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ORIGINAL ARTICLE

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Xylem embolism and stomatal regulation in two rubber clones (*Hevea brasiliensis* Muell. Arg.)

Abstract Vulnerability to water-stress-induced embolism of stems, petioles, and leaf midribs was evaluated for two rubber clones (RRIM600 and RRIT251). The xylem conduits were relatively vulnerable to cavitation with 50% of embolism measured for xylem pressures between –1 and –2 MPa. This feature can be related to the tropical-humid origin of the species. A distinct basipetal gradient of vulnerability was found, leaf midribs being the least vulnerable. Substantial variation in vulnerability to cavitation was found between the two clones only at the petiole level. A correlation was found between the stomatal behavior and the development of cavitation. Stomata were nearly closed when the xylem pressure reached the point of xylem dysfunction. Stomata may thus contribute to controlling the risk of cavitation. However, for one clone a poor correlation was found between stomatal regulation and petiole vulnerability. This was consistent with a high degree of embolism measured in the petioles after a soil drought event. Therefore, xylem cavitation might represent a promising criterion to evaluate the performance of rubber clones under drought conditions.

Keywords Water relations · Hydraulic properties · Cavitation · Stomatal conductance · Rubber tree

Introduction

Due to lack of available land and competition with other crops, rubber plantations tend to extend toward the northeastern part of Thailand where they inevitably encounter a long dry season. Growth reduction, longer immaturity period (Manmeun et al. 1993) and up to 30% lower latex production (Wichitchonchai and Manmeun 1992) have been reported in such areas. Similar results were obtained in the dry subhumid climate of India (Chandrashekar et al. 1996, 1998). In order to improve rubber cultivation under these conditions, more drought-efficient trees and adapted cultivation systems have to be developed. Rubber tree breeding being a very long process, it is critical to identify reliable and pertinent parameters in the early stage of tree development. One possible way toward this objective is to focus on the physiological traits determining rubber tree performance under water stress.

Like any plant, rubber tree growth and latex production is to a great extent determined by the carbon budget (Chandrashekar 1997). Therefore, the understanding of rubber tree stomatal function is a key step in the understanding of drought performance. Stomatal behavior is probably one of the most complex processes in plants. Numerous internal or external factors are know to influence stomatal aperture, e.g., light, air humidity, soil water content, ABA concentration, leaf water status etc.

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However, under drought conditions, a striking relation has been found between stomatal function and plant hydraulics (Sperry 1986; Jones and Sutherland 1991; Sperry et al. 1993; Cochard et al. 1996, 2002; Fuchs and Livingston 1996; Salleo et al. 2000). It has been suggested that stomata may respond to an increase in plant hydraulic resistance with the effect of preventing deleterious cavitation events in the xylem conduits. Xylem cavitation occurs when sap pressure drops below a specific threshold (Sperry and Tyree 1988). By reducing water loss, stomatal closure may maintain the pressure above the threshold.

Plant hydraulics might therefore provide a sound basis for an early selection for drought-efficient rubber trees. Thus, the first objective of this study was to test the hypothesis of a correlation between stomatal closure and cavitation avoidance in rubber tree. We are aware of only one study on rubber tree hydraulics (Ranasinghe and Milburn 1995) but the above hypothesis was not evaluated. The second objective of the study was to evaluate a potential variability of rubber tree hydraulics among different clones. Substantial variations in hydraulic properties have already been reported between different plant genotypes (Neufeld et al. 1992; Kavanagh et al. 1999; Tausend et al. 2000) including rubber tree (Ranasinghe and Milburn 1995). We have selected two clones for this study, 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 (RRIT 1999). The RRIM 600 clone represents approximately 80% of total rubber planted area in Thailand. In dry areas, this clone grows moderately when compared with four other clones, while its production is the highest (Wichitchonchai and Manmeun 1992; Chandrashekar 1997; Jacob et al. 1999). 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 in RRIM 600 (RRIT 1999). Its behavior under water stress conditions has not yet been documented.

Materials and methods

Plant material

Experiments were conducted on 1.5-year-old rubber clones *(Hevea brasiliensis* Muell. Arg. clone RRIM 600 and RRIT 251) during June–July 2002. 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 Department of Agronomy, Faculty of Agriculture, Kasetsart University, Bangkok, Thailand (13.850°N; 100.750°E). Plants were watered daily until a drought treatment was started. The irrigation of one plant per clone was successively stopped at 1-week intervals during June 2002. The pots were covered with a plastic sheet to prevent rainfall. Thus, at the beginning of July we obtained five plants per clone with a range of soil dehydration corresponding to 0 (control) to 4 weeks without irrigation. At time of harvest, plants were between 2 and 3 m tall.

Xylem pressure potential and stomatal conductance

Minimum xylem pressure potentials were determined for branches (P_{branch}) and petioles (P_{petiole}) with a pressure chamber. The covered leaf technique was used to estimate xylem pressures (Turner 1981). Rubber trees have trifoliated leaves with leaflets of comparable sizes. We enclosed either whole leaves or one leaflet in a bag at least 2 h before measurement. This had the effect of preventing leaf water loss and thus equilibrating the bulk leaf water potential (Ψ_{leaf}) with the xylem pressure at the base of the bag. The leaflet and the whole leaf balance pressures were estimates of the xylem pressure in the leaf petiole (P_{petiole}) and in the branch (P_{branch}). Our technique overestimated P_{petiole} because only two thirds of the leaf area was still transpiring. For each tree, one replicate of P_{branch} and two replicates of P_{petiole} were obtained.

Leaf stomatal conductance (g_s) was measured with an AP4 Porometer (Delta-T Devices, Cambridge, England). Measurements were performed on eight leaflets randomly chosen on each tree between 1000 and 1200 hours concurrently with the xylem pressure estimates.

Xylem embolism and vulnerability curves

The percentage loss of hydraulic conductivity (PLC) was measured at the end of the drought treatments on branches, petioles and midribs with the technique described by Sperry et al. (1988). We used the new XYL'EM apparatus (Embolism Meter, INRA Licensed Instrumentec, France). Petiole, branch or midrib segments (approx. 3 cm long) were excised under water to prevent air entry into the conduits and connected to XYL'EM apparatus. Midribs segments were wrapped with Teflon tape to prevent lateral leaks. The initial conductivity (K_i , mmol m s^{-1} MPa^{-1}) of each segment was measured with a hydrostatic pressure gradient (P) of ca. 3 kPa using deionized, degassed and filtered (0.2 μm) water. The segments were then perfused at a pressure of 0.15 MPa for 5 min to dissolve and expel air bubbles. The hydraulic conductivity of the segments was determined again and the flushes were repeated until the maximum conductivity, K_m, was obtained. PLC then was calculated from:

$$\mathrm{PLC} = 100(K_m - K_i)/K_m \tag{1}$$

Vulnerability curves (VC) were constructed by dehydrating branches or leaves to different xylem pressure and measuring the corresponding PLC values. We used the air pressure dehydration technique (Cochard et al. 1992) to construct the curves. Branches or whole leaves were enclosed in a pressure chamber with the cut end protruding outside. The air pressure in the chamber was increased at a rate of 5 kPa s^{-1} up to different pressures ranging from 1 to 3.5 MPa. The pressure was maintained at its target value until sap no longer exuded (which meant the leaf had reached a balance pressure). The pressure was then released at 2 kPa s^{-1} to atmospheric. Dehydrated branches or leaves were then kept overnight in an air-tight bag (to allow air equilibration in the samples) and xylem embolism measured as described above.

Segments were excised under water at least 15 cm away from the cut end. The low PLC values measured in the stems at −1 MPa indicated that the degree of embolism caused by air entry at the base of the samples before pressurization was negligible. For each sample, PLC values were obtained for 2 or 3 segments. The following logistic function was fitted to the different curves (Cochard et al. 1999):

$$\mathrm{PLC}(P) = 100/[1 + (P/P_{50\mathrm{PLC}})^s] \tag{2}$$

where $P_{50\mathrm{PLC}}$ is the pressure inducing 50PLC and s a parameter affecting the slope of the curve [the slope at $P = P_{50\mathrm{PLC}}$ (inflexion point) is $-25\ s/P_{50\mathrm{PLC}}$].

Results

Drought treatments provoked a strong stomatal closure and a decrease in xylem pressure. One week after irrigation was stopped, g_s was substantially more reduced for the RRIT251 clone (80% decreased) than for the RRIM600 clone (60% decreased) (Fig. 1a). Thereafter, g_s was reduced to cuticular levels for both clones. Minimum xylem pressures in the petioles for control plants varied between –0.7 and –0.8 MPa (Fig. 1b). Four weeks after the onset of the drought treatment, P_{petiole} was reduced to –1.7 and –2 MPa for the RRIM600 and RRIT251 clones, respectively. Less negative xylem pressure values were measured in the branches (see Fig. 2). The dependencies of g_s on P_{petiole} (Fig. 2a) and P_{branch} (Fig. 2b) show that no substantial differences were found between the two clones with respect to the above parameters.

VC were constructed by plotting PLC versus xylem pressure. The VCs for different organs of both clones are shown in Fig. 3 and the parameters of the logistic fitting are given in Table 1. For both clones, strong differences were found between organs, with branches being the most vulnerable and leaf midribs the least. $P_{50\text{PLC}}$ were usually statistically different at P=0.05 between organs for each clone, but slope parameters were similar (Table 1). Petioles of the RRIT 251 clone were distinctly more vulnerable than that of RRIM600 (about a 0.5 MPa shift, significant difference at P=0.10) whereas stem and midribs were not statistically different (compare open and filled symbols in Fig. 3). PLC values obtained on pot-dehydrated samples were in agreement with branch-pressurized values although usually lower (compare circles and squares in Fig. 3). This might have been caused by vessel plugging by tylosis or latex in intact plants. At the end of the drought treatment the degree of xylem embolism was below 10PLC in the midribs for both clones (Fig. 3a, squares). Embolism developed significantly in the petioles only for RRIT 251 clone (about 40PLC) (Fig. 3b, open squares). More substantial levels of embolism were observed in the branches, especially in the RRIM 600 clone (up to 75PLC, Fig. 3c).

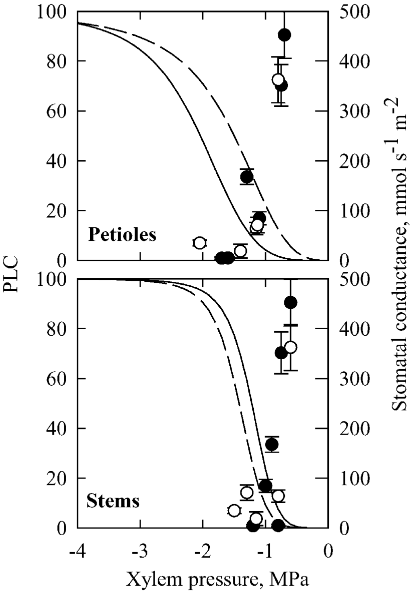

Fig. 2 Leaf stomatal conductance versus xylem pressure in the petioles (*upper panel*) and the branches (*lower panel*) of RRIM600 (*filled symbols*, *plain lines*) and RRIT251 (*open symbols*, *dotted lines*) rubber clones. The lines are logistic fits of the vulnerability curves from Fig, 3. *Error bars* represent 1 SD

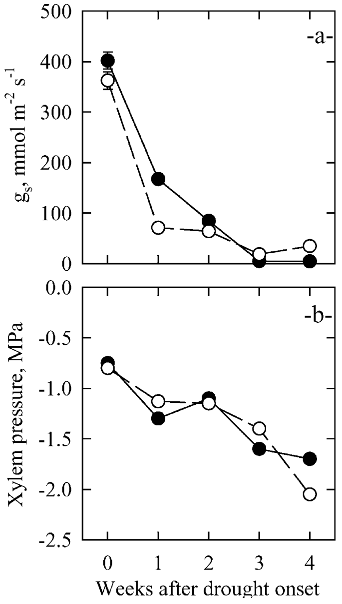

Fig. 1 Time course of leaf stomatal conductance (*upper panel*) and xylem pressure potential (*lower panel*) for RRIM 600 (*filled symbols*) and RRIT 251 (*open symbols*) after pot watering was stopped at time 0. *Error bars* represent 1 SD

Table 1 Parameters of the logistic function fitted to the vulnerability curves. P_{50PLC} data correspond to the xylem pressure (MPa) provoking 50% embolism and s is a slope parameter. Values ± SE. For each clone, organs having a letter in common are not statistically different at P=0.05. Between clones, significant differences at P=0.1 are indicated by *

	RRIM600			RRIT251		
	Midrib	Petiole	Branch	Midrib	Petiole	Branch
$P_{50\text{PLC}}$	−2.72±0.09a	−2.04±0.20b*	−1.22±0.20c	−2.69±0.07a	−1.50±0.30b	−1.42±0.08b
s	−6.13±1.23a	−4.40±1.35a	−5.95±2.57a	−5.73±0.82a	−3.09±1.15bc	−6.58±2.18ac

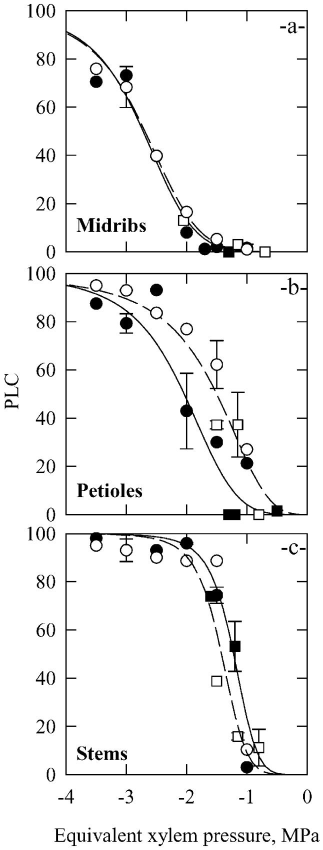

Fig. 3 Midribs, petioles and branches vulnerability curves for RRIM660 (*filled symbols*, *plain lines*) and RRIT251 (*open symbols*, *dotted lines*) rubber clones. *Circles* correspond to air pressure->dehydrated samples and squares to measures on soil-dehydrated plants. *Lines* are logistic fits through the data. *Error bars* represent 1 SD

Discussion

Vulnerability to cavitation

Since the introduction of the hydraulic techniques to assess xylem embolism (Sperry et al. 1988) the vulnerability of a relatively high number of woody species have been documented and it is now possible to rank species according to this parameter. The xylem vessels of the rubber trees in this study were found to embolise in the range of −1 to −2.5 MPa. Fifty percent of embolism was noted in the petioles for xylem pressures between −1.5 and −2 MPa. This is in accordance with the results of Ransinghe and Milburn (1995) who measured 40PLC for tensions of −1.8 to −2.0 MPa. Such $P_{50\mathrm{PLC}}$ values are relatively high compared to temperate or Mediterranean species (Cruiziat et al. 2002). The high vulnerability of rubber trees seems to be a feature common to other tropical species adapted to rainforest-type environmental vulnerabilities (Tyree and Zimmermann 2002) although some tropical species might also exhibit very low vulnerability (Cochard et al. 1994; Tyree et al. 2003). This is a first important result for our project because one may speculate that because of its high vulnerability rubber trees might be prone to serious xylem dysfunctions outside of their natural humid habitat.

A second feature of the hydraulic system of rubber tree is its vulnerability segmentation. This feature refers to the fact that different organs in a same tree exhibit different vulnerabilities. There are few reports of vulnerability segmentation in the literature, the case of *Juglans regia* (Tyree et al. 1993) being probably the most spectacular. A clear basipetal gradient was found in this study, with leaf midribs been the least vulnerable. The differences were rather substantial because $P_{50\mathrm{PLC}}$ of midribs and stems differed by ca. 1.5 MPa. If characterizing the hydraulic structure is rather easy, identifying the physiological consequences of such a construction is much more challenging because this requires a more thorough description of the hydraulic architecture of the whole sap pathways. What we can note is that the gradient of vulnerability in rubber was correlated with the presumed gradient in xylem pressure. However, the PLC data measured in situ suggested that the distal parts were less prone to cavitation. Nevertheless, high embolism rates in more proximal parts may have only a limited impact because the hydraulic resistance of these organs is relatively low. If the benefit of having cavitation resistant midribs is conceivable, the benefit for having more vulnerable stems is still unclear. Three hypotheses have been proposed in the literature. First, early cavitation events in the proximal parts may release water to sustain the transpiration demand. However, the amount of water release by cavitation is usually very small compared to leaf evaporation rates. Second, there might be a tradeoff between xylem efficiency and xylem safety. Wider xylem conduits may confer a higher conductive capacity but at the expanse of increased vulnerability. However, the correlation between xylem safety and efficiency is very weak when different species are compared (Tyree et al. 1994) or even between different branches of the same plant (Cochard et al. 1999). Hacke et al. (2001) suggested a third hypothesis. A less vulnerable xylem structure may require thicker conduit walls and an overall higher wood density in order to prevent wall collapses. Consequently there might be an energetic cost for cavitation resistance. Rubber trees have a with relatively low-density wood. This may corroborate the hypothesis.

A third hydraulic feature of rubber trees revealed by this study is clonal variation. Petiole vulnerability for the two clones we have evaluated was contrasted contrary to our measurements of midribs and stems. However, a larger sample size would be required to confirm this trait. This finding was nevertheless confirmed by the fact that, after a soil drought event, xylem embolism developed only in the petioles of the most vulnerable clone. This result confirms the potential genotypic variability around this hydraulic trait (Neufeld et al. 1992; Kavanagh et al. 1999; Tausend et al. 2000). This is an important result in our context of a long-term breeding program.

Xylem embolism and stomatal function

The main objective of our study was to evaluate the hypothesis of a correlation between stomatal closure and cavitation avoidance in rubber trees. To evaluate the hypothesis, we have represented the relations between the xylem pressure and both g_s and the degree of embolism in Fig. 2. We show the results for branches and petioles because the xylem pressure in the midribs was not measured in this study. The figure suggests that the stomata were nearly closed at the onset of xylem cavitation. More quantitatively, we found a near 1 to 1 relation between the xylem pressure provoking 10 PLC and the pressure corresponding to 10% of the maximal g_s. Only for petioles of the RRIT510 clone was the relation not verified (open circles in Fig. 2b). This was consistent with the high level of embolism measured in situ for this clone. These results highlight the essential role that stomata may play in the control of xylem embolism. Models have been developed to analyze the dependence of these two parameters (Sperry 2000; Cochard et al. 2002). The models show that stomatal closure minimizes the risk of cavitation while maximizing the transpiration rate and thus the assimilation rate. The models also suggest that any deviation from behavior translates into massive xylem dysfunction. Again, the substantial amount of embolism noted that in the petiole of RRIT251 clone might be a consequence of an inability of stomata to control cavitation when soil drought persists.

Conclusion

The main conclusions of this study are (1) the xylem conduits in rubber trees are relatively vulnerable to cavitation, a feature that is sometimes related to a tropical-humid origins; (2) substantial variation in vulnerability to cavitation was found in a comparison of two clones; and (3) a correlation was found between the stomatal behavior and the development of cavitation. Therefore, the analysis of xylem embolism, especially in the petioles, may provide a sound criterion for the evaluation of rubber tree clone behavior under drought conditions. On the basis of the results of this study, we can predict that more cavitation-resistant clones will exhibit less xylem dysfunction after a drought period. We can also predict that such clones may perform better in terms of carbon assimilation during a water shortage because they may maintain their stomata open for a longer period. It is critical in this analysis to combine the stomatal and hydraulic behavior. Our data suggest that these two parameters may be de-coupled during clone selection. This may result in a nonstomatal control of embolism, a problem that may become critical in drier areas. However, it is still quite difficult to predict rubber tree performance under drought conditions in terms of growth or rubber yield on the basis of our results. Indeed, the process governing rubber production might be uncoupled from the mechanism triggering stomatal closure and cavitation avoidance. It is well known that tree growth is affected in the early stage of a drought period, well before any cavitation occurs in the xylem. Cavitation resistance is a parameter that pertains more to drought survival than growth performance under drought conditions. For instance, grain yield under drought conditions was not correlated with vulnerability to cavitation in four maize genotypes (Cochard 2002). Drought survival is important in the northern part of Thailand where long dry periods may threaten tree survival the first year after planting.

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