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Variations in water use by a mature mangrove of *Avicennia germinans*, French Guiana

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Abstract

- In the tropical intertidal zones, little is known on water uptake by mangroves. Transpiration rates are generally measured at leaf level, but few studies exist on water use at tree or stand levels.
- The objective of this study was to measure sap flow in trees of different sizes to appreciate the range of variation in water use that may exist in a site dominated by 80% mature *Avicennia germinans*.
- The results showed that from the dry to the wet season the mean water use increased from 3.2 to 5.3 dm³ d⁻¹ in small trees (DBH ~ 13 cm), from 11.5 to 30.8 dm³ d⁻¹ in medium trees (~24 cm) and from 40.8 to 64.1 dm³ d⁻¹ in large ones (~45 cm).
- Sapwood remained active up to a depth of 8 cm with radial variations within the stem. Weak correlations were obtained with VPD and net radiation.
- This study confirmed that transpiration was larger under low levels of salinity. Water use at stand level (~1900 living stems ha⁻¹) was estimated to be in the range of 5.8 to 11.8 m³ ha⁻¹ d⁻¹ according to the season.

Résumé – Variations de la consommation d'eau d'une mangrove adulte à *Avicennia germinans*, en Guyane française.

- Dans les zones intertidales tropicales, des taux de transpiration sont généralement mesurés au niveau des feuilles, mais il existe peu d'études sur la consommation d'eau à l'échelle de l'arbre ou de la parcelle.
- L'objectif de cette étude était de mesurer les flux de sève dans des arbres de différentes tailles pour apprécier la gamme de variation de la consommation d'eau qui peut exister dans un site dominé à 80 % par des *Avicennia germinans* adultes.
- Les résultats montrent que la consommation moyenne d'eau, entre une saison sèche et humide, augmente de 3.2 à 5.3 dm³ jour⁻¹ chez les petits arbres (DHP ~13 cm), de 11.5 à 30.8 dm³ jour⁻¹ chez les arbres moyens (~24 cm) et de 40.8 à 64.1 dm³ jour⁻¹ chez les plus gros (~45 cm).
- L'aubier restait actif jusqu'à une profondeur de 8 cm avec des variations radiales dans le tronc. Les corrélations avec le DPV ou le rayonnement se sont révélées globalement faibles.
- Cette étude confirme que les mangroves transpirent plus avec des salinités faibles et indique qu'au niveau de la parcelle (~1900 pieds vivants ha⁻¹) la consommation d'eau varie de 5.8 à 11.8 m³ ha⁻¹ jour⁻¹ selon la saison.

1. INTRODUCTION

Mangroves develop widely in the tropical intertidal zones over 170 000 to 200 000 km² (Saenger, 2002). Species distribution is strongly influenced by the substrate (from soft to firm mud), by periodic flooding under tidal influence and by the soil salinity, which can reach several times the salt concentration of sea water. One consequence of this drastic environment is the limited number of species that can survive

and develop. The poor floristic and taxonomic composition of mangrove trees in the Atlantic Ocean and on the Pacific coast of the Americas was noticed early, with only 8 species, compared with the eastern group from East Africa to South-East Asia and Australia with 40 species (Tomlinson, 1986). From Florida to South Brazil, three species dominate, i.e. *Avicennia germinans*, *Rhizophora mangle* and *Laguncularia racemosa*. In French Guiana, *A. germinans* occupies about 80% of the mangrove stands (Fromard et al., 1998; Lescure and Tostain, 1978) and has the lowest genetic diversity of all the Atlantic Ocean sites (Dodd et al., 2002).

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Water use by trees in the intertidal environment has always been considered as a key process for understanding the unique life traits of mangroves. However, this process is still relatively unknown. Scholander (1968) first showed that the xylem water potential of mangroves was very low (-30 to -60 bars) and sufficient to counterbalance the low water potential of sea water or saline soils (e.g. -25 bars for a 3% concentration of sodium chloride). However, an excess of salt may lead to vessel blockage and stem death (Ewers et al., 2004). In the past, in the absence of direct measurements, there was some controversy as to whether mangroves had high or low rates of transpiration. Tomlinson (1986) showed that mangroves tolerate or prefer salt only to a limited degree. Recent studies based on non-destructive methods have shown that mangrove transpiration rates are actually low when compared with non-saline plants, but not intrinsically low as they vary with the salt concentration in the environment (Saenger, 2002). For example, *A. germinans* displays higher rates during the wet season (around $4 \text{ mmol m}^{-2} \text{ s}^{-1}$ around noon) than during the dry season ($< 1 \text{ mmol m}^{-2} \text{ s}^{-1}$) and even higher rates when grown without salt (Sobrado, 1999; Suarez et al., 1998). Salinity is therefore a key factor for understanding the variation in water use and for any comparison between species and sites.

Mangroves have developed salt resistance. They absorb salt together with water and are constantly confining it by transferring it to the leaves or to other tissues (Popp, 1995). The absorbed salt is primarily excreted metabolically by salt glands in the leaves. In non-secreters such as *Rhizophora*, the salt concentration in xylem sap is less than one-hundredth of that of sea water but still almost 10 times more concentrated than that in non-mangrove plants such as *Eugenia* and *Hibiscus*. Therefore, mangroves tend to accumulate salt but this is partly compensated for by losing it through salt glands, cuticular transpiration or leaves. Mangroves as a group have acquired a conservative water use strategy (namely, low transpiration rates and elastic cell walls). In this respect, *A. germinans* seems to be the most efficient, as demonstrated by Sobrado (2000) in Venezuela in the middle of a wet season. At midday, the author measured not only significantly lower transpiration rates in *A. germinans* ($6.18 \text{ mmol m}^{-2} \text{ s}^{-1}$) than in *R. mangle* and *L. racemosa* (6.95 and $6.83 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively) but also significantly higher photosynthetic rates and water-use efficiency. These results confirmed those of Lin and Sternberg (1992), Medina and Francisco (1997), and Sobrado (1999). However, when the trees are growing in exactly the same habitat there may be no significant differences in terms of transpiration rate, stomatal conductance, net primary productivity and instantaneous transpiration efficiency (Snedaker and Arujo, 1998).

It is therefore clear that water use among the same mangrove species is highly variable and must be considered in relation to local salinity, season and tree size. In the above studies, the measurements mainly dealt with transpiration rates using portable plant leaf chambers. It is necessary to extrapolate from the leaf to the entire canopy (which is not a simple matter) to obtain an estimate of the whole-tree water use. An alternative approach is based on sap flow measurements in the stem which provide easier integrative indications once the ac-

tive sapwood sections of stems are known. Surprisingly, very few sap flow measurements have been undertaken to monitor mangrove stands. Difficulties in instrument maintenance in the mangal environment may explain this lack of data. Becker et al. (1997) used a heat pulse velocity method and observed maximum sap velocities close to 0.13 mm s^{-1} and daily sap flow in the range 0.78 to $3.0 \text{ m}^3 \text{ d}^{-1} \text{ m}^{-2}$ of basal area. Measurements were made over three days in Brunei and on two species, *Avicennia* cf. *alba* Blume and *Rhizophora apiculata* Blume. No data have been published yet about long-term records of sap flow over seasons and contrasted climates to document seasonal variation in water use in mangroves.

The extreme conditions for the mangroves on the coast of the Guianas (including French Guiana, Suriname and Guyana) can be partly explained by the influence of the Amazon River. About 20% of the enormous mud supply of the Amazon is deflected north-west towards this coast due to oblique wave approach (Balzer et al., 2004; Froidefond et al., 2004). The particulate flux is transported in shoreface-attached and subtidal mudbanks, thus creating the longest mud coastline in the world, from Brazil to Venezuela. These non-stable mudbanks migrate at a rate of about 1.4 km per year and the upper intertidal fringe is colonized by mangroves (Allison et al., 2000; 2004). Historical maps of the shoreline demonstrate that the accretion and erosion associated with mudbank passage have followed ~30-y cycles over the last two and a half centuries (Plaziat and Augustinus, 2004). One consequence of these Amazon-influenced dynamics is that mangroves must develop on very recent mud deposits and that they rarely survive longer than 15–20 y.

In this restricted environment, which is still virtually free from human intervention, *A. germinans* seems especially well adapted. The root system consists of superficial (25–30 cm) long horizontal “cable” tracing roots on which pencil-like pneumatophores are erected upwards emerging through the substrate and downwards small second-order vertical anchoring roots more or less alternating with the pneumatophores (Tomlinson, 1986). Fine dense third- and higher-order roots considerably increase the absorption capacity. However, the effective depth of roots probably does not exceed 1 m. Observation of dead trees uprooted by erosion on the sea front indicated no vertical larger anchoring roots. *A. germinans* is an efficient pioneer species, primarily because of its reproductive capability and its unique biological features, notably vivipary. Populations of *A. germinans* develop in bands parallel to the coastline. This zonation in space corresponds to a zonation in time with increasing age as the distance from the sea increases. Meanwhile, the mud becomes more and more stable along an increasing slope gradient from the sea to the land. *A. germinans* forms populations without succession and without stratification, as generally no understorey develops.

The objective of this study was to measure water use by a mature *A. germinans* forest in a high saline environment in French Guiana. It was assumed that, since salinity decreases slightly during the wet season, water use by trees would increase consecutively. The first objective was therefore to quantify these changes and to observe the range of variability in water use that may exist between seasons. Additional goals were

to try to relate sap flow to local meteorological parameters and to see how far water use modeling was possible. One uncertainty was the radial depth into the stem at which sapwood remained active and how far sap flow was homogeneous within the stem.

2. MATERIALS AND METHODS

2.1. Study site

The study site was chosen near the village of Sinnamary (French Guiana) along the former coastal road which is parallel to the sea. The road was partly destroyed by an erosion phase in the 1970s. It was built on the sand bank (chenier) which represents the permanent coast line. The mangrove of Sinnamary is now in an extension phase and covers a large stretch between the remaining road and the open sea (30 km long and 4 km wide). A gradual zonation is visible from the sea to the land with trees of increasing age. In the back mangrove the tree density is lower due to dying out as contact with the sea decreases, the accumulation of fresh water, concentration of sulfites and acidification of the soil (Lambs et al., 2007; Marchand et al., 2004). The study site was located at a distance of 3.5 km from the village and 300 m from the road (Easting 52° 56' 05"; Northing 5° 23' 22").

2.2. Environmental measurements

Three measurement campaigns were organized in November 2003, November 2004 and March 2005. Two piezometers were installed in the site and one was equipped in 2004 and 2005 with a Diver automated pressure gauge (Eijelkamp, NL) to monitor continuous fluctuations in groundwater level. Salinity measurements were made in the field, on groundwater, sea water, and on drops of soil solution. When large water samples could be obtained, a field multiparameter (WTW, Germany) with a Tetracon electrode provided the measurements of salinity. For small samples, salinity levels were determined on drops using an Atago refractometer. Drops of soil interstitial water were extracted from soil samples through a filter paper using a hand garlic-press.

Two trees were equipped with air temperature (T) and relative humidity (RH) sensors located 1.5 m above the ground with data acquisition at the same rate as sap flow data, in order to calculate the air vapor pressure deficits (VPD). Rainfall data and insolation data were obtained from the Savane-Combi meteorological station 5 km from the village of Sinnamary by MétéoFrance. Over the measurement period, in the weather stations of INRA Paracou (20 km) and in the Guiana Space Center (CSG) in Kourou (30 km) rainfall and global radiation were available but not Penman evapotranspiration (PET).

2.3. Information about plants in the study site

The characterization of the forest stand was based on stem diameter and not age as many tropical trees do not form annual rings, which prevents easy calculation of tree age from tree ring cores. The wood of *A. germinans* presents irregular and anastomotic rings which consist of bands of hard and persistent xylem, alternating with bands

of conjunctive tissue including strands of phloem which decay relatively rapidly (Tomlinson, 1986). The successive rings of xylem and phloem are produced from successive cambia, but do not correspond to annual rings. They are linearly correlated with the stem diameter and are under endogenous control (Tomlinson, 1986).

Detailed observations were made over 1600 m² of the mature forest of *A. germinans*. The following information was collected on each mangrove tree: species, X, Y coordinates, diameter at breast height (DBH), height, health status (+, –, dead) and dominance (yes/no). Juice was extracted from fresh leaves using a manual juicer for salinity measurements in the field with the WTW multiparameter. Drops of sap were extracted from sapwood cores using a hand-made pressure chamber (Lambs and Berthelot, 2002) mounted on a standard portable 8-ton car jack. A test to determine tree age was also carried out on five wood cores with ¹⁴C.

2.4. Sap flow measurements

No information was available on sap flow for *A. germinans*. A preliminary study was done during the dry season (November 2003), on three neighboring *A. germinans* trees, with DBH ranging from 12 to 16 cm, each with differing health status. The following year, the most declining tree was dead. The measurements were repeated during the following dry season (November 2004) and during a rainy season (March 2005). Six trees were fitted with instruments in order to cover the range of variation in stem diameters, namely the remaining previous two small trees (DBH = 12–15 cm), two medium trees (DBH = 23–25 cm) and two large trees (DBH = 43–47 cm). The characteristics of the 7 trees used for the sap flow measurements are summarized in Table I.

Sap flow measurements were made by inserting 2-cm heat dissipation probes in each stem. Each sensor is a thermocouple and consists of two identical needles (UP GmbH, Germany). They were initially designed by Granier (1985). The upper needle is heated and positioned 10 cm above the lower. An increase in sap flow decreases the temperature difference between the two needles. The probes were thermally isolated and protected with Trisodur material (4 reflective aluminium foils alternating with three thermo-insulator Dacron layers). The heating of the probes was maintained using 12-Volt DC batteries. Sap flows were measured within a stem by inserting probes at three increasing radial depths (0–2 cm, 2–4 cm and 4–6 cm). Measurements were made every 30 s and data were averaged and recorded every 5 min in dataloggers (Skye Instruments Ltd, UK). The dataloggers, current regulators and batteries were housed in a weatherproof box fixed against the trunk on wooden poles 1 m above soil level. Each sensor provided 288 measurements daily, each corresponding to the mean value over 5 min. Data were acquired and stored as tensions (in millivolts) in the dataloggers and later downloaded into a laptop. They were then converted into sap flow densities (SFD) following the standard procedure detailed by Granier (1985), and expressed in a volume of sap per time unit and per area unit of sapwood, typically in dm³ h⁻¹ dm⁻². This instantaneous flow varies continuously through time and has a minimum early in the morning and a maximum close to midday.

At the depth *i* in a stem, the effective daily flow Q_i (in dm³ d⁻¹) was computed by adding the 288 measurements collected every day and by multiplying them by the corresponding sapwood area A_i (i.e. the 2-cm-wide ring at the depth *i*), following the equation

$$Q_i = A_i * \sum_{288} SFD_i.$$

Table 1. Characteristics of the *A. germinans* trees, used for the sap flow measurements. S, M and L correspond to size class small, medium and large respectively. In March 2005, trees M1 and L1 were used for a test at 6–8 cm, and L1 for a test in three distinct orientations.

Measurement campaigns	Tree code	Health status	Height (m)	DBH (cm)	Ring section (dm ²)					% of the stem section	
					0–2 cm	2–4 cm	4–6 cm	6–8 cm	Stem	over 0–6 cm	over 0–8 cm
November 2003	S1	++	14	11.8	0.61	0.36	0.11	0.00	1.09	100.0	100.0
	S2	+	20	14.6	0.79	0.54	0.29	0.06	1.68	96.7	100.0
	S3	–	19	15.6	0.85	0.60	0.35	0.10	1.91	94.7	100.0
November 2004 and March 2005	S1	++	14	12.0	0.63	0.38	0.13	0.00	1.13	100.0	100.0
	S2	+	20	14.7	0.80	0.55	0.30	0.06	1.70	96.6	100.0
	M1	++	30	23.7	1.36	1.11	0.86	0.61	4.41	75.6	89.4
	M2	++	25	24.3	1.40	1.15	0.90	0.65	4.64	74.4	88.3
	L1	++	35	43.9	2.63	2.38	2.13	1.88	15.14	47.2	59.6
	L2	++	38	46.6	2.80	2.55	2.30	2.05	17.06	44.9	56.9

The whole-tree daily sap flow Q was obtained by adding all daily sap flows Q_i computed at each depth i , following the equation

$$Q = \sum_i Q_i = \sum_i (A_i * \sum_{288} SFD_i).$$

These values Q and Q_i are therefore sensitive to the tree size. At the time of the experiments, no probes were manufactured for measurements at depths beyond 6 cm, and it had to be implicitly assumed that water use by trees occurred only within the external 6 cm of the stems. However, in order to verify if sap flow existed beyond a radial depth of 6 cm a test was done in March 2005 by inserting probes in trees M1 and L1 at a depth of 6–8 cm. First, a hole was dug in the stem (one-cm square by two-centimeters deep), then the longest available probes (6 cm) were inserted. An additional test was done in March 2005 in tree L1, to verify the homogeneity of sap flows in three distinct orientations within the same stem.

2.5. Statistical treatment

Statistical tests and analysis of variances and linear regressions were done using Statgraphics Centurion XV (StatPoint, Inc.). Confidence limits around the means are provided in the text by ± 2 *standard errors.

3. RESULTS

3.1. Environmental measurements

During the three sap flow measurement campaigns (dry season 2003, dry season 2004 and wet season 2005), mean global radiation was 1967, 1998 and 1812 J cm⁻² d⁻¹, the mean insolation 7.9, 7.8 and 6.5 h d⁻¹ and mean daily temperatures 25.8, 25.7 and 26.0 °C, respectively. The mean daily rainfall was 3.8, 1.1 and 4.4 mm, respectively. Cumulated rainfall in October and November was slightly lower in 2004 than in 2003 (148 vs. 162 mm). Thus, measurements in the dry season 2004 were made under more severe conditions than in 2003. However, the water table level was close to –0.94 and –0.92 m, respectively. At the end of the dry season 2004, it reached a minimum of –172 cm on December 26. The rainy season started on December 27. In one month the total rainfall reached 517 mm

and the water table level steadily rose, reaching the soil surface on January 15th. At the end of the month, the site was permanently inundated with 40 cm of water up to March 2005 when the last sap flux measurements were made.

During the dry seasons, soil salinity was in the range 30–50‰ in the organic-rich surface, 61–74‰ at 20 cm and 65–82‰ at 50 cm (i.e. almost twice open sea water salinity, 35‰). The groundwater salinity remained close to 65‰. During the wet season the salinity of the permanently stagnant water was low (3–6‰). The juice of fresh leaves extracted in situ from 12 mature *A. germinans* trees over several days during the wet season had salinities ranging from 18 to 26‰. Within one tree, a test on 4 branches indicated that the salinity was very homogeneous, with variations below 1‰ salinity. Another test done on 5 neighboring trees at 11 a.m. and at 2 p.m. showed overall variations in salinity in the range of 18–23‰, but no significant differences between trees. In contrast, the leaves of 1-3-year-old *A. germinans* located in front of the sea had lower salinity (15–20‰) and the first two leaves collected on young seedlings within the mature forest under study had the lowest salinity with 10‰. In November 2004, the salinity of the sap extracted from the 6 trees was in the range 100 to 120‰, i.e. around three times higher than sea water, which is considerably higher than the salinity reported by Scholander (1968), namely one-tenth that of sea water. During the rainy season, sap salinity decreased slightly to 80‰.

3.2. Structural characteristics of the mangrove forest

Measurements in the forest stand of 1600 m² revealed a very high density of trees, with 2790 individuals per hectare, including 827 dead trees per ha (about 30%) and 1963 living trees per ha (70%). Of the dead trees, only 7 had a diameter above 12 cm. In other words, most of the dead trees were young individuals which could not reach mature stages. Among the dead trees 92.5% were *A. germinans*, 6.8% were *L. racemosa* and 0.7% were *R. mangle*. By contrast, among the living trees, 80% were *A. germinans* and 20% *L. racemosa*. No *R. mangle* was alive. No living *L. racemosa* had a diameter above 3.8 cm, indicating that, in this environment, the only

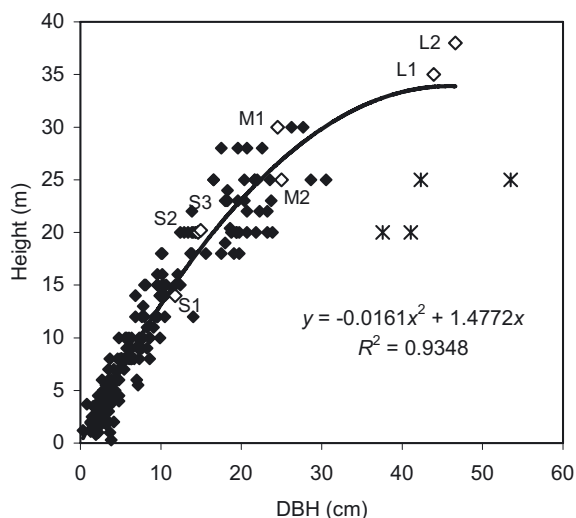


Figure 1. Diameter-height relationship for living *A. germinans* ($n = 246$ trees). The letters S, M and L and the white dots indicate the positions of the small, medium and large trees selected for sap flow measurements.

species able to reach a mature stage was *A. germinans*. During the rainy season, young seedlings had a mean density of 26 individuals per m^2 . All were *A. germinans*. Not one survived.

A diameter-height relationship was obtained among the dominant living adults of *A. germinans* using a polynomial model (Fig. 1). The degree-2 polynomial was necessary to model the relative decrease in height which exists among the larger trees where dieback is frequently observed on the higher branches. Four large declining trees with heights in the range 20–25 m were excluded from the model. For trees with $\text{DBH} < 30$ cm a simple linear model could describe quite well the diameter-height relationship using the equation $y = 1.1962x$ ($R^2 = 0.90$). Thus, in this mangrove forest the height (in meters) of the living *A. germinans* can be roughly estimated as 1.2 times the DBH (in cm), for trees with diameters between 1 and 30 cm. With ^{14}C analysis carried out on 3 wood samples we noticed that the growth rate was about 1.0 cm per year in radius. This was consistent with a possible establishment in a newly settled mudbank in 1989–90 as seen from satellite photos (Fromard et al., 2004).

3.3. Dieback effect on water use

The initial measurement period was 11 days during the dry season (9–19 November 2003) with a comparison of sap flow in only three small mature *A. germinans* trees (S1, S2 and S3). Trees S1 and S2 were healthy while tree S3 showed signs of decline, with a smaller canopy and the bark in bad condition (Tab. I). Together, they were similar in terms of DBH (~12–16 cm). The three sap flow probes inserted radially at 0–2 cm, 0–4 cm and 0–6 cm in each stem provided a good estimate of the whole-tree water use as they could integrate sap flows over 95 to 100% of the total stem sections. The results showed that over this first measurement period, the whole-tree water use (Q) ranged from 3.2 to 5.1 $\text{dm}^3 \text{d}^{-1}$ for S1, from 4.6

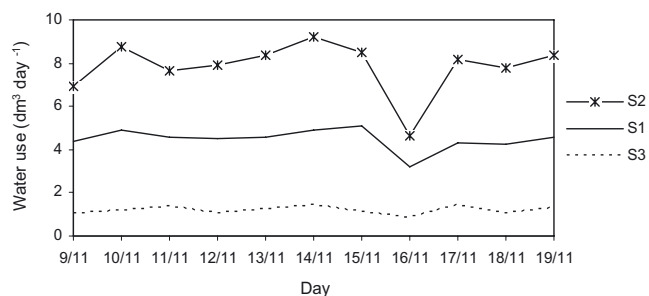


Figure 2. Comparison of the daily water use by three small *A. germinans* during the dry season 2003. The decrease in water use on 16th November was due to a rainfall.

to 9.2 $\text{dm}^3 \text{d}^{-1}$ for S2 and from 0.9 to 1.4 $\text{dm}^3 \text{d}^{-1}$ for S3 (Fig. 2). The mean daily Q values over 11 d were 4.5, 7.8 and 1.2 $\text{dm}^3 \text{d}^{-1}$, respectively. Trees S2 (healthy) and S3 (dominated and declining) were almost the same height (20 m and 19 m) and the same diameter (14.6 cm and 15.6 cm) but had very distinct water uses which differed by a factor of 6. The dieback status of S3 clearly explains its very low daily water use.

3.4. Variation in water use with the tree size and the season

The following year, S3 had no more leaves, was considered to be dead and no more measurements were made on it. Sap flow measurements were made during a second dry season over 17 d (21 November–7 December 2004), i.e. slightly later than in the dry season 2003 (9–19 November 2003). The results indicated that the daily water use (Q) was from one-third to one-half lower than in 2003. It ranged from 2.0 to 3.7 $\text{dm}^3 \text{d}^{-1}$ for S1 and from 1.8 to 4.1 $\text{dm}^3 \text{d}^{-1}$ for S2, with mean Q values of 3.0 and 3.4 $\text{dm}^3 \text{d}^{-1}$, respectively (Fig. 3). Measurements made simultaneously on medium and large trees showed that the mean water use was 7.3 and 15.7 $\text{dm}^3 \text{d}^{-1}$ for trees M1 and M2, and 29.7 and 52.0 $\text{dm}^3 \text{d}^{-1}$ for trees L1 and L2.

Three months later, during the short wet season, measurements were repeated on the same six trees over 12 d (10–22 March 2005). The site remained permanently inundated during the measurement period. For S1, S2, M1, M2, L1 and L2 the mean daily Q values were 3.1, 7.5, 25.1, 36.5, 65.0 and 63.2 $\text{dm}^3 \text{d}^{-1}$, respectively (Fig. 3). Compared with the dry season, the overall mean daily water use in the wet season, computed over the six trees, increased from 18.5 to 33.4 $\text{dm}^3 \text{d}^{-1}$, i.e. by 15 $\text{dm}^3 \text{d}^{-1}$ per tree. Water use patterns were also more variable from one day to the next than during the dry season (e.g. standard deviations in March were twice as high as in November).

3.5. Variation in sap flux densities

The SFD (in $\text{dm}^3 \text{dm}^{-2} \text{h}^{-1}$) corresponds to sap flow ($\text{dm}^3 \text{h}^{-1}$) per unit area of sapwood (dm^2) and facilitates comparisons between radial depths and between trees and provides

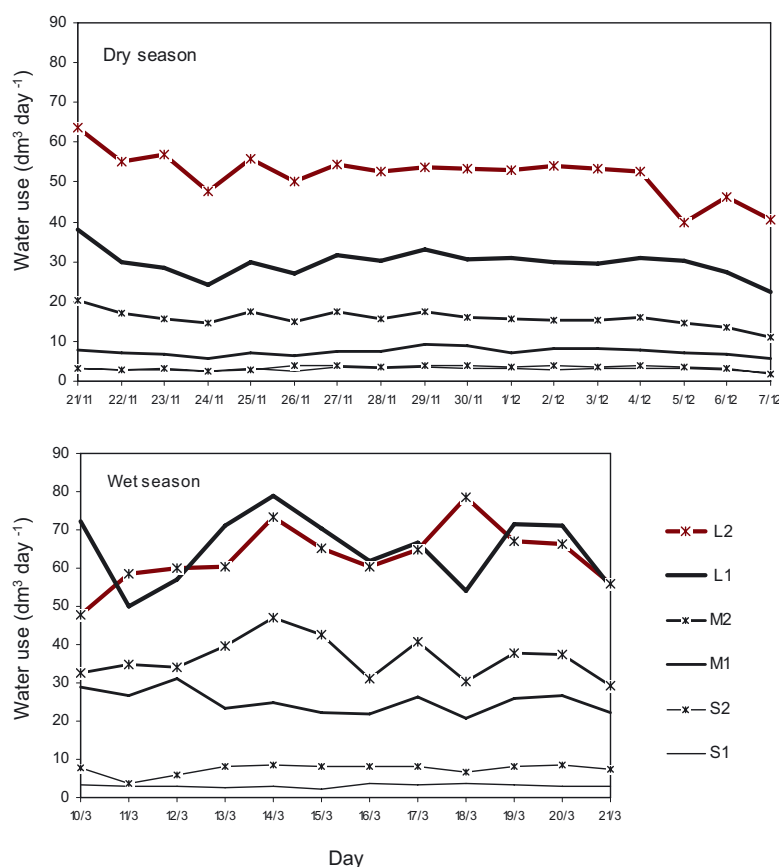


Figure 3. Comparison of the daily water use of six *A. germinans* trees in November 2004 (dry season) and March 2005 (wet season). S, M and L correspond to size class small, medium and large, respectively.

an explanation of the effective daily water use computed at the tree level. The results indicated that in *A. germinans* sap flows were not limited to only the external rings of the trees but continued to be active at more internal radial depths as well. Daily patterns of sap flow densities remained fairly stable within a season (Fig. 4). The day factor was never significant. The peak in daily SFD values gave an indication of the maximum activity level, e.g. for S1, $\sim 0.8 \text{ dm}^3 \text{ h}^{-1} \text{ dm}^{-2}$ in the dry season 2003, $0.6 \text{ dm}^3 \text{ h}^{-1} \text{ dm}^{-2}$ in the dry season 2004 and $1.4 \text{ dm}^3 \text{ h}^{-1} \text{ dm}^{-2}$ in the wet season 2005. However, for a better comparison, SFD were also computed on a daily basis (in $\text{dm}^3 \text{ dm}^{-2} \text{ d}^{-1}$). For the smaller trees, very highly significant differences ($P = 0.000$) were observed between the 3 seasons in the SFD (3.82 ± 0.32 , 2.49 ± 0.16 and $4.99 \pm 0.19 \text{ dm}^3 \text{ dm}^{-2} \text{ d}^{-1}$, respectively), with a drop during the severe dry season 2004 and the highest activity during the wet season 2005. The 6 trees were comparable only during the dry season 2004 and wet season 2005. An ANOVA with all data ($n = 522$) showed that the 3 factors of variation, namely the seasons, the tree size and the sapwood depth were all very highly significant ($P = 0.0000$). The corresponding adjusted linear model explained $R^2 = 65.3\%$ of the variability of SFD. For an overall mean of $5.65 \pm 0.16 \text{ dm}^3 \text{ dm}^{-2} \text{ d}^{-1}$, the mean SFD was 3.81 ± 0.21 in the dry season 2004 and 7.49 ± 0.26 in the wet season. A general trend of increas-

ing SFD with tree size was suspected (3.3 , 4.3 , 4.4 , 7.7 , 6.5 and $7.6 \text{ dm}^3 \text{ dm}^{-2} \text{ d}^{-1}$, respectively, with the same confidence intervals ± 0.40), probably in relation to the dominance status of the trees. The trend was more obvious when trees were grouped by tree size categories with $3.7 \pm 0.14 \text{ dm}^3 \text{ dm}^{-2} \text{ d}^{-1}$ for S, 6.2 ± 0.28 for M and 7.0 ± 0.27 for L ($P = 0.0000$) (Fig. 5). The general SFD depth profile for the two seasons and the six trees was characterized by very highly significant differences in SFD with depth (5.9 , 6.2 and $4.8 \text{ dm}^3 \text{ dm}^{-2} \text{ d}^{-1}$, respectively, $P = 0.0000$, confidence intervals ± 0.28). However, this general pattern varies significantly with season and tree size (Fig. 5). *A. germinans* decreased SFD during the dry season and increased it during the wet season. This trend was more pronounced from the innermost rings toward the most external ones. In the case of severe dieback, a different pattern was observed, with very highly significant SFD drops both in the external and the innermost rings, as shown with tree S3 in the dry season 2003 (0.49 , 1.19 and $0.18 \text{ dm}^3 \text{ dm}^{-2} \text{ d}^{-1}$, $P = 0.0000$, confidence limits ± 0.09).

3.6. Underestimation of water use in medium and large trees

In large trees, only a fraction of the total sections was taken into account by the sensors at three depths, i.e. about

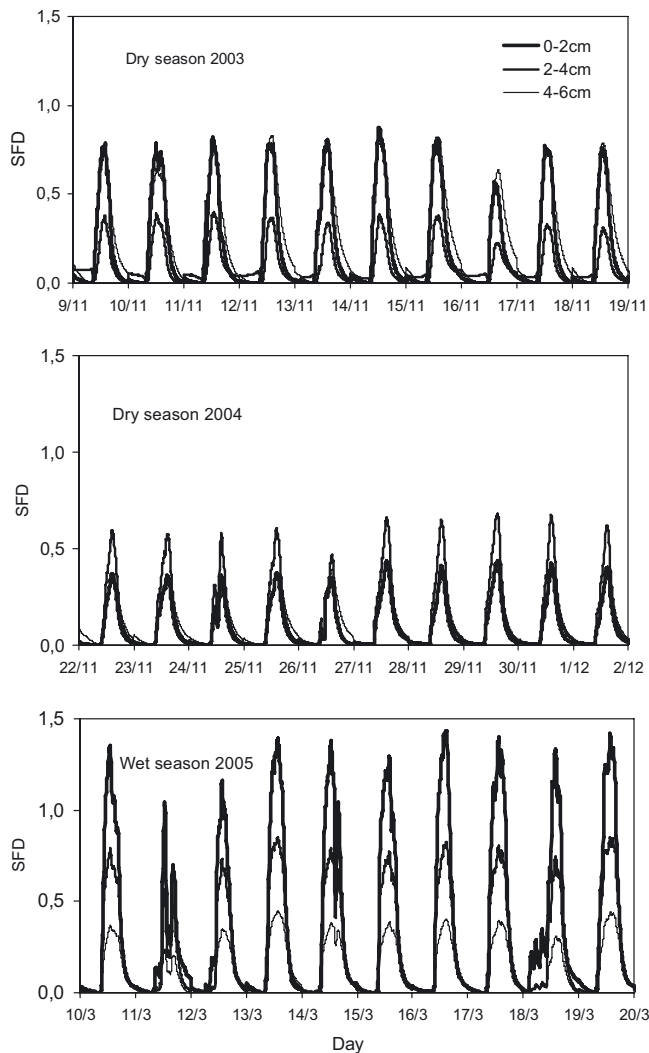


Figure 4. Examples of diurnal and seasonal changes in sap flux densities ($\text{dm}^3 \text{h}^{-1} \text{dm}^{-2}$) for the small *A. germinans* tree S1, during 10 consecutive days. SFD.

75% for M1 and M2 trees and about 45% for L1 and L2 (Tab. I). However, L1 and L2 were among the largest trees of the forest (Fig. 1). A test was done in March 2005 to estimate SFD at depths greater than 6 cm and to evaluate underestimation of water use in large trees. The test was realized on a medium tree (M1) and a large tree (L1) over 5 d. The results showed that SFD remained at 6–8 cm and was not significantly different from SFD observed at 4–6 cm (3.1 and $3.0 \text{ dm}^3 \text{dm}^{-2} \text{d}^{-1}$, respectively). However, the interaction tree*depth was highly significant ($P = 0.0001$). Mean values at 6–8 cm were $3.42 \pm 0.56 \text{ dm}^3 \text{dm}^{-2} \text{d}^{-1}$ in the medium tree and 2.14 ± 0.56 in the large one, compared with 2.51 ± 0.56 and 4.02 ± 0.56 , respectively, at 4–6 cm. The contribution of the 6–8 cm sapwood depth to the mean whole-tree water use of $27.0 \text{ dm}^3 \text{d}^{-1}$ for M1 was $2.1 \text{ dm}^3 \text{d}^{-1}$, an underestimation of 7.2%. The corresponding correction factor to be applied to water use computed between 0 and 6 cm was +7.8%. For the large

Table II. Comparison of mean sapflux densities over 9 d, at three radial depths (0–2 cm, 2–4 cm, 4–6) and in three distinct azimuths (A, B and C) in the stem L1 (in $\text{dm}^3 \text{dm}^{-2} \text{d}^{-1}$, coefficient of variation CV in %).

depth	Orientation			mean	SD	CV
	A	B	C			
0–2 cm	8.6	7.5	11.1	9.1	2.0	21.7
2–4 cm	10.4	7.0	7.8	8.4	1.9	22.1
4–6 cm	9.0	3.8	5.2	6.0	2.7	45.1
mean	9.4	6.1	8.0	7.8	2.2	29.6

tree L1, the mean whole-tree water use was $48.9 \text{ dm}^3 \text{d}^{-1}$ (over 0–6 cm). The underestimation was $4.0 \text{ dm}^3 \text{d}^{-1}$ (7.4%) and the correction factor to be applied +8.2%. Of course, in the absence of verification, it is possible that sap flow does even exist over 8 cm stem depth. However, visual observations on large stems indicated that the hearts of the stems are darker and often dead or empty at depths over 8 cm. Thus, one may consider that if there is sap flow beyond 8 cm, it is fairly negligible. Therefore, in the absence of any additional test, and as a provisional rule of thumb, the suggestion is to apply a general correction factor of +8% on water uses of *A. germinans* trees with DBH > 12, when measurements are made at 0–6 cm only.

3.7. Variation in sapwood activity with the azimuth

In March 2005, a test was carried out over 9 d to verify the homogeneity of SFD with the azimuth in stem L1. Sensor probes were inserted simultaneously in three distinct azimuths (namely A, B and C) and at the three radial depths (0–2 cm, 2–4 cm and 4–6 cm). Azimuth A was on the North side of the stem as for all previous measurements, while B and C were on the South-West and South-East sides, respectively. No significant difference was observed between days but the azimuth factor was very highly significant at the three depths and the depth factor was very highly significant at the three azimuths ($P = 0.0000$, $n = 27$ in both cases, $F = 30.4$ and 28.9 , respectively) (Tab. II). One may conclude that the variability in SFD introduced by depth is equivalent to the variability introduced by the azimuth. Coefficients of variation increased by a factor of two at 4–6 cm, indicating a higher relative SFD variability in the innermost sapwood.

3.8. Difficulty in modeling water use

When examining a single tree, the shape of the diurnal SFD curves clearly showed that soon after the maxima (generally between 12:00 and 14:00 local time), a decrease in SFD occurs in the afternoon. On cloudy days and during rainfall SFD can be drastically reduced. SFD were actually very sensitive to small changes in weather conditions with quasi-simultaneous reactions at all radial depths as shown, for example, on March 14th (Fig. 6). However, daily water use was not always well correlated with environmental parameters. The available PET

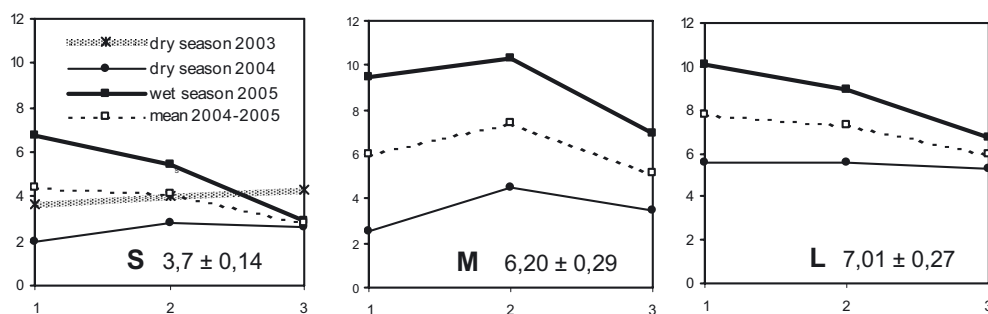


Figure 5. Comparison of the SFD depth profile for the small trees (S), the medium trees (M) and the large trees (L), in $\text{dm}^3 \text{d}^{-1} \text{dm}^{-2}$.

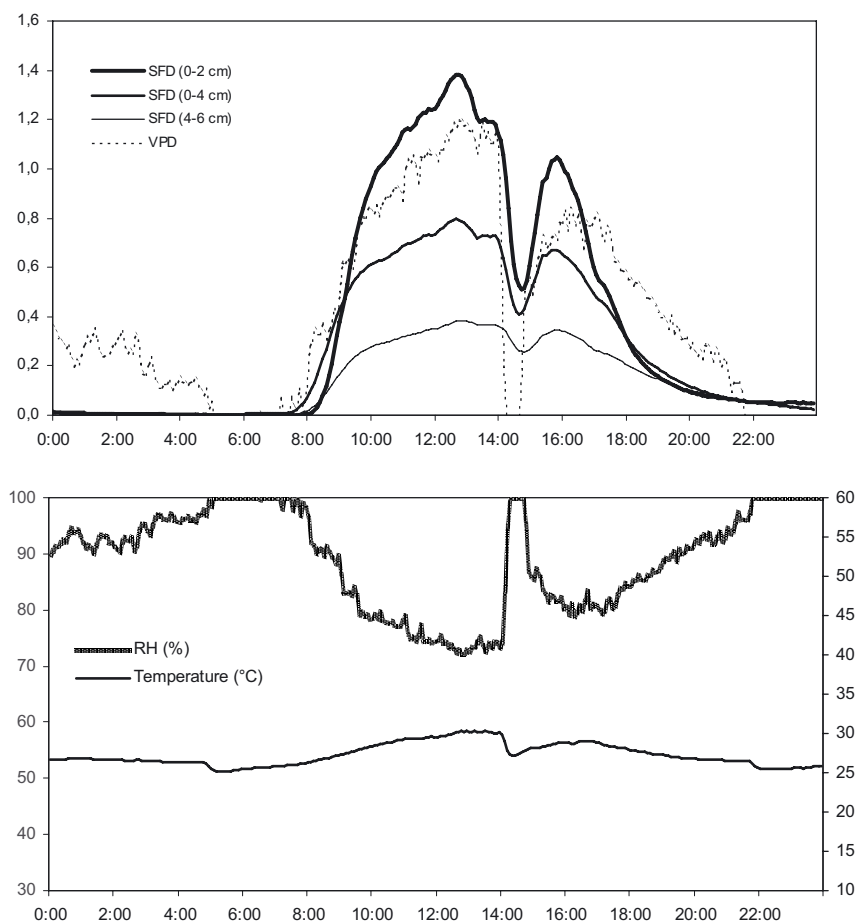


Figure 6. Sensitivity of SFD to changes in vapor pressure deficit on March 14, 2005, following a short rainfall (recorded as 1.5 mm in the nearest weather station at 3 km, but probably locally more significant). The episode lasted about 45 min, around 2 p.m.

data, which were measured too far away from the study site, did not show any correlation with the water use. VPD was the best predictor. Insolation was slightly more efficient than the global radiation. Regressions were weaker during the rainy season (Tab. III).

4. DISCUSSION

In this old mangrove, observation campaigns actually revealed that trees were disconnected from direct tidal influence

but remained in a highly saline environment. SFD measurements were made only in two extreme periods, in two dry seasons and in a wet season with permanent stagnant water. As expected, the water use by individual trees was affected by tree size and season. In the wet season, a strong increase in the mean daily water uptake was observed compared with the dry season, 5.3 vs. 3.2 $\text{dm}^3 \text{d}^{-1}$ in small trees (DBH ~ 13 cm), 30.8 vs. 11.5 $\text{dm}^3 \text{d}^{-1}$ in medium trees (DBH ~ 24 cm) and 64.1 vs. 40.8 $\text{dm}^3 \text{d}^{-1}$ in the largest ones (DBH ~ 45 cm). These values were low compared with trees in the neighboring Guiana

Table III. Quality of linear regressions of the daily water use with three drivers (in bold, significant relations with $R^2 > 0.40$).

Measurement campaigns	Tree code	Radiation		Insolation		VPD	
		R^2	P	R^2	P	R^2	P
dry season 2003	S1	0.42	0.0194	0.64	0.0030	0.57	0.0071
	S2	0.69	0.0014	0.85	0.0001	0.82	0.0001
	S3	0.32	0.0716	0.32	0.0661	0.30	0.0795
dry season 2004	S1	0.33	0.0143	0.49	0.0018	0.70	0.0000
	S2	0.64	0.0001	0.69	0.0000	0.82	0.0000
	M1	0.40	0.0062	0.42	0.0047	0.66	0.0001
	M2	0.17	0.0933	0.45	0.0032	0.38	0.0089
	L1	0.17	0.0971	0.41	0.0050	0.65	0.0001
	L2	0.20	0.676	0.38	0.0087	0.18	0.0827
wet season 2005	S1	0.01	0.7490	0.02	0.6030	0.04	0.8545
	S2	0.25	0.0977	0.22	0.1180	0.51	0.0086
	M1	0.30	0.5772	0.30	0.8633	0.01	0.9443
	M2	0.51	0.0090	0.66	0.0013	0.12	0.2644
	L1	0.06	0.4251	0.26	0.0861	0.09	0.3333
	L2	0.47	0.0132	0.47	0.0140	0.45	0.0169

rainforest located less than 20 km from our study site, where large dominant trees with diameters similar to L1 or L2 transpire $250\text{--}300\text{ dm}^3\text{ d}^{-1}$ in the dry season (Granier et al., 1996), i.e. 6 to 7 times more than *A. germinans*. In the rainforest, sap flow was linearly related to PET. The mean ratio of stand sap flow to PET was close to 0.75, with a tendency to decrease down to 0.60–0.65 during a 30-d rainless period, and to increase up to 0.80–0.85 after a rain event. They also obtained good correlation with the VPD (Granier et al., 1996).

The conservative water use strategy of *A. germinans* may also explain the difficulty in modeling water use. Sobrado and Ewe (2006) have shown significant seasonal changes in leaf water content of *A. germinans* but not in *L. racemosa*, which always had higher water contents. They found that both species could adjust the xylem osmolalities diurnally. However, in *A. germinans* osmolality was higher than in *L. racemosa* and contributed to 15.7% and 9.1% of predawn and midday water potential, respectively. The authors also showed that in highly saline environments, *A. germinans* were better adapted to develop lower water potential without turgor loss than *L. racemosa* and that the water potential declined significantly from predawn to midday during both the dry and the wet season. *A. germinans* is also known to have higher salt secretion rates than *L. racemosa* under comparable salinities (Sobrado, 2000). These physiological adjustments probably prevent the transpiration of *A. germinans* from being driven by a single environmental factor alone as for other forest species (Köcher et al., 2009; Ma et al., 2008) and may explain the high dominance of the species in the Guyanese mangroves.

The salinity, which is considered as a limiting factor for the transpiration rate of *A. germinans* in many mangrove studies (Passioura et al., 1992; Sobrado, 1999; Sobrado and Ewe, 2006), may contribute to the weakness of correlations between water use and the VPD, even during the wet season. The health status of the trees was also an additional uncontrolled driving

factor of water uptake, as measured during the dry season 2003 when the small declining tree S3 used only about $1\text{ dm}^3\text{ d}^{-1}$ (i.e. ten times less than healthy trees of similar size). Unfortunately, the health status cannot be estimated or quantified easily as it is linked to the tree's more or less dominant status.

The specific structure of the sapwood of *A. germinans* and the variability in its activity with the radial depth, the azimuth, the season and the tree age, prevent easy modeling of the distribution of SFD in the stems as in Lüttschwager and Remus (2007) for temperate species. In the rainforest, Granier et al. (1996) made measurements using a single probe in the external tree ring and data were extrapolated to the entire sapwood whose apparent thickness was estimated visually from tree cores. They always observed sapwood thickness of less than 5 cm. Thus, apparently in the nearby local rainforest trees, sapwood depth is less than in the mangrove trees and more homogeneous. With *A. germinans* the sapwood is active up to a depth of at least 8 cm.

The survival of this back mangrove forest located in a highly saline environment was made possible at the expense of a high mortality (30%) and a reduced water use by the surviving trees. In a recent complementary study based on stable isotopes and ion analysis, it was shown that local inflows of freshwater percolating into the sandbars from the inland marshes and reaching this mangrove forest could have contributed to the survival of trees (Lambs et al., 2008). This may explain the surprising absence of barren salty area (tanne) in the back mangrove along the coast of the Guianas.

Complementary studies are expected to compare water use along transects towards the sea to understand better the influences of salinity, tide and fresh water not only in the wet and the dry seasons but over a transition period as well. However, as SFD remained up to 8 cm, with a high variability with the azimuth, new sap flow measurement campaigns will require a high density of sensors which will impose higher practical

and cost constraints than in other forest environments. Another issue should be estimating the possible contributions of the mangrove trees in the progressive salinization of the local substrates, which is generally considered as dominated by only physical processes such as evaporation or convection processes (Marchand et al., 2006).

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