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Original article

Transpiration and stomatal conductance of two rain forest species growing in plantations (*Simarouba amara* and *Goupia glabra*) in French Guyana

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Summary — Water relations of 2 tree species from the tropical rain forest of French Guyana were studied in young plantations of *Simarouba amara* and *Goupia glabra*. Experiments took place in 1988 and 1989. Sap flow was recorded continuously for several months including a dry season. On bright days, sap flux densities (*eg* sap flow per unit of conducting area) exhibited high values of ≈ 3.5 to 4.0 $kg.dm^{-2}.h^{-1}$. Total sap flow differed from one tree to another depending on individual sapwood areas. In spite of the increase of global radiation and of the vapour pressure deficit, sap flow remained constant for *Simarouba* and even decreased for *Goupia* between 10:00 and 15:00 h as a consequence of stomatal closure. Sap flow measurements allowed the calculation of stand transpiration, which for bright days represented only 50% of Penman potential evapotranspiration (PET). This low transpiration level was explained by incomplete canopy closure and hence a low LAI of the plots. Canopy conductances were calculated from the Penman–Monteith equation. They demonstrated the inhibiting effect of vapour pressure deficits > 4 hPa. These results confirm those of Huc and Guehl (1989), that for tropical rain forest species, transpiration may be limited by stomatal closure notwithstanding a high annual rainfall.

transpiration / sap flow / stomatal conductance / air humidity / tropical species / canopy conductance

Résumé — Transpiration et conductance stomatique de deux espèces tropicales humides en plantation (*Simarouba amara* et *Goupia glabra*) en Guyane française. *Le fonctionnement hydrique de 2 espèces de la forêt tropicale humide a été étudié en Guyane française dans des jeunes plantations. Ces études ont porté sur le* Simarouba (Simarouba amara) *en 1988 et 1989, puis sur le* Goupi (Goupia glabra) *en 1989. Le flux de sève brute a été mesuré en continu sur plusieurs arbres de chaque espèce pendant une période de plusieurs mois, incluant une saison sèche. Lors des journées ensoleillées, on a pu mettre en évidence, au sein de chaque espèce, une évolution des densités de flux (flux par unité de surface de bois d'aubier) similaire chez les différents arbres. Les densités de flux ont atteint des valeurs élevées, de l'ordre de 3,5 à 4,0* $kg.dm^{-2}.h^{-1}$. *Les flux totaux étaient par contre différents, puisqu'en relation directe avec la dimension des arbres mesurés. Malgré l'augmentation du rayonnement global et celle du déficit de saturation de l'air dans la journée, les flux de sève restaient stables* (Simarouba), *voire diminuaient* (Goupia) *dans la journée, pendant les heures chaudes, en relation avec une importante régulation stomatique. Les mesures de flux de sève ont* *permis d'évaluer la transpiration des placeaux, ne représentant environ que 50% de l'ETP Penman pour les belles journées. Ce faible pourcentage a été rapproché du faible indice foliaire de ces jeunes plantations non encore fermées. Un calcul des conductances de couvert a été réalisé à partir de la formule de Penman-Monteith, en assimilant les flux de sève à la transpiration. Les valeurs de conductance ainsi obtenues ont montré un effet négatif important de la sécheresse de l'air, dès que le déficit de saturation dépassait 4 hPa. Les comportements ainsi mis en évidence confirment, après les résultats de Huc et Guehl (1989) que chez ces espèces, une fermeture stomatique peut intervenir, malgré une pluviométrie annuelle élevée.*

transpiration / flux de sève / conductance stomatique / humidité de l'air / espèces tropicales / conductance du couvert

INTRODUCTION

Tree species and natural forest stands of the tropical rain forest remain poorly studied with respect to their water relations. Although in the North Amazonian regions water availability is not usually a limiting factor, 1–2 dry seasons may occur, sometimes leading to temporary water deficits (Guehl, 1984). Limitations of CO_2 uptake and water consumption may result from sensitivity of local species to atmospheric drought, which affects the stomatal regulation and the functioning of photosynthetic apparatus in leaves (Huc and Guehl, 1989).

From an ecological point of view, data on water fluxes in these ecosystems are still missing, mainly regarding the 2 components linked to the canopy structure: transpiration and interception of precipitation. Mention should be made, however, of the studies of Roche (1982), Ducrey and Guehl (1990) in French Guyana, Odum and Jordan (1970) in Puerto Rico and those of Shuttleworth *et al* (1984) and Shuttleworth (1989) in Brazil.

The perspectives of management of forest wood resources in French Guyana are mainly centered along 2 axes:

- silviculture of natural forest stands ensuring regeneration of valuable tree species;
- to a lesser extent, plantations of trees of commercial interest.

The present article concerns research on water relations, in artificial stands, for 2 species belonging to a group of tree species which are likely to be favored in plantations.

Sap flow measurements were used in order to estimate transpiration for individual trees as well as entire stands.

MATERIAL AND METHODS

Experimental site

The experiments were conducted on experimental plots of CIRAD–CTFT (Forest Tropical Technical Center) located at Paracou, Sinammary, close to Kourou in French Guyana (53°W, 5.2°N, elevation 40 m). These plantations were established after the natural forest was clear cut and the soil was mechanically prepared. The understorey was completely removed at the start of the experiment. The rainfall is ≈ 2 200 mm per year, with a minimum occurring between August and November. Average potential evapotranspiration is ≈ 4 $mm.d^{-1}$ (Roche, 1982). The characteristics of the plots of the 2 studied species, *Simarouba amara* (Simaroubaceae) and *Goupia glabra* (Goupiaceae) are given in table I. The soil of the experimental site is an oxisol on precambrian bedrock with a microaggregated structure. Clay content increases continuously from

Table I. Main characteristics of the 2 studied stands.

		Simarouba	Goupia
Age	(year)	3	5.5
Stems.ha^{-1}		4 398	1 066
Mean height	(m)	4.7	8.8
Mean circumference	(cm)	18.2	27.4
Ground area	(m^2.ha^{-1})	11.6	7.1
Sapwood area	(m^2.ha^{-1})	10.8	6.9
LAI	m^2.m^{-2}	3.5	3.7

15–20% in the sandy upper layers to a maximum of 40–50% in the lower layers.

Methods

Sap flow

Tree transpiration was estimated from sap flow measurements with a constant heating radial flowmeter (Granier, 1985, 1987). This sensor averages the sap flux density (*ie* flow per unit of conductive area) along its length. One sensor is composed of 2 20-mm long and 2-mm thick probes, covered with an aluminum cylinder which are radially inserted into the sapwood of the trunk. The upper one (20 cm above the lower one) is continuously heated by Joule effect, while the lower one remains at wood temperature. Thermocouples in each probe allow measurement of the temperature difference between them. The maximum temperature difference (typically 10–12 °C) is attained when no sap flow occurs. When sap flow commences, convective heat flux is added to diffusive flux into the wood and the temperature difference decreases. A calibration relationship was established in the laboratory on different species allowing the calculation of the sap flux density Ju (kg.dm^{-2}.h^{-1}):

$$Ju = 4.28\,[\Delta T(0)\,/\,\Delta T(Ju) - 1]^{1.23} \qquad (1)$$

in which $\Delta T(0)$ and $\Delta T(Ju)$ are the temperature differences between both probes (°C), for sap flux densities 0 and Ju respectively.

Total sap flow F (kg.h^{-1}) for each tree is calculated from the sapwood cross-sectional area sa (dm^2) of the trees at the heated probe level:

$$F = Ju\,.\,sa \qquad (2)$$

Stand transpiration T (mm.h^{-1}) was computed for 1-h intervals from sap flow measurements on individual trees by taking into account the representativeness of each tree in the stand. Five *Simarouba* and 6 *Goupia* selected from different crown classes were monitored in their respective plots. Stand transpiration:

$$T = SA\,.\,\Sigma Ju_i\,.\,p_i \qquad (3)$$

in which SA is the stand sapwood area per unit of ground area (dm^2.m^{-2}), Ju_i is the sap flux density of tree i, and p_i is the proportion of sapwood of class i with respect to stand sapwood area.

Other measurements

Measurements of leaf water potential were taken every 1–2 h over 2 days in both stands using a pressure chamber. Leaves were chosen both in the upper and the lower part of the crowns for calculating an average value of leaf water potential.

Stomatal conductance was measured every 2 h with a LI-COR 6200 gas exchange system during 2 bright days in the *Goupia* stand but not in the *Simarouba* stand because of technical problems.

Air temperature, humidity and global radiation were recorded from a weather station located at the top of the canopies on a scaffolding tower; wind speed was measured 2 m above.

Climate and sap flow data were collected on a Campbell Ltd 21X data logger at a rate of one measurement every 10 s, from which hourly averages were calculated and stored.

In the *Simarouba* experiment, sap flow was recorded from October 27, 1988 to April 12, 1989, and in the *Goupia* experiment from May 18, 1989 to November 17, 1989.

Hydraulic and canopy conductances

Whole-tree hydraulic conductance was calculated from linear regressions between diurnal measurements of sap flux density and leaf water potential. Correlation coefficients were high, ranging between 0.90 and 0.95.

Canopy conductance was evaluated hourly from sap flow and climatic measurements using the Monteith transformation (1973) of the Penman formula, and assuming that vapour flux was equal to sap flux. Net radiation, not measured, was assumed to be 70% of the global radiation. Aerodynamic conductance was calculated with the Monteith formula, from wind speed and mean height of the stands. Early morning values (6–8 am) were eliminated from this calculation because evaporation of dew adversely affects the estimates of canopy conductance with the Penman–Monteith equation.

RESULTS

Spatial variations of sap flow

Typical daily evolutions of sap flow in different trees of each stand are shown in figure 1. Diurnal variations were in phase for the different trees, but maximum values

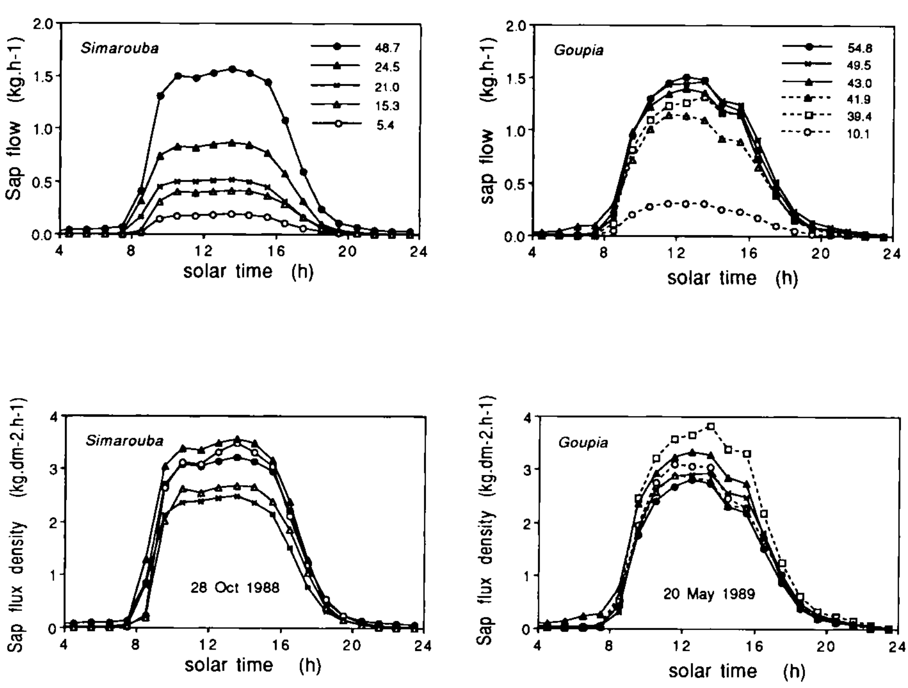

Fig 1. Top: diurnal evolution of total sap flow of *Simarouba* (left) and *Goupia* (right) for the different trees during 2 bright days. Sapwood area (cm^2 at dbh) of each tree is also indicated. Bottom: corresponding sap flux density evolution for the same trees and days.

and daily sap flow showed marked differences: total daily sap flow ranged from 1.4 $kg.d^{-1}$ to 13.3 $kg.d^{-1}$ for *Simarouba*, and from 2.3 $kg.d^{-1}$ to 11.4 $kg.d^{-1}$ for *Goupia*. The most important variable was the size, and hence the sapwood area of the individuals (see eq (2)). The sap flux density shown in figure 1 for the same days was less variable from tree to tree. Coefficients of variation ranged only between 15–20%.

As shown in figure 1, the between-tree variability in the *Goupia* experiment was less important, due to a greater homogeneity of the stand, as compared with the *Simarouba* one. During the brightest days, maximum sap flux density attained 3.5–4.0 $kg.dm^{-2}.h^{-1}$.

Diurnal evolution of water relations

Figure 2 shows diurnal time-courses of sap flow, water potential and stomatal conductance measured for several trees of both species, concurrently to the evolution of the climatic factors. Vapour pressure deficit *(vpd)* remained relatively low during the day, which is a characteristic of these equatorial areas where minimum relative humidity is about 70%. Diurnal sap flow increased sharply in the morning, from 8 to 10 am after dew evaporation. While global radiation and vpd continued to increase after 10 am, sap flow remained approximately constant for *Simarouba*, and began to decrease for *Goupia*, indicating stomata were closing at this time. A continuous decrease of stomatal conductance was observed all day from the earlier measurements (11:00) to the later ones (17:00). It was probably a consequence of the inhibiting effect of increasing *vpd* on stomatal conductance. In a first approximation *Ju* is proportional to the product of stomatal conductance times *vpd*, which explains why *Ju* fell about 30% while stomatal conductance decreased > 50%.

Measured predawn leaf water potentials were high for both species and close to zero (–0.2 to –0.1 MPa), indicating a high water availability in the root zones. Diurnal minimum values were similar for the studied trees, ranging from –1.5 to –1.8 MPa. Stand structure may explain this low variability in leaf water potential. A large distance between the planted trees allows significant available energy penetration into the crowns, even for the smallest trees.

Whole-tree hydraulic conductance was similar for both species: 0.351 10^{-5} $mol.m^{-2}.s^{-1}.Pa^{-1}$ for *Simarouba* and 0.319 10^{-5} $mol.m^{-2}.s^{-1}.Pa^{-1}$ for *Goupia*.

Average daily accumulated values of sap flow were 5.7 $kg.tree^{-1}$ for *Simarouba* and 11.2 $kg.tree^{-1}$ for *Goupia* for the days shown in figure 2. On a stand basis, extrapolating measures of sap flow (see eq 3) this yielded 2.8 $mm.d^{-1}$ and 2.1 $mm.d^{-1}$ respectively. Such low stand transpiration was due to low potential evapotranspiration (PET) (3.7 and 3.3 $mm.d^{-1}$ for the 2 d of measurement), as a consequence of high air humidity and shortness of the daylight period.

Stand transpiration and potential evapotranspiration

The relationship between stand transpiration *(T)* and potential evapotranspiration *(PET)* is given in figure 3 for the 2 stands; maximum values of *T* and *PET* were 2.8 and 5.5 mm respectively. The relationship was not significantly different between *Goupia* and *Simarouba*. It can be observed that *T* was not linearly related to *PET* above 4 $mm.d^{-1}$. For days with a highest evaporative demand, *T* was about only 50% of Penman evapotranspiration, as a consequence of the effect of quite high vapour pressure deficit on stomatal conductance.

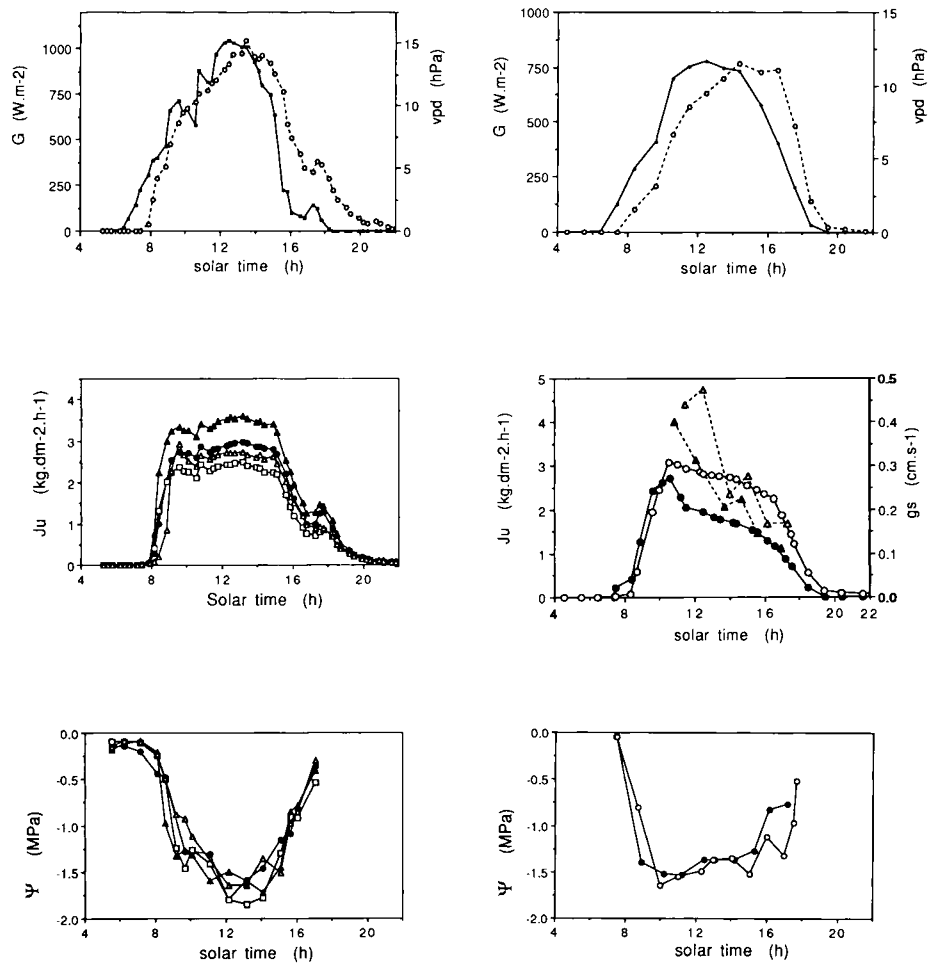

Fig 2. Diurnal evolution of: top: global radiation *(G)* ----, vapour pressure deficit *(vpd)* o----o; middle: sap flux density *(Ju)* and stomatal conductance *(gs)*; bottom: leaf water potential *(ψ)*, measured on 4 *Simarouba* (left) and 2 *Goupia* (right) during 2 bright days.

The relationship between vapour pressure deficit and canopy conductance, as calculated from sap flow and Penman–Monteith equation, is given in figure 4 for the 2 plots. The inhibiting effect of *vpd* on canopy conductance can be observed for both species, even at low values (4 hPa), as previously seen on stomatal conductance. For higher *vpd*, *Simarouba* exhibited higher canopy conductance than *Goupia*. This difference became significant above 8 hPa, leading to 20% greater values for *Simarouba* than for *Goupia* which appeared to be more sensitive to vapour

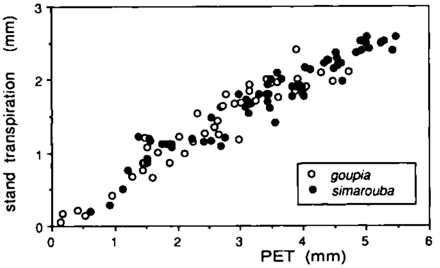

Fig 3. Relationship between stand transpiration computed from sap flow, and Penman potential evapotranspiration *(PET)* for the 2 species. Each point is a daily value.

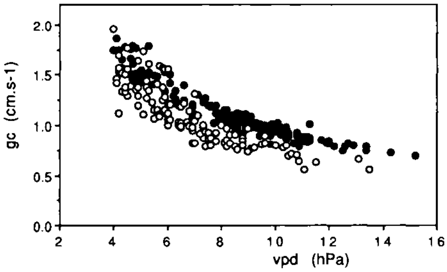

Fig 4. Effect of vapour pressure deficit *(vpd)* on calculated canopy conductance (gc) of the 2 plots; data are hourly values during days without rain. Same symbols as used in figure 3.

pressure deficit of the air. For both species, canopy conductance dropped below 1.0 cm.s^{-1} when *vpd* increased > 10 hPa. On *Goupia*, a good agreement was found between estimations of canopy conductance from i), stomatal conductance, *vpd* and leaf area index *LAI* giving values decreasing from 1.48 cm.s^{-1} to 0.72 cm.s^{-1} and ii), Penman–Monteith equation giving values ranging from 1.67 cm.s^{-1} to 0.60 cm.s^{-1}.

DISCUSSION AND CONCLUSION

These experiments show higher sap flux densities than those measured on temperate species whose maximum rates range typically between 2 and 3 kg.dm^{-2}.h^{-1} either for coniferous species, such as *Pinus pinaster* (Granier *et al,* 1990) or broadleaved species such as *Quercus petraea* (Bréda and Granier, unpublished data). In tropical rain forests, values as high as 4 kg.dm^{-2}.h^{-1} seems to indicate a very efficient hydraulic conducting system in the tree, as the evaporative demand is generally not very important. Experiments reported by Huc and Guehl (pers comm) in pioneer species like *Jacaranda copaia* showed a high hydraulic efficiency, calculated as the ratio of stomatal conductance to soil-to-leaf water potential gradient.

The computed stand transpirations yielded quite low ratios of transpiration: potential evapotranspiration. For bright days, without rain events, the average ratios were 0.51 for *Simarouba* (over 64 d) and 0.48 for *Goupia* (90 d). This is likely a consequence of low sapwood basal areas and *LAI* of these young plantations; evaluations of *LAI* in the studied stands gave values < 4.0 (table I). Alexandre (1981) estimates in natural forest were close to 7.0. It may be considered that it ranges from 5.5 to 8.2, according to the structure of the forest and its phenology. Measurements made by Shuttleworth *et al* (1984) over a natural stand in the Amazonian forest gave values of transpiration of ≈ 70% of Penman evaporation during bright days, and in non-limiting soil water conditions. Nevertheless, total evapotranspiration of these forests may exceed *PET* when interception of precipitation is taken into account (Shuttleworth, 1989).

Estimations of surface conductance of the 2 studied plots, and the measurements of stomatal conductance shown in figure 2 during days without rainfall indicate a high sensitivity of stomata to *vpd*; these observations have been previously reported by Huc and Guehl (1989) in several other species from French Guyana. The threshold of stomatal closure appears (see figs 2, 4) for air vapour deficits close to 5 hPa, a value attained between 9:00 and 10:00 for bright days. On the other hand, dew evaporation typically lasted until 8:00. Thus for the 2 studied species transpiration showed a very sharp increase during the morning, from 8:00 to 10:00, at which time sap flow was close to its maximum. This high sensitivity to *vpd* produces a sap flow figure showing a plateau or a slight decrease during mid-day (10:00 to 15:00). Therefore for both species, increasing *vpd* did not increase plot transpiration, which levels off around 2.5 $mm.d^{-1}$. Transpiration of natural tropical forests will probably show a different behaviour, as it has a complex mix of species and also because of its multi-layered structure. The combination of an upper layer fully exposed to the sun with lower ones at lower *vpd* should lead to a greater consumption of available energy. Nevertheless, even for closed stands, latent flux estimates of Shuttleworth *et al* (1984) showed a strong control of transpiration, as a consequence of the high sensitivity of tropical forest species to low air *vpd*.

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