Is growth performance in rubber (*Hevea brasiliensis*) clones related to xylem hydraulic efficiency?

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Abstract: Hydraulic efficiency, xylem pressure, and stomatal conductance were measured in two *Hevea* clones having contrasting growth performances in their immature phase. Hydraulic efficiency was estimated by the xylem resistance on a leaf area basis on stem, petiole segments, and whole branches. The fast-growing clone exhibited significantly higher xylem efficiency, higher stomatal conductance, and higher xylem pressure. The difference in xylem pressure between the two clones was quantitatively consistent with the differences in hydraulic resistance and leaf transpiration rates. Our results suggest that variations in xylem efficiency may explain variations in stomatal conductance and xylem pressure, and hypothetically, growth performance between *Hevea* clones.

Key words: xylem, hydraulic conductance, hydraulic architecture, water relations, rubber tree, *Hevea*.

Résumé : L'efficience hydraulique, la pression hydrostatique du xylème et la conductance stomatique ont été mesurées chez deux clones d'*Hevea* ayant des potentialités de croissance contrastées pendant leur phase immature. L'efficience hydraulique a été estimée par la conductance hydraulique du xylème par unité de surface foliaire, pour les tiges, les pétioles et les branches entières. Les résultats montrent que le clone ayant la plus forte croissance possède également la meilleure efficience hydraulique, la conductance stomatique la plus élevée et des pressions de xylème moins négatives. Les différences de pressions entre les deux clones sont quantitativement cohérentes avec les différences de résistances hydrauliques et de transpiration foliaires. Nos résultats suggèrent que des variations d'efficience hydraulique pourraient expliquer des variations de conductance stomatiques, de pressions de xylème, et, hypothétiquement, de potentialités de croissance entre clones d'*Hevea*.

Mots clés : xylème, conductance hydraulique, architecture hydraulique, relations aquatiques, arbre à gomme, *Hevea*.

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Introduction

Growth rate during the immature period is one of the key parameters for evaluating the performance of rubber tree clones (Webster and Baulkwil 1989). Indeed, trees can be

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tapped for latex production only when trunks have reached a minimum circumference of approximately 50 cm at breast height. It is thus important to identify physiological parameters that may explain the genetic variability of growth performance among rubber clones as related to environmental factors.

Among these factors, water stress has become of first importance because of the lack of available land in traditional areas, resulting in plantations tending to extend to dryer areas in many countries (Chandrashekar et al. 1996; Jacob et al. 1999). Under soil drought conditions, growth is drastically reduced (Kozlowski 1971), and trees form narrow annual rings. For well-watered trees, there is also experimental evidence for a growth reduction caused by high transpiration rates and low xylem pressures (Berman and Dejong 1997). For rubber trees, the ability to grow during the mid-season, under moderate water stress, determines the cumulative differences in growth performance among clones in a dry, sub-humid climate (Chandrashekar et al. 1998).

From a physiological point of view, growth reduction has at least two explanations. First, stomata may close in response to water stress, which lowers the carbon gain, and, eventually, the quantity of carbohydrates available for growth. Second, soil drought lowers the xylem pressure po-

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tential (ψ_{xp}), which may impair turgor pressure in growing cells and, hence, growth. A biophysical relationship between cell growth and xylem pressure has been proposed by Lockhart (1967).

According to the soil–plant–atmosphere continuum model of water flow in trees, ψ_{xp} can be calculated according to the following equation (Tyree et al. 1993a; Cochard et al. 1997):

$$[1] \qquad \psi_{xp} = \psi_{soil} - E \times LA(R_r + R_s)$$

where ψ_{soil} is the soil water potential (MPa), E is the transpiration rate (mmol $H_2O \cdot m^{-2} \cdot s^{-1}$), LA is the leaf area ($m^2$), R_r is the hydraulic resistance of the root compartment (MPa·s·mmol^{-1}), and R_s is the hydraulic resistance of the shoot system (MPa·s·mmol^{-1}). R_s is the sum of trunk, branch, petiole, and leaf resistances.

Equation 1 shows that plant hydraulic resistance is a key parameter in understanding variations in ψ_{xp} values between plants. Plants with high hydraulic resistance will exhibit more negative xylem pressure. Consequently, a putative impact of plant hydraulics on plant growth has been hypothesized (Tyree 2003) but remains largely undocumented (Domec and Gartner 2003; Vanderwilligen and Pammenter 1998; Wang et al. 2003).

The objective of our study was to analyse the hydraulic properties and water relations of two rubber clones with contrasted growth performance during the immature phase (RRIM 600 and RRIT 251). These clones are categorized in the first class among clones recommended for commercial plantation by the Rubber Research Institute of Thailand (Rubber Research Institute of Thailand 1999). The RRIM 600 clone represents approximately 80% of the total rubber-planted area in Thailand. In dry areas, this clone was considered to have the best stomatal and growth performance when compared with eight other clones (Chandrashekar 1997), while its production is the highest (Wichitchonchai and Manmeun 1992). The RRIT 251 clone is a new, promising Thai high-yielding clone (Susewee 2001), but its average growth during the immature period is lower than that of the clone RRIM 600 (Rubber Research Institute of Thailand 1999).

Materials and methods

Plant materials

Experiments were conducted on 1.5- to 2-year-old rubber (*Hevea brasiliensis* Muell. Arg.) clones RRIM 600 and RRIT 251 during June 2002 – July 2003. Budded scions were grown in small containers until they had produced two flushes of leaves and then transplanted in February 2001 into 150-L plastic pots containing Pakchong soil. Plants were placed in a nursery located at the Department of Agronomy, Faculty of Agriculture, Kasetsart University, Bangkok, Thailand (13°85′N; 100°75′E). A total of 10 trees for each clone were used in this study.

Water relations

Minimum xylem pressure potentials (ψ_{xp}) were determined for stems using a pressure chamber. Following Turner (1981), whole leaves were enclosed in a bag to prevent water loss and thus equilibrate the bulk leaf water potential (Ψ_{leaf})

with the xylem pressure at the base of the bag. Ψ_{leaf} was then an estimate of ψ_{xp}.

Leaf stomatal conductance (g_s) was measured with an AP4 porometer (Delta-T Devices Ltd., Cambridge, UK). Measurements were performed between 0900 and 1600 on a clear day, on 120 leaves per clone, randomly chosen among all the trees.

Hydraulic characteristics of xylem segments

Xylem hydraulic conductance was measured on branch and petiole segments using the technique described by Sperry et al. (1988) by means of a XYL'EM apparatus (Instrutec-France). Approximately 3 cm long segments were excised under water to prevent air entry into the conduits and connected to the XYL'EM apparatus. Stem segments were cut in the internodes. The conductivity (K_{max}, mmol·m·s^{-1}·MPa^{-1}) of each segment was measured with a hydrostatic pressure gradient (P) of approximately 3 kPa using deionized, degassed, and filtered (0.2 μm) water. The segments were first perfused at a pressure of 0.15 MPa for 5 min to dissolve and expel possible air bubbles. On average, K_{max} was measured for 30 branch and petiole segments for each clone.

Hydraulic characteristics of whole branches

Hydraulic resistance to water flow in whole branch, leaf, and petiole was measured using a high-pressure flow meter (HPFM, Tyree et al. 1993a; Cochard et al. 1997). Branches had a basal diameter (bark excluded) of 0.4–1.9 cm and a total leaf area between 0.2 and 1.1 m^2. Branches were cut in the air, and the basal 0.1 m of the stems were immediately recut under water to remove the embolism that formed upon excision. The base of the stem was connected to a compression fitting and perfused with water at a pressure (P) between 0.2 and 0.3 MPa, until water was dripping from the leaf blades (after 1–2 h). The water flow rate (F, mmol·s^{-1}) entering the branch was then constant. Water flow was calculated by measuring the pressure drop across a 0.177 m long PEEK capillary having a 250-m internal diameter. Whole branch resistance (r_{branch}) was calculated from:

$$[2] \qquad r_{branch} = P/F$$

The entire branch leaf area specific resistance (r^*_{branch}) computed as:

$$[3] \qquad r^*_{branch} = P \times LA/F$$

where LA is branch leaf area (m^2).

To measure the branch xylem resistance (r_{xylem}), all the leaf blades were then excised with a razor blade. The mean leaf blade resistance (r_{leaf}) was calculated from:

$$r_{leaf} = r_{branch} - r_{xylem}$$

Whole branch measurements were performed on 10 branches for each clone.

Results

Water relations

The fast-growing RRIM 600 clone exhibited significantly higher stomatal conductance and higher (less negative) mid-

Table 1. Midday stomatal conductance (g_s), midday xylem pressure (Ψ_{xp}), leaf-area-specific whole-branch hydraulic resistance (r^*_{branch}), and leaf-area-specific whole-branch xylem hydraulic resistance (r^*_{xylem}) for two rubber clones.

	RRIM 600			RRIT 251			
	Mean	SE	n	Mean	SE	n	P
g_s (mmol·s^{-1}·m^{-2})	667	24	120	522	26	120	5.3×10^{-5}
ψ_{xp} (MPa)	0.67	1.7×10^{-2}	10	0.77	1.9×10^{-2}	10	2.7×10^{-3}
r^*_{branch} (MPa·s·mmol^{-1}·m^2)	1.17×10^{-1}	5.8×10^{-2}	10	2.13×10^{-1}	1.37×10^{-1}	10	5.8×10^{-2}
r^*_{xylem} (MPa·s·mmol^{-1}·m^2)	8.77×10^{-2}	5.4×10^{-2}	10	1.65×10^{-1}	1.15×10^{-1}	10	6.9×10^{-2}

Note: Mean values with SE are shown (n replicates). P values are from a Student's t test.

Fig. 1. Hydraulic conductivity of petiole (*a*, *c*) and stem (*b*, *d*) xylem segments for RRIM 600 (●, solid lines) and RRIT 251 (○, dotted lines) clones. Segment conductivity is expressed as a function of segment xylem area (*a*, *b*) or segment distal leaf area (*c*, *d*). Lines are linear regressions through the log values.
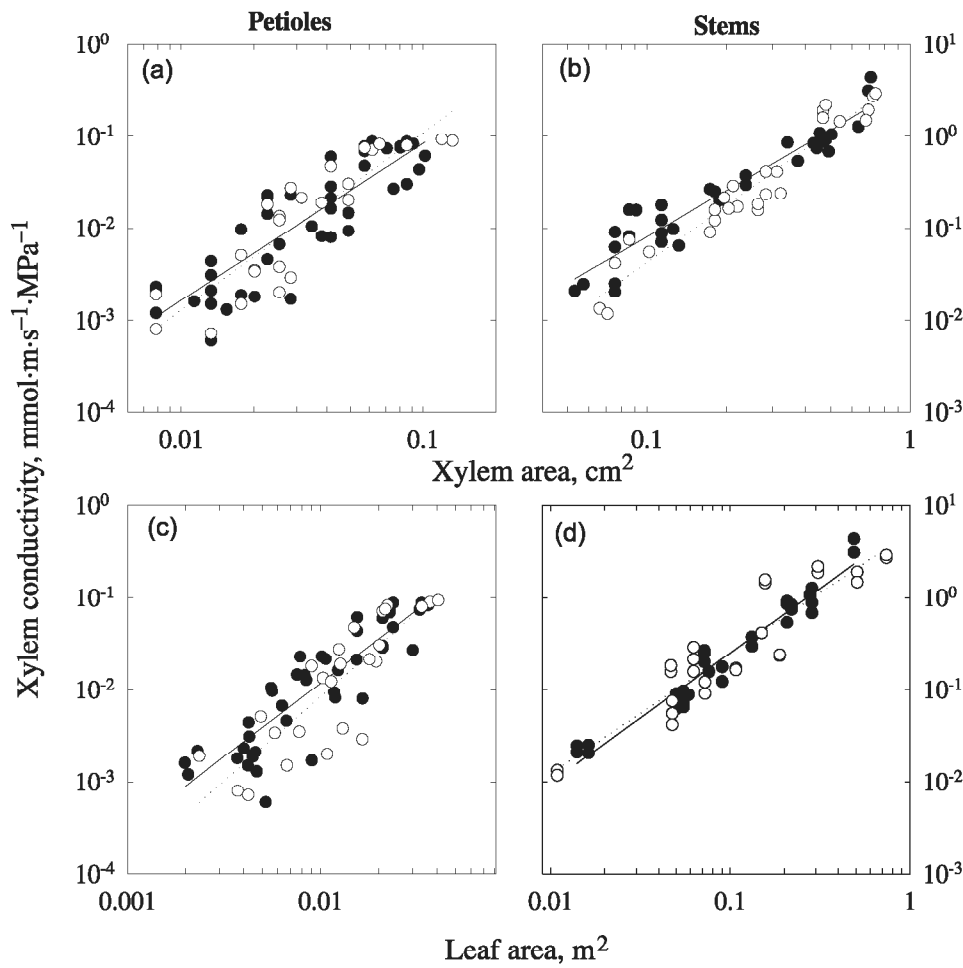
day xylem pressure (Table 1). On average, the xylem pressure differed by 0.1 MPa, and stomatal conductances differed by 28%.

Hydraulic characteristics of xylem segments

The hydraulic conductivity after embolism dissolution (K_{max}) as a function of petiole and branch xylem area and distal leaf area is shown in Fig. 1. The relationships for both segments were positive and linear (on a log–log scale). The

differences were small between the two clones. However, we noted substantially higher K_{max} values for the fast-growing RRIM 600 clone (closed symbols), especially for the stem segments with small diameters (Fig. 1*b*) and the petiole segments with low leaf areas (Fig. 1*c*).

Hydraulic characteristics of whole branches

The dependences of whole-branch (r_{branch}) and whole-branch xylem (r_{xylem}) resistance on branch basal xylem area

Fig. 2. Hydraulic resistance of leafy (*a*, *c*) and leafless (*b*, *d*) branches for RRIM 600 (●, solid lines) and RRIT 251 (○, dotted lines) clones. Whole-branch resistance is expressed as a function of basal branch xylem area (*a*, *b*) or total branch leaf area (*c*, *d*). Lines are linear regressions.
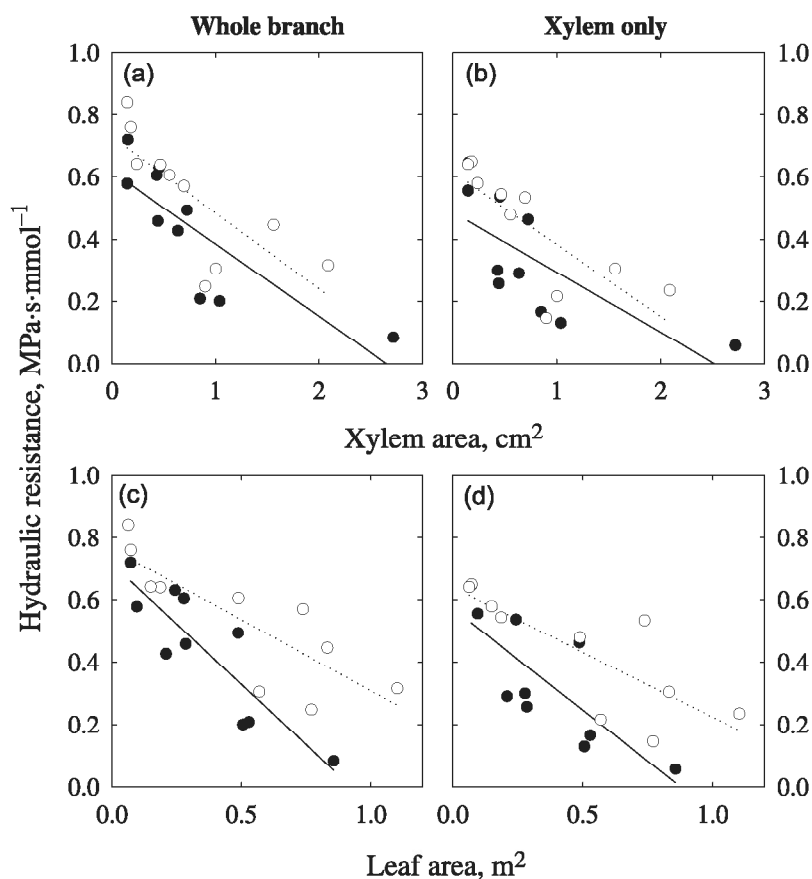
or total branch leaf area are shown in Fig. 2. The fast-growing RRIM 600 clone (closed symbols) exhibited significantly lower values. As a result, the leaf-area-specific hydraulic resistances were about twofold greater in RRIT 251 compared with RRIM 600 (Table 1).

The partitioning of whole-branch hydraulic resistance into stem, petiole, and leaf-blade resistances showed that the greatest share was located in the stems (about 75%), with no difference between clones (Fig. 3).

Discussion

The two *Hevea* clones having contrasting growth performance that we have analyzed in the present study exhibited significantly different water relations and hydraulic traits. Higher stomatal conductance and higher xylem pressures in the fast-growing RRIM 600 clone were associated with higher hydraulic conductances at the whole-branch level and, to a lesser extent, at the xylem-segment level.

The hydraulic characteristics of *Hevea* are in the range of previous reports for tropical trees (Tyree and Ewers 1991; Cruiziat et al. 2002; Tyree and Zimmermann 2002). The fact that the two clones exhibited contrasting characteristics at the branch level and less contrast at the level of xylem internode segment is not surprising for two reasons. First, the dif-

Fig. 3. Partitioning of whole-branch resistance into stem, petiole, and leaf blade resistances for two rubber clones. Error bars are SE (*n* = 10).
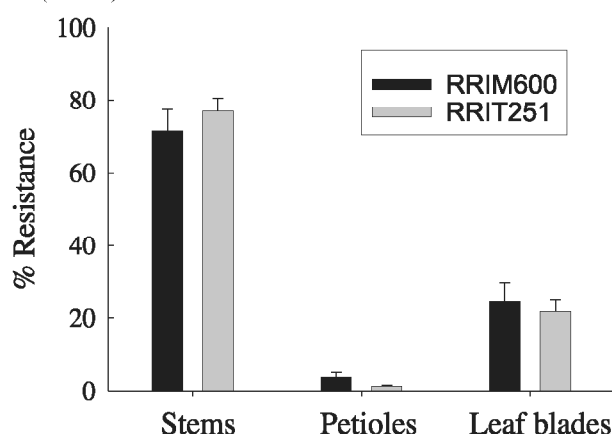
ferences at the segment level were mostly in the terminal parts. These parts are the most resistive and, as resistances are serial and additive along the sap pathway, they will mostly determine the overall branch resistance. Second, the whole-branch xylem resistance is also determined by the

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length of the sap pathway and, more significantly, by extra resistances located in the nodes and branch junctions (Tyree and Alexander 1993). These two parameters are not taken into account when internodes are measured.

A surprising result of our study was the relative high share of the xylem resistance. Partitioning of r_{branch} into different components has been studied for several temperate tree species. As a rule, the highest share is located in the leaf blade (e.g., 80%–90% in *Quercus* spp., Tyree et al. 1993*a*; 80% in *Juglans regia*, Tyree et al. 1993*b*; 40%–60% in *Acer* spp., Yang and Tyree 1994). In the present study, r_{leaf} represented less than 25% of the total branch resistance. However, Cochard et al. (1997) have demonstrated that within a *Fraxinus excelsior* tree, the share of the xylem resistance can vary between 10% and 90% according to the age and the developmental stage of the different branches.

According to eq. 1, a causal relationship exists between plant hydraulic resistance, water potential, and leaf evaporation rate. As these different parameters were measured independently in this study, it is possible to test the consistency of our findings. It is not possible to test the consistency of the absolute xylem pressure values with our data, because hydraulic resistances were measured only in the aerial tree parts. However, we can compute the relative impact of different branch resistances on branch water relations. Assuming a mean transpiration rate (E) of 2 mmol·s^{-1}·m^{-2} (?, unpublished data), we can predict that the lower leaf-area-specific xylem resistance for the RRIT 251 clone r^{*}_{xylem}, (Table 1) will induce a 0.16-MPa more negative xylem pressure. If we now consider that the lower stomatal conductance for the RRIT 251 clone was reduced E to 1.56 mmol·s^{-1}·m^{-2}, a 0.08-MPa reduction is expected. The predictions are thus in close agreement with our measurements (0.1-MPa difference, Table 1). A similar computation can show that the stomatal conductance of the RRIT 251 clone must equal 50% that of the RRIM 600 clone to obtain similar xylem pressure drops in the two clones. The above computations illustrate the strong dependence of leaf transpiration on xylem hydraulic resistance in *Hevea*. Because the share of the xylem resistance is high, a compromise between high water losses and low xylem pressures seems to exist for this species. High water losses are likely to favor high CO_2 uptake and carbohydrate production but induce low xylem pressures, which may impair cambium growth. Conversely, high xylem pressures are at the expense of low stomatal conductances, and hence, low assimilation rates. The higher growth performance of the RRIM 600 clone is thus consistent with its higher xylem efficiency, which correlates with higher stomatal conductance (higher CO_2 uptake) and higher xylem pressure (possible higher cambial growth).

In a previous study (Sangsing et al. 2004), we demonstrated a striking correlation between xylem vulnerability to cavitation and stomatal closure during water stress for the same *Hevea* clones. Our results illustrate the importance of the xylem characteristic on the stomatal behavior, both under well-watered and drought conditions. Interestingly, the fast-growing RRIM 600 clone exhibits both higher xylem efficiency (the present study) and safety (Sangsing et al. 2004). This suggests that the two phenomena are independent and that there is a potential for selecting fast-growing and drought-resistant *Hevea* clones on the basis of their hydraulic traits.

Acknowledgements

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