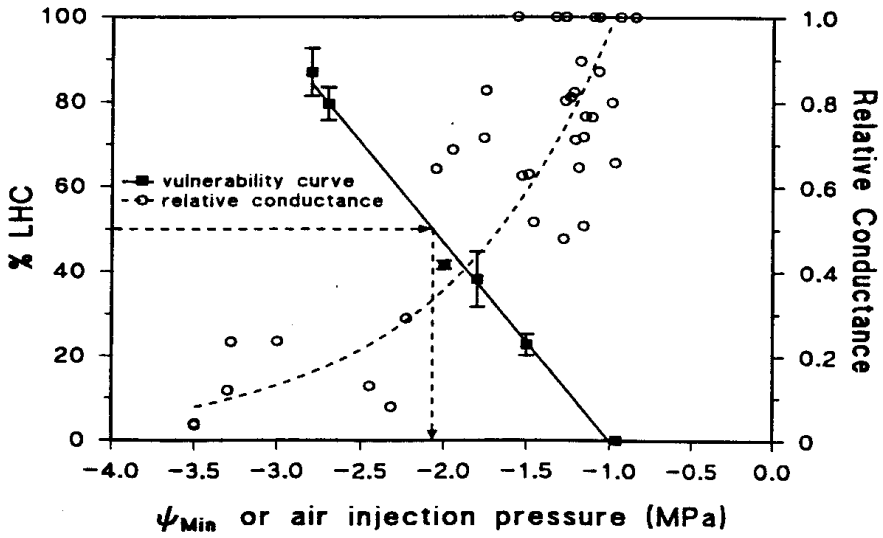

Figure 2 - Percent loss of hydraulic conductivity due to xylem embolism and midday relative stomatal conductance *vs* leaf water potential. Embolism significantly increased in petioles and twigs when Ψ_{Min} became lower than -2.0 MPa, the point where stomatal conductance was reduced to about 40 % of its maximal value.

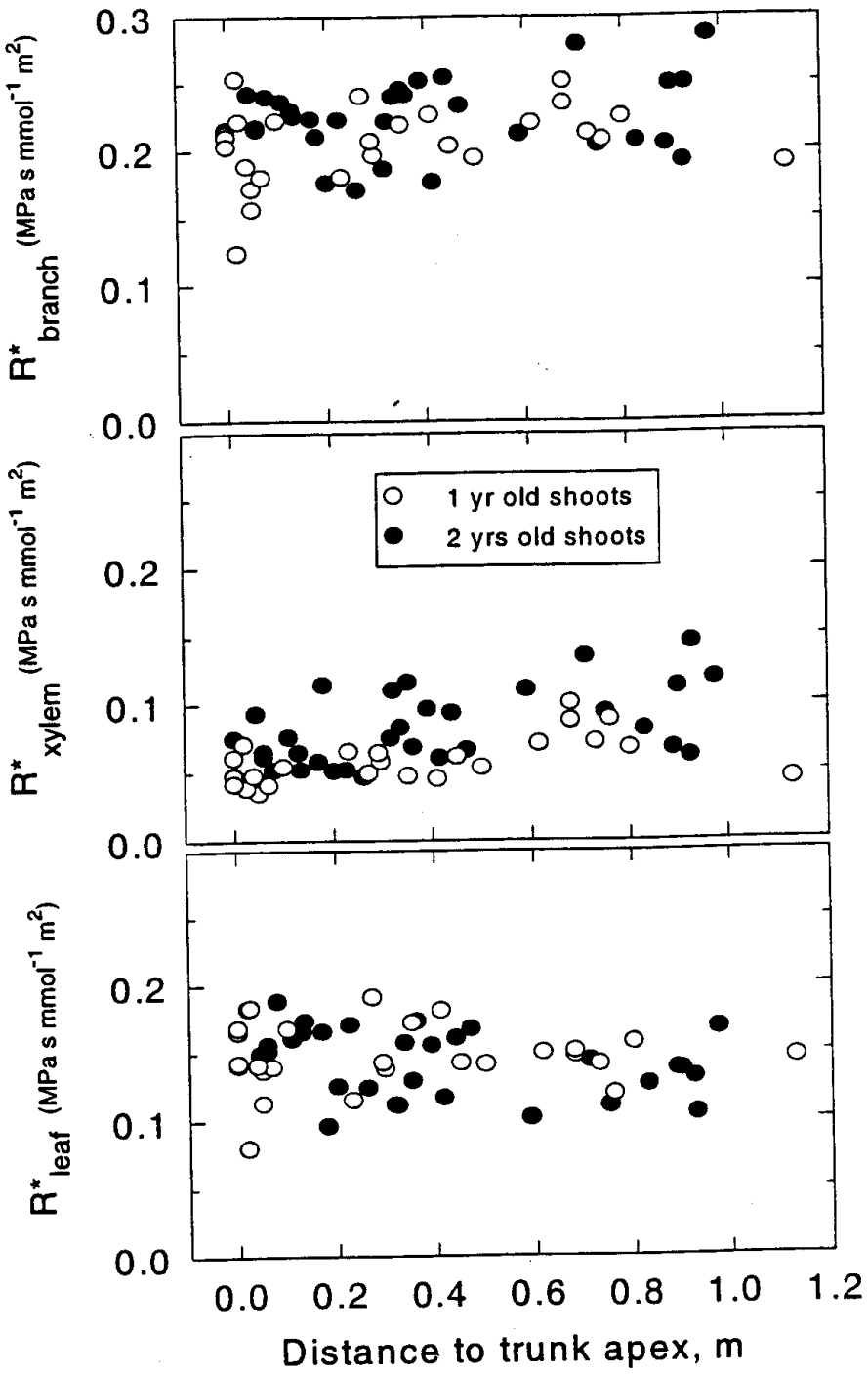

Figure 3 - Hydraulic characteristics of peach branches. We measured whole branch leaf area specific hydraulic resistances (R^*_{branch}, upper graph) and divided it into xylem resistance (R^*_{xylem} middle) and leaf resistance (R^*_{leaf}, lower). We compared one year-old branches (open circles) and two year-old branches (closed symbols) both developing on the trunk. The results are expressed as a function of the position of the branch on the trunk. R^*_{branch} and R^*_{leaf} were constant along the trunk and comparable for the two types of branches. R^*_{xylem} was slightly but significantly lower for one-year old branches.