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Seasonal changes in the water status of three woody legumes from the Atlantic forest, Caratinga, Brazil

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ABSTRACT. The Atlantic forest of Brazil is considered to be a high priority for conservation in South America. Despite its importance, few phenological and ecophysiological data are available for plants of this area. In this study the seasonal changes in the water potentials (ψ) and the phenological behaviour of three woody legumes are related to environmental conditions, particularly air vapour pressure deficit (VPD). The values of ψ at predawn were greater than –0.75 MPa for all species even during the dry season (May–September). The minimal daily value of ψ was –3.8 MPa. The maximum daily amplitude of ψ (Δ parameter) was correlated with the air vapour pressure deficit, showing high correlation coefficients in linear equations. A high recovery rate of ψ after rain (greater than 0.80) was registered for all species, suggesting a high hydraulic conductivity. The high values of ψ at predawn during the year and the strong relationship between the daily amplitude of ψ and VPD suggested that the changes in the canopy cover are related more to atmospheric drought than to soil water deficit.

KEY WORDS: Atlantic forest, phenology, vapour pressure deficit, water potential, woody legumes

INTRODUCTION

The mosaic of vegetation types of eastern Brazil varies from arid formations, with pronounced dry seasons (Caatinga of the north-eastern region), to humid rain forest along the coast (Atlantic forest) where there is no or virtually no dry season, and very little water stress (Brown & Prance 1987). The Atlantic forests are of particular interest to biologists because of their high degrees of endemism in all groups of organisms, and have been recognised as a top priority for conservation in South America (Dinerstein *et al.* 1995, Mori 1989).

There are few data on water status for woody plants of tropical South America. The majority of studies come from the savanna areas of Venezuela

(Goldstein *et al*. 1986, Medina & Francisco 1994, Meinzer *et al*. 1983, Sarmiento *et al.* 1985) and Brazil (Ferri 1977, Moraes & Prado 1998, Perez & Moraes 1991). Some data on humid forest in Brazil are presented by Roberts *et al.* (1995) for seasonal and diurnal changes in plant water relations, leaf gas exchange and leaf area index of rain forest and pasture at three localities in Amazonia. They pointed out that no evidence has emerged from their studies at the rain forest sites that the soil moisture deficit influences stomatal conductance, on the other hand Perez & Moraes (1991) studing nine tree species in 'cerradão' (savanna forest) of southern Brazil, found that a decrease in the values of relative water content, water and osmotic potentials were accompanied by low values of stomatal conductance in the dry season.

Studying a number of tree species in a dry forest in Costa Rica, Borchert (1994) pointed out that the seasonal changes in water status varied with the availability of soil water and biotic factors, including the structure and leaf-span of leaves, time of leaf shedding, wood density and capacity for stem water storage, and depth and density of the root system. Holbrook *et al.* (1995) reviewed the drought responses of neotropical dry forest trees and concluded that, in general, the leaf water relations and gas exchange parameters of dry forest trees appeared not to differ markedly from values reported from wetter regions, and that leaf abscission was the most significant response to low soil moisture and high evaporative demand during the dry season.

Seasonal changes in the physiognomy of tropical forests are determined mainly by the total annual rainfall and its seasonal distribution (Borchert 1998). Phenological events such as leaf shedding, flowering and shoot flushing are strongly correlated with seasonal changes in tree water status, and both the phenology and distribution of tree species in tropical dry forests are determined mainly by the soil and tree water storage capacity (Borchert 1994). In a study of eight trees in the northern Australian savanna, Duff *et al.* (1997) showed that the patterns of canopy cover were strongly influenced by both soil moisture and vapour pressure deficit (VPD), with an increase in canopy cover coinciding with a decrease in the VPD prior to any increases in soil moisture.

Phenological studies in moist forests of eastern Brazil have been published by Alvim & Alvim (1978), Jackson (1978), Morellato *et al.* (1989), and Mori *et al*. (1982), but ecophysiological studies of the relationships between seasonal climatic changes, plant water status and phenological behaviour are restricted to the study of the coastal forest of southern Bahia of Alvim & Alvim (1978), who related growth periodicity with the climate. There are no data on the water status of woody plants of the Atlantic forest inland, and questions concerning phenological and ecophysiological responses to the climate seasonality remain to be answered. In view of this, we report here on our studies concerning three principal questions regarding seasonal changes in the water status of three woody species of legumes of the Atlantic forest: (1) Is there a seasonal soil limitation to the water status of the legume trees? (2) To what extent does the evaporative demand determine the changes in the water status? (3) Are seasonal changes in the water status related to canopy cover? Answers to these questions will contribute to our understanding of seasonal changes in the physiognomy of the Atlantic forest of southern Brazil.

STUDY SITE

This study was carried out at the Biological Station of Caratinga (BSC) (19° 50′S, 41° 50′W), in the state of Minas Gerais, Brazil. This area is in the basin of the Rio Doce, and is part of the forested mountainous domain of Ab'Saber (1996). The soil is predominantly an alic red-yellow latosol (Silva 1993). The mean annual rainfall recorded from 1985 through 1994 was 1032 mm and the mean air temperature 21.5 °C. There is a marked dry season from April to October, with 5 mo having less than 50 mm of rainfall and a wet season from November to March (Figure 1a). The seasonal variation of the rainfall is greater than the changes in temperature, a feature of climate of tropical deciduous forests (Reich & Borchert 1982).

The 880 ha of the remnant inland Atlantic forest covers hills and valleys with altitudes ranging from 400–680 m (Strier 1991). The valley bottoms have the multi-layer structure typical of tropical moist forests, including tall emergents (up to 35 m high), a main middle canopy (*c*. 20 m) and a lower tree layer (*c*. 10 m). Two-layered, tall secondary forest and young regenerative forest, with trees 10–15 m high occur on steep slopes and on hill tops (Hatton *et al.* 1984). The forest is rich in epiphytic bromeliads, orchids and lianas. The Leguminosae is the most widely represented family with *c*. 100 species (Mendonça-Filho 1996) followed by Lauraceae, Anacardiaceae, Bignoniaceae and Moraceae. Hardwoods are still to be found, including the 'jacarandás' *Machaerium, Dalbergia*, the 'jequetibás' *Cariniana legalis* and the 'angicos' *Anadenanthera, Acacia* (Hatton *et al*. 1984). Leaves, flowers and fruits are exploited by the 'Muriqui' (*Brachyteles arachnoides*), one of the most endangered species of the South American primates (Strier 1989, 1991).

MATERIALS AND METHODS

The woody legumes studied, *Anadenanthera peregrina* (L.) Speg., *Senna multijuga* (L.C. Rich.) Irwin & Barneby, and *Machaerium floridum* (Mart. ex Benth.) Ducke, also present at other Atlantic forest sites (Lewis 1987), are common distributed at BSC, occurring at all altitudes. *A. peregrina* has a dense wood with values between 0.84 and 1.1 g cm^{-3}, *S. multijuga* is a soft wood, with densities between 0.45 and 0.51 g cm^{-3} (Carvalho 1994). Wood density for different species of *Machaerium* vary from 0.66 to 1.12 g cm^{-3} (Lorenzi 1998). All species lose their leaves partially or totally according to where they occur and the severity of the dry season. Three individuals of each species were selected in the valley bottoms, and their phenology and water status were recorded. All were adults, at

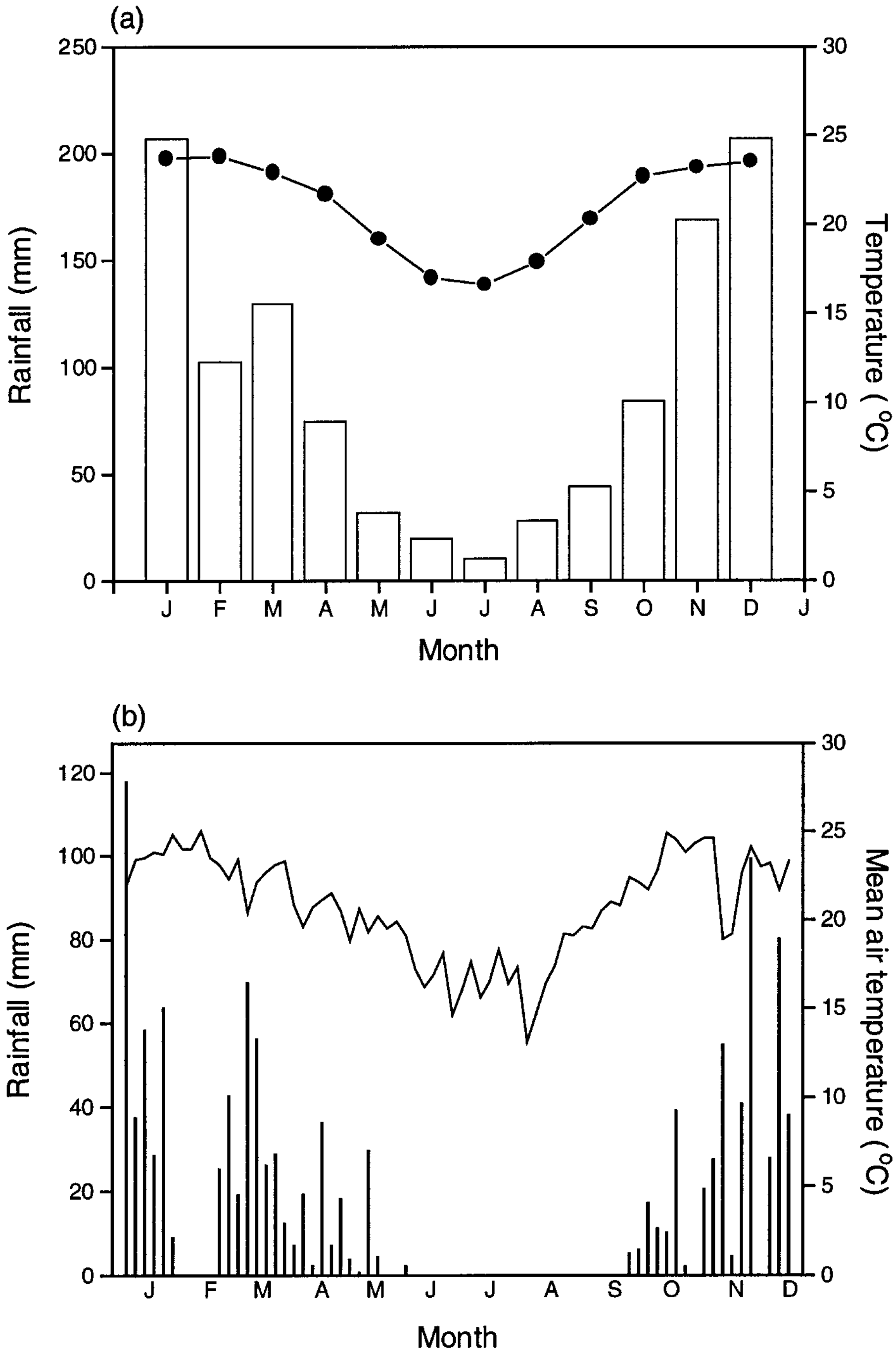


Figure 1. Climate at the Biological Station of Caratinga. (a) Monthly mean temperature (line) and rainfall (bars), 1985–1994, and (b) accumulated rainfall and mean air temperature for every 5 d during 1994.

least 12 m high and partially shaded in the forest margins. A psychrometer was set up in the shade, near to the selected trees, in order to measure the vapour pressure deficit (VPD).

Monthly visits were made to record phenological changes (leaf fall and flush, flowering and fruiting). The water potential (ψ) was measured with a pressure chamber (Scholander *et al.* 1965). One vegetative branch was selected from each plant and cut ± 10 cm from the apex for the determination of the water status parameters. The branches were located under shade on the lower portion of the crown and clipped by a tree pruner on a 5-m long pole. The parameters listed below were determined following Berger *et al.* (1996): the water potential predawn (ψ_{PD}), giving the maximum value of the ψ at the start of the day; the minimum water potential of the day (ψ_{MD}), and the delta parameter (Δ_ψ), that gives the daily maximum amplitude of the water potential, and permits an indirect evaluation of the transpirational flux.

Another parameter, the post-rain recovery rate, was obtained from the values of the water potential 1 h after the onset of rain (ψ_{AR}). This parameter shows the rate (R_R) at which the plant restores the water potential after an episode of rain. These parameters were used by Berger *et al.* (1996) to determine the recovery rate using values of the post sunset xylem pressure potential.

$$R_R = 1 - [(\psi_{PD} - \psi_{AR})/(\psi_{PD} - \psi_{MD})]$$

Linear equations were fitted to see if the changes in the water potentials were related to changes in the transpiratory demand. The values of delta (Δ_ψ) were fitted to the difference in the value of the VPD at the time of the highest evaporative demand and that at predawn.

RESULTS

The accumulated rainfall and the mean air temperature recorded every 5 d each month of 1994 at the Biological Station of Caratinga are shown in Figure 1b. The highest temperature was observed on February (25.0 ± 0.91 °C), during the short drought period, and the lowest temperature was recorded in the middle of August (13.1 ± 0.48 °C). The heavy rains at the beginning of the year ceased on January 28, with a short dry period until February 22. During this short summer dry period and even in the sunny days of March, the relative humidity decreased to values lower than 60%. An extended drought period began in May, and there was no rain in July, August and September. The rainy season began in October. The reduced rainfall when compared to data from other years (Figure 1a), indicated an unusually intense dry season during the study period. In September, at the end of the dry season, relative humidity decreased to values lower than 40%, and there was no dew in the early morning.

Most of the phenological changes occurred at the end of the dry season and at the beginning of the rainy season, with fruit dispersal, leaf fall and flushing,

Table 1. Periods of leaf fall, flushing, flowering and fruit dispersal of three woody legumes at the Biological Station of Caratinga.

Species	Leaf fall	Leaf flushing	Flowering	Fruit dispersal
Anadenanthera peregrina	Sep–Oct	Sep–Oct	Sep–Oct	Sep
Machaerium floridum	Sep–Nov	Nov	Jan	Aug
Senna multijuga	Sep	Sep	Apr–May	Sep

occurring between August and November (Table 1). Following the criteria of the canopy cover changes adopted by Duff *et al.* (1997) to characterize leaf phenology, none of the species studied could be considered deciduous. *A. peregrina* showed leaf fall, but leaf flushing and flowering followed straight after. *M. floridum* plants showed a long period of leaf fall, but below 50%. These two species can be characterized as semi-deciduous plants. *S. multijuga* retained up to 75% of its canopy even during the drought. However, in drier sites of the forest leaf fall was more accentuated for this species.

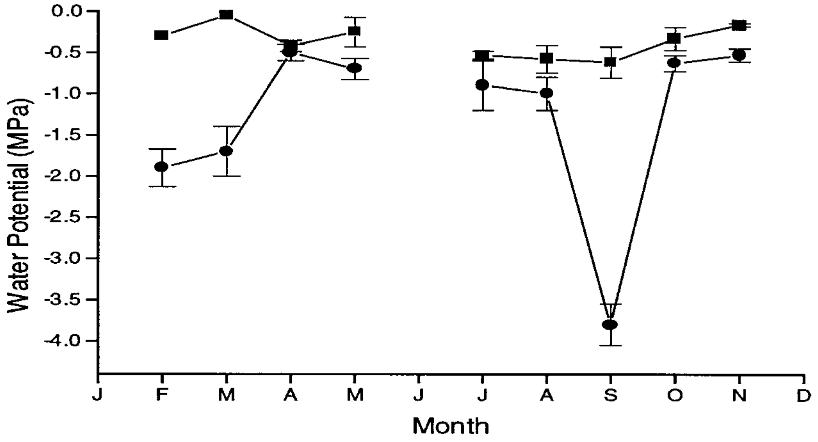
The leguminous trees showed remarkable seasonal changes in their water potentials (Figure 2). The predawn values (ψ_{PD}) decreased in the dry season, and no statistical difference ($P < 0.05$) was observed for the minimum value between the three species studied, the mean was −0.57 ± 0.14 MPa. The high ψ_{PD} values even throughout the dry season suggested that the leguminous species are deep-rooted, accessing the subsoil moisture. Although there was no soil water limitation, during the late summer (February and March) under high evaporative demand, the water potential at midday (ψ_{MD}) decreased to nearly −2.0 MPa in all three species. In September, at the end of the dry season and with the highest air pressure vapour deficit, ψ_{MD} decreased to −3.8 ± 0.2 MPa in *A. peregrina*, −2.6 ± 0.5 MPa in *S. multijuga*, and −2.4 ± 0.4 MPa in *M. floridum*.

The short period of no or low rainfall during the rainy season in the summer (Figure 1b), does not lead to the same patterns of senescence and leaf fall as observed at the end of the dry season. In both periods, however, the values of ψ_{MD} showed a significant decrease with the higher evaporative demand in the three species studied (Figure 2). The data suggest that the summer dry spell, as pointed out by Holbrook *et al.* (1995), is not severe enough to trigger abscission, or that this phenological trait is a result of differential leaf age-related responses to the soil water availability and/or evaporative demand.

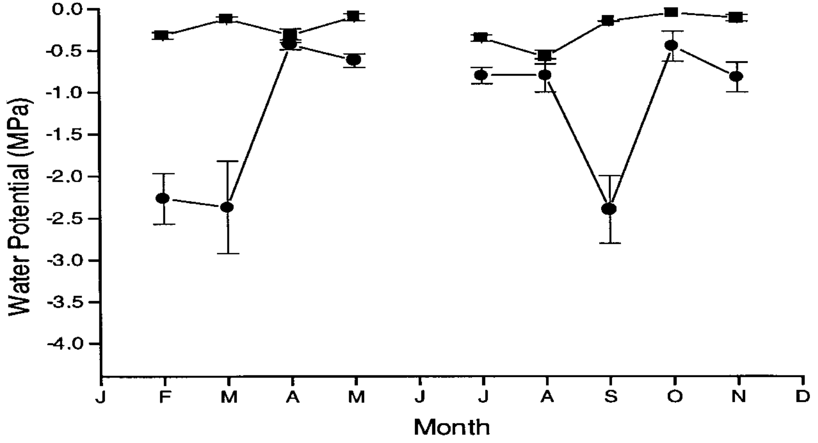
The delta parameter ($\Delta_\psi = \psi_{MD} - \psi_{PD}$) was highest in September for all species (Table 2). Compared with the other two species, *A. peregrina* showed the highest Δ_ψ value suggesting a higher transpirational flux and/or higher flow resistance. The seasonal changes in Δ_ψ values were related to the daily difference in the vapour pressure deficit between predawn and at midday ($\Delta VPD = VPD_{MD} - VPD_{PD}$), since a linear equation with significant correlation coefficient ($P < 0.01$) were obtained for all species (Table 3).

Water potentials in February and March, including the predawn values (ψ_{PD}), those under high evaporative demand (ψ_{MD}) and 1 h after a short rain

(a) *A. peregrina*



(b) *M. floridum*



(c) *S. multijuga*

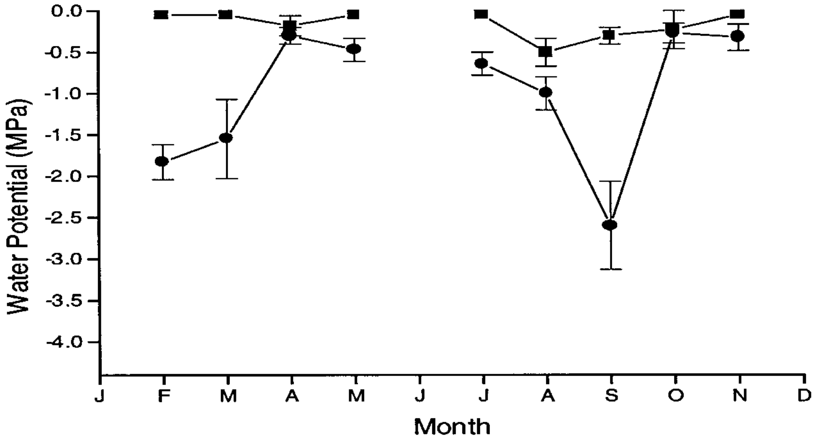


Figure 2. Water potentials at predawn (squares) and after the high solar angle (circle) for (a) *Anadenanthera peregrina*, (b) *Machaerium floridum*, and (c) *Senna multijuga* at the Biological Station of Caratinga, during 1994. Potentials were measured on a day lying between the 19th and 30th. Note: June 1994 had no measurements.

Table 2. Maximum daily amplitude of the vapour pressure deficit ($\Delta VPD = VPD_{MD} - VPD_{PD}$), and maximum amplitude of the xylem water pressure potential ($\Delta_\psi = \psi_{MD} - \psi_{PD}$) for three leguminous trees (mean ± SD, n = 3). See Table 1 for full names.

Date in 1994	ΔVPD (KPa)	Δ_ψ (MpA)		
		A. peregrina	*M. floridum*	*S. multijuga*
22 Feb	2.22	1.63 ± 0.23	1.95 ± 0.29	1.78 ± 0.21
19 Mar	1.23	2.45 ± 0.30	2.28 ± 0.29	1.50 ± 0.48
27 Apr	0.13	0.08 ± 0.10	0.12 ± 0.15	0.12 ± 0.15
27 May	0.32	0.45 ± 0.27	0.51 ± 0.08	0.42 ± 0.14
26 July	0.62	0.37 ± 0.25	0.45 ± 0.26	0.62 ± 0.14
20 Aug	1.00	0.41 ± 0.20	0.66 ± 0.26	0.50 ± 0.10
23 Sep	2.83	3.15 ± 0.13	2.25 ± 0.38	2.30 ± 0.46
30 Oct	0.38	0.30 ± 0.23	0.40 ± 0.18	0.03 ± 0.01
27 Nov	0.17	0.37 ± 0.07	0.69 ± 0.33	0.27 ± 0.16

Table 3. Linear equations for the maximum daily amplitude of the xylem water pressure potential (Δ_ψ) and the maximum daily amplitude of the vapour pressure deficit (ΔVPD), for three leguminous species. See Table 1 for full names.

Species	Equation	SE (b)	r^2	*P*
A. peregrina	$\Delta_\psi = 0.023 + 1.011\ \Delta VPD$	0.217	0.757	0.0023
M. floridum	$\Delta_\psi = 0.268 + 0.775\ \Delta VPD$	0.175	0.737	0.0031
S. multijuga	$\Delta_\psi = 0.048 + 1.123\ \Delta VPD$	0.133	0.911	0.0001

(ψ_{AR}), and the recovery rate (RR) are shown in Table 4. Except for *S. multijuga* the ψ_{PD} values were lower in February than in March. This was related to the decrease in soil water availability (Figure 1a), since the values of ψ_{PD} were determined on the last day of the short drought period in February. Even considering the limit of precision of the measurements at higher water potential values (see Berger *et al.* 1996), the data indicated a high rate of water recovery after rain, with minimum values greater than 0.80. The higher values of the post-rain recovery rate in February than in March in *A. peregrina* and *M. floridum* were related to the lower values of water potential at predawn than before the start of the new rainy season.

The high wood density of *A. peregrina* plants (*c*. 1.0 g cm^{-3}), suggests, according to Borchert (1994), a lower stem water storage capacity in comparison

Table 4. Values of the water potential at predawn (ψ_{PD}), after the high solar angle (ψ_{MD}), 1 h after the rain (ψ_{AR}), and the value of the post-rain recovery rate (R_R) for leguminous trees at the Biological Station of Caratinga on 21 February and 19 March 1994 (mean ± SD). Full species names are given in Table 1.

Species	Xylem pressure potential (MPa)			Post-rain recovery rate R_R
	ψ_{PD}	ψ_{MD}	ψ_{AR}	
22 February 1994				
A. peregrina	−0.28 ± 0.03	−1.90 ± 0.23	−0.28 ± 0.03	1.00 ± 0.04
M. floridum	−0.31 ± 0.04	−2.27 ± 0.30	−0.16 ± 0.03	1.07 ± 0.01
S. multijuga	−0.07 ± 0.03	−1.80 ± 0.21	−0.25 ± 0.09	0.89 ± 0.06
19 March 1994				
A. peregrina	−0.07 ± 0.03	−2.50 ± 0.30	−0.16 ± 0.05	0.96 ± 0.03
M. floridum	−0.12 ± 0.03	−2.40 ± 0.55	−0.53 ± 0.32	0.83 ± 0.09
S. multijuga	−0.07 ± 0.03	−1.50 ± 0.46	−0.12 ± 0.03	0.94 ± 0.05

with *S. multijuga*, which has a lower wood density (<0.5 g cm^{-3}). Despite these different wood densities, the recovery rate after rain was high for all species, suggesting that, independent of the differential water storage capacity under no soil water stress (high values of ψ_{PD}), there is a rapid increase in stem water content in response to the rise in atmospheric humidity.

DISCUSSION

The values of the water potentials at predawn (ψ_{PD}) for the three woody species of Atlantic forest observed here were, as expected, higher than those observed for plants of Sahelian woody species by Berger *et al.* (1996), with values as low as −2.4 MPa in *Acacia senegal* and −5.0 MPa in *Boscia senegalensis*. Sobrado (1986) observed −3.0 MPa as the minimum value of predawn water potential (ψ_{PD}), for deciduous species in a tropical dry forest of Venezuela. Higher minimum values of ψ_{PD} (−1.5 MPa) were observed by Goldstein *et al.* (1986) for evergreen trees of a Venezuelan savanna. In a study in the Northern Australian savanna, Myers *et al.* (1997) showed that, despite the severe drought, the ψ_{PD} values remained high, between −1.3 to −1.5 MPa for evergreen species and −0.5 to −1.5 MPa for deciduous species. Considering that the leaf water status at predawn is related to the soil water availability (plants tend to equilibrate overnight with the wetter zones of the bulk soil, see Schimidhalter 1997), and can be used as an approximation of the soil water potential (Andrade *et al.* 1998), the high values of ψ_{PD} for the leguminous trees in this study indicate that there was no severe soil water limitation even at the end of the dry season. The site where the measurements were made is a typical site of a remnant primary forest, located at the bottom of the valley, near to the drainage line. Despite there being no severe soil water limitation, the minimum daily water potentials (ψ_{MD}) of the Atlantic forest legumes were lower than the values determined for four woody species in a Venezuelan savanna by Meinzer *et al.* (1983). However, a lower value (−4.0 MPa) for leaf water potential was recorded by Roberts *et al.* (1995) at the top of the forest canopy of the rainforest of Amazonia.

The high values for the daily amplitude of the water potential (delta parameter, Δ), for all plants studied (with values > 3.0 MPa for *A. peregrina*) could suggest a high transpirational flux. However, as pointed out by Berger *et al.* (1996), this interpretation of the delta parameter is problematic, since it also depends on the hydraulic conductivity of the soil–plant system. In spite of that, the relatively high values of the predawn water potentials during the year (> -0.75 MPa) even during the drought period, suggest the lack of greater seasonal changes in the hydraulic conductivity of the soil–plant system. The high values for the proportion of the water potential recovery after rain (> 0.80), even with high daily amplitude values (Table 4), indicates a rapid recovery of the water bulk with air vapour saturation. These data give further evidence for high hydraulic conductivity.

Daily changes in leaf water status in tropical trees has been related to the hydraulic conductance of the soil/root/leaf pathway (Meinzer *et al.* 1995), and with the stem water storage capacity (Borchert 1994). Higher internal water storage may partially compensate the increase of axial hydraulic resistance with tree size, and thus play an important role in regulating the water status of leaves exposed to large diurnal evaporative demand (Goldstein *et al.* 1998). The higher ψ_{MD} observed at the end of the dry season in *S. multijuga*, that also showed lower leaf abscission compared with *A. peregrina*, could be related to the higher internal water storage capacity, as observed by Borchert (1994) in a study at Costa Rica. The reduction of the canopy area in *M. floridum* and the higher water storage capacity in relation to *A. peregrina*, could explain the comparatively lower ψ_{MD} decrease.

In a comparative study with drought-deciduous and evergreen tropical trees, Sobrado (1993) found that in deciduous species the hydraulic conductivity is much lower at the time of leaf abscission than during the wet season, suggesting an increase in xylem cavitation during the transition from the wet to the dry season. The data suggesting high soil/plant/leaf conductivity for the three leguminous species studied at BSC were obtained during the wet season, and thus a decrease in conductivity in the dry season, mainly in hardwood species, is likely. Endogenous leaf-age related processes such as senescence and the reduction of stomatal control in old leaves (Reich & Borchert 1988) could also be related to the high ψ_{MD} decrease at the end of the dry season.

The seasonal changes in the diurnal amplitude of the water potentials ($\Delta\psi$) were statistically related to the diurnal amplitude of the vapour pressure deficit (Δ VPD), suggesting the importance of the atmospheric vapour saturation status in the water relations of these species. Several studies have pointed out the importance of the vapour pressure deficit. In Amazonian conditions, Roberts *et al.* (1990), showed that the stomatal conductance (g_s) was negatively correlated to the specific humidity deficit. In the Brazilian Cerrado, Miranda *et al.* (1997) found that much of the total seasonal variation of the ecosystem surface conductance was associated with variations in the leaf-to-air vapour pressure deficit and the solar irradiation, and they provided evidence that there was not a large direct effect of soil water deficit on ecosystem surface conductance in the dry season. The ecophysiological study of Duff *et al.* (1997) in Australian savanna, emphasized the role of the vapour pressure deficit (VPD), showing that the decrease in canopy cover coincided with decrease in soil moisture and an increase in VPD. They also showed that the recovery of the canopy cover at the end of the drought period coincided with a decrease in VPD prior to the increase of the soil moisture with the onset of the wet season. The phenological behaviour of the leguminous trees in this study showed that most of the canopy cover changes occurred between the end of the dry season and the beginning of the rainy season, and that they are certainly more related to the changes in the VPD than those in the soil water availability, since there was no great decrease in the predawn water potentials. In fact, the most drastic changes in the physiognomy of the forest in the Caratinga region occur in the higher sites, suggesting a higher soil and atmospheric drought. At the bottom of the valleys, small canopy cover changes are associated with the higher soil water availability and the higher frequency of vapour saturated air.

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