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ROSADO, BRUNO H.P.; DE MATTOS, EDUARDO A.

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Chlorophyll fluorescence varies more across seasons than leaf water potential in drought-prone plants

BRUNO H.P. ROSADO¹ and EDUARDO A. DE MATTOS²

¹Departamento de Ecologia, Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier, 524, PHLC, sala 220, Maracanã, 20550-900 Rio de Janeiro, RJ, Brasil

²Departamento de Ecologia, Instituto de Biologia, CCS, Universidade Federal do Rio de Janeiro, Caixa Postal 68020, 21941-970 Rio de Janeiro, RJ, Brasil

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ABSTRACT

Among the effects of environmental change, the intensification of drought events is noteworthy, and tropical vegetation is predicted to be highly vulnerable to it. However, it is not clear how tropical plants in drought-prone habitats will respond to this change. In a coastal sandy plain environment, we evaluated the response of six plant species to water deficits across seasons, the relationship between their morphophysiological traits, and which traits would be the best descriptors of plants' response to drought. Regardless of leaf succulence and phenology, responses between seasons were most strongly related to chlorophyll fluorescence. In this study we have demonstrated that a better comprehension of how tropical species from drought-prone habitats cope with changes in water availability can be based on seasonal variation in leaf water potential and chlorophyll fluorescence. Temporal variation in leaf water potential and chlorophyll fluorescence was found useful for differentiating between groups of sandy soil species that are responsive or unresponsive to water availability. However, chlorophyll fluorescence appeared to be a more sensitive descriptor of their seasonal and short-term responses.

Key words: drought, functional traits, plant-water relations, photoinhibition, seasonal habitats.

INTRODUCTION

In the current scenario of large-scale environmental change, the search for functional traits which will allow us to predict the response of communities and species to changes in conditions and resources has been identified as one of the 100 fundamental questions in ecology (Sutherland et al. 2013). Among the effects of environmental change, the intensification of drought events is noteworthy

(McDowell et al. 2008, 2011), and several studies have identified plant physiological traits that may be descriptors for the responses of plants to water availability (Bartlett et al. 2012, Choat et al. 2012, Bhaskar and Ackerly 2006). In tropical environments seasonality is largely reflected in changes in water availability (Franco 2002), and temporal fluctuations in water availability are particularly important for plants growing in sandy environments, due to the low water retention capacity of sandy soils (Noy-Meir 1972). Although several studies of plant responses to drought

Correspondence to: Bruno Henrique Pimentel Rosado
E-mail: brunorosado@gmail.com

in tropical dry forests and savannas have been published (Bucci et al. 2005, Franco 2002, Choat et al. 2006, Méndez-Alonzo et al. 2012), it is still unknown how tropical plants in other tropical drought-prone habitats (e.g. coastal sandy plains) will respond to drought, and which are the best traits for predicting this response.

Plants growing on sandy soils show higher water potential than those growing on clay soils, since sandy soils hold water at high water potential (Sperry et al. 2002). One important process that facilitates highly conservative water use is homeostasis of leaf water potential (Ψ_L) at midday across seasons (Bucci et al. 2005, Maseda and Fernández 2006). The ability to maintain constant Ψ_L might be achieved by mechanisms such as greater stomatal control and hydraulic adjustments, which reduce transpiration (Maseda and Fernández 2006). Species with less stomatal control may exhibit greater decreases in Ψ_L (Franks et al. 2007, Maseda and Fernández 2006). An important aspect of species that are able to maintain high Ψ_L is related to the avoidance of embolism (Sperry et al. 2002, Maseda and Fernández 2006). However, species with lower Ψ_L can maintain CO_2 gas exchange for longer periods during drought, under low soil water availability and/or high air vapor pressure deficit (VPD). On the other hand, such species might be more susceptible to water loss (Maseda and Fernández 2006). Importantly, the greater the degree of stomatal closure (associated with high Ψ_L), the dissipation of excitation energy by photosynthetic carbon assimilation will be more reduced (Maseda and Fernández 2006). In addition, greater stomatal closure may result in an increase in carbon starvation due to a decrease in photosynthesis (McDowell et al. 2008, van der Molen et al. 2011).

A further drawback of stomatal closure is that it may lead to light stress, i.e., photoinhibition caused by excess light that is not used in photosynthesis. Changes in the ratio of the yield of variable (F_v)

and maximum (F_m) chlorophyll fluorescence in dark-acclimated leaves can be used to characterize the degree of photoinhibition in plants subjected to environmental stress (Baker 2008). A decrease in the F_v/F_m ratio indicates increased photoprotection, in which excess excitation energy is dissipated as heat, and to direct photodamage to photosystem II (PS II) centers (Krause 1988, Walker 1992). In addition, an increase in thermal dissipation in PS II is associated with a decrease in F_m and minimum chlorophyll fluorescence (F_0), whereas damage to the reaction centers increases only F_0 (Krause 1988, Porcar-Castell et al. 2008).

Rosado and de Mattos (2010) observed variations between wet and dry seasons in the pressure-volume relationship in species on the Brazilian coastal sandy plains, a species assemblage known as restingas. As expected for plants growing on dry sandy soils, they observed high values of Ψ_L at the turgor loss point (Ψ_{TLP}), less negative osmotic pressure, and a low bulk modulus of elasticity in restinga species (Rosado and de Mattos 2010). However, most species have an average predawn F_v/F_m of less than 0.83 during the dry season, which indicates chronic photoinhibition. To date, however, no information is available about the physiological responses of restinga plants to seasonal variation in water availability, or the possible relationship between such physiological responses and leaf phenology.

In this study we chose the two dominant species, which are able to maintain a high minimum Ψ_L during the dry season (Rosado and de Mattos 2010), and four less dominant restinga species. These six species occur in a restinga in southeastern Brazil and exhibit a range of leaf succulence, from 147 to 1105 g m^{-2} , and leaf phenology characteristics, from successive to concentrated leaf production in wet seasons (Rosado and de Mattos 2007, 2010). Leaf succulence reflects the amount of water stored in leaves and may act as a buffer for water loss (Lamont and Lamont 2000),

and variations in leaf phenology are commonly associated with the ability to deal with water deficits (Reich and Borchert 1982, Borchert 1994). We thus addressed the following hypotheses: 1) the six species have different strategies to maintain high Ψ_L across seasons based on distinct arrays of leaf phenology and leaf morpho-physiological traits; 2) seasonal responses of chlorophyll fluorescence are dependent on seasonal variation in Ψ_L and both Ψ_L and chlorophyll fluorescence are redundant in the description of species' seasonal responses to water availability. Although soil moisture availability is a function of input minus output of water and rooting depth, the number of rainless days (NRD) might be a useful surrogate for soil moisture availability, especially in sandy soils whose water retention capacity is low (Sperry et al. 2002). Given the low water retention capacity of sandy soils and the occurrence of dry spells in both wet and dry seasons (Cavalin and de Mattos 2007), coastal sandy plants may be differentially predisposed to water shortage during rainless days with varying VPD during wet and dry seasons. Our third hypothesis is therefore as follows: Ψ_L responds to higher VPD only when NRD is low, but responds to an increase in NRD, regardless of VPD.

MATERIALS AND METHODS

STUDY AREA AND PLANT SPECIES

Our study was conducted in the Restinga of Jurubatiba National Park, (14 140 ha), located in the northern part of the state of Rio de Janeiro, Brazil (extending north-south between 22°00'S and 22°23'S and east-west between 41°15'W and 41°35'W). The maximum temperature (around 30 °C) occurs in January and the minimum (around 20 °C) in July (Henriques et al. 1986). The mean annual temperature is 22.6 °C. The sandy soil is characterized by low water retention capacity, low nutrient content and low organic matter content. Average annual rainfall is 1100–1300 mm, with a

monthly minimum of 41 mm in dry seasons and a monthly maximum of 189 mm in wet seasons (Araujo et al. 1998). The soil water deficit is highest during the months of July and August (Henriques et al. 1986). Open *Clusia* scrub is the most common vegetation type, characterized by vegetation patches composed of shrubs and trees 0.5–8.0 m in height, surrounded by white bare sand that can reach 70 °C on typical summer days. *Clusia* scrub covers 40% of the park and is dominated by two species: *Clusia hilariana* Schltdl. (Clusiaceae) and *Protium icariba* (DC.) Marchand (Burseraceae) (Araujo et al. 2004). The annual rainfall in 2004 and 2005 was 1319 mm and 1388 mm, respectively. In the months studied, cumulative rainfall was 246 mm in 2004 and 770 mm in 2005, with September 2004 and August 2005 receiving the lowest rainfall (Fig. 1). The rainless period in September 2004 was 30 days long, whereas in August 2005 it lasted 15 days.

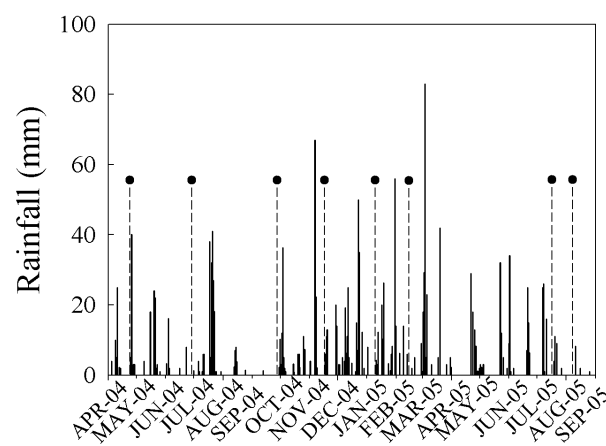


Figure 1 - Daily rainfall (mm) during the period of study. The dashed lines indicated by black circles represent the months in which Ψ_L and chlorophyll *a* fluorescence were measured.

We selected six shrub species based on variation in leaf succulence and phenology (Rosado and de Mattos 2007) in an area 300 m from the ocean: *Clusia hilariana* (average leaf succulence: 1105 g m⁻²) and *Byrsonima sericea* DC. (Malpighiaceae)

(239 g m⁻²) are classified as successive leaf producers because they produce leaves throughout the year, while *Protium icicariba* (147 g m⁻²), *Ocotea notata* (Nees) Mez (Lauraceae) (169 g m⁻²), *Eugenia umbelliflora* Berg (Myrtaceae) (358 g m⁻²), and *Erythroxylum ovalifolium* Peyr. (Erythroxylaceae) (194 g m⁻²) concentrate their leaf production during the wet season. *Erythroxylum* is the only species that shows brevi-deciduous behavior. For simplicity, we will refer to each species by its genus name. *Clusia* is an obligatory CAM plant (Franco et al. 1996), whereas all other species are C₃ plants.

LEAF WATER POTENTIAL AND CHLOROPHYLL FLUORESCENCE

Leaf water potential was measured using a pressure chamber (Model 1000, PMS Instruments, USA) at predawn (Ψ_{pd}) and midday (Ψ_{md}). The measurements were made using two completely exposed mature leaves from the north-facing side of the canopy of the same three individuals of each species throughout the study. For *Erythroxylum* measurements, samples were taken from terminal shoots because the leaves and petioles were too small to be used in the pressure chamber. When the difference in Ψ_L between two leaves of each individual was greater than 0.5 MPa, we measured a third leaf to estimate the average. From April 2004 to August 2005, measurements of Ψ_L were made during eight months chosen to represent the variation between the wet and the dry seasons. Twelve measurements were made at predawn and 18 at midday for each individual. To represent these data graphically we chose the days with the minimum values for each individual per month. The minimum values are good descriptors of species' responses to water deficits (Sperry et al. 2002) because they indicate the maximum xylem tension that a given species is able to tolerate while being able to maintain physiological activity (Bhaskar and

Ackerly 2006). At the same time, measurements of chlorophyll *a* fluorescence were performed using a pulse-amplitude modulated fluorometer with a fiber optic (FMS-2, Hansatech, UK), on the same two leaves from each individual. The fiber optic was kept at a constant distance and angle to the leaf surface using a leaf clip. The potential quantum yield of PSII, which is dependent on minimal (F_0) and maximal fluorescence yield (F_m), was measured by applying a pulse of light strong enough to saturate all the PSII reaction centers after the leaf was dark-adapted for 30 min (de Mattos and Luttge 2001). The F_v/F_m ratio was determined just before dawn (F_v/F_{mpd}) and at midday (F_v/F_{mmd}) by dark-adapting leaves for 30 min. Despite the usual high variability between leaves and individuals, we found it useful to use the absolute values of F_0 and F_m to indicate temporal variation in photoprotection or photodamage associated with stress (Porcar-Castell et al. 2008). The averages were calculated in the same way as for Ψ_L . On each sampling occasion we measured relative humidity and air temperature at 30 min intervals, starting at predawn and ending at midday.

STATISTICAL ANALYSES

To test hypothesis 1, we evaluated the differences in Ψ_{pd} , Ψ_{md} and F_v/F_{mpd} , F_v/F_{mmd} , and F_0 and F_m between seasons and among species using a two-way repeated-measures ANOVA ($P < 0.05$). Additionally, to evaluate changes in the response of species (ecophysiological performance) between seasons, we constructed a correlation matrix using the mean values of each variable for each species in the wet and dry season, respectively. The wettest period comprised the months between November 2004 and February 2005. We analyzed the correlation matrix with a Principal Component Analysis (PCA) using program MULTIV (Pillar 1997). We also used PCA to describe the association between Ψ_L and the chlorophyll variables (hypothesis 2).

To test hypothesis 3, we ran a multiple linear regression to determine the contribution of VPD and NRD to variation in Ψ_{md} and Ψ_{pd} . We chose the highest VPD on each day when Ψ_L and F_v/F_m were measured at both predawn and midday, and NRD during the one, two, three or four weeks before the measurements were taken. We performed a separate multiple regression for each week because we used cumulative NRD. Two-way ANOVAs and multiple linear regressions were carried out in R 2.11.1 (<http://www.R-project.org>).

RESULTS

LEAF WATER POTENTIAL

The physiological measurements from September 2004 were taken after 30 days of drought, and those from August 2005, after six days of drought (Fig. 1). The highest VPD values were observed during the dry seasons, i.e. September 2004 (46.1 Pa KPa⁻¹) and August 2005 (36.5 Pa KPa⁻¹) (Table I). The lowest VPD was observed on a cloudy day in July 2005 (12.3 Pa KPa⁻¹).

TABLE I
Daily maximum air vapor pressure deficit (VPD), measured on the days on which leaf water potential (Ψ_L) and chlorophyll *a* fluorescence were measured.

| Month and year | VPD (Pa KPa ⁻¹) |
|----------------|-----------------------------|
| Apr-04 | 28.9 |
| June-04 | 16.1 |
| Sept-04 | 46.1 |
| Nov-04 | 27.8 |
| Jan-05 | 33.9 |
| Feb-05 | 21.2 |
| July-05 | 12.3 |
| Aug-05 | 36.5 |

The Ψ_{pd} and Ψ_{md} values ranged from almost zero to around -1.70 MPa and from almost zero to -4.23 MPa, respectively. All species showed the greatest decline in Ψ_{pd} in September 2004 and August 2005 (Figs. 2a, 2b). In contrast to other species, *Protium* and *Clusia* showed constant values

of Ψ_{md} throughout the year, which were greater than those of other species (Tables II and III). *Clusia* showed a slightly lower Ψ_{md} than *Protium*, but the difference was not significant. *Clusia* and *Erythroxylum* showed significantly lower values of Ψ_{pd} in the dry season in comparison to the wet season, but *Erythroxylum* was the only species with a significantly lower Ψ_{md} in the dry season (Tables II and III). In July 2005, when measurements were made on a cloudy day, all species showed increases in Ψ_{md} .

CHLOROPHYLL A FLUORESCENCE

In all species, predawn and midday F_v/F_m varied in the ranges of 0.60-0.90 and 0.55-0.85, respectively. *Byrsonima*, *Eugenia* and *Clusia* showed a decline in F_v/F_{mpd} in September 2004. *Eugenia* had the lowest F_v/F_{mpd} value of all species (Table II, Fig. 2c). With the exception of *Protium*, all species showed a decline in F_v/F_{mpd} in the dry season (Tables II and III). A decline in F_v/F_{mmd} in all species was also observed in September 2004. *Clusia* and *Protium* showed the highest F_v/F_{mmd} in the wet season (0.80 and 0.79, respectively), while *Eugenia* showed the lowest (0.66) (Table II, Fig. 2d). The highest F_v/F_{mmd} values were observed for all species during July 2005. There were no significant differences between seasons for any species (Tables II and III).

The F_{opd} values varied from 180 to 450, with the lowest values observed in August 2005 (Fig. 3). *Byrsonima*, *Clusia* and *Eugenia* showed significant differences between seasons, with the highest values observed in September 2004 (Tables II and III). *Eugenia* showed the greatest variation in F_{opd} throughout the year (Fig. 3a). F_{mpd} varied from 800 to 2000 (Fig. 3b). With F_{opd} , *Eugenia* showed the greatest variation between seasons. Most species displayed a simultaneous marked decline in F_{mpd} in September 2004 and August 2005. Only *Eugenia* showed significant differences between seasons, with the lowest values of F_{mpd} measured in the dry season (Table II).

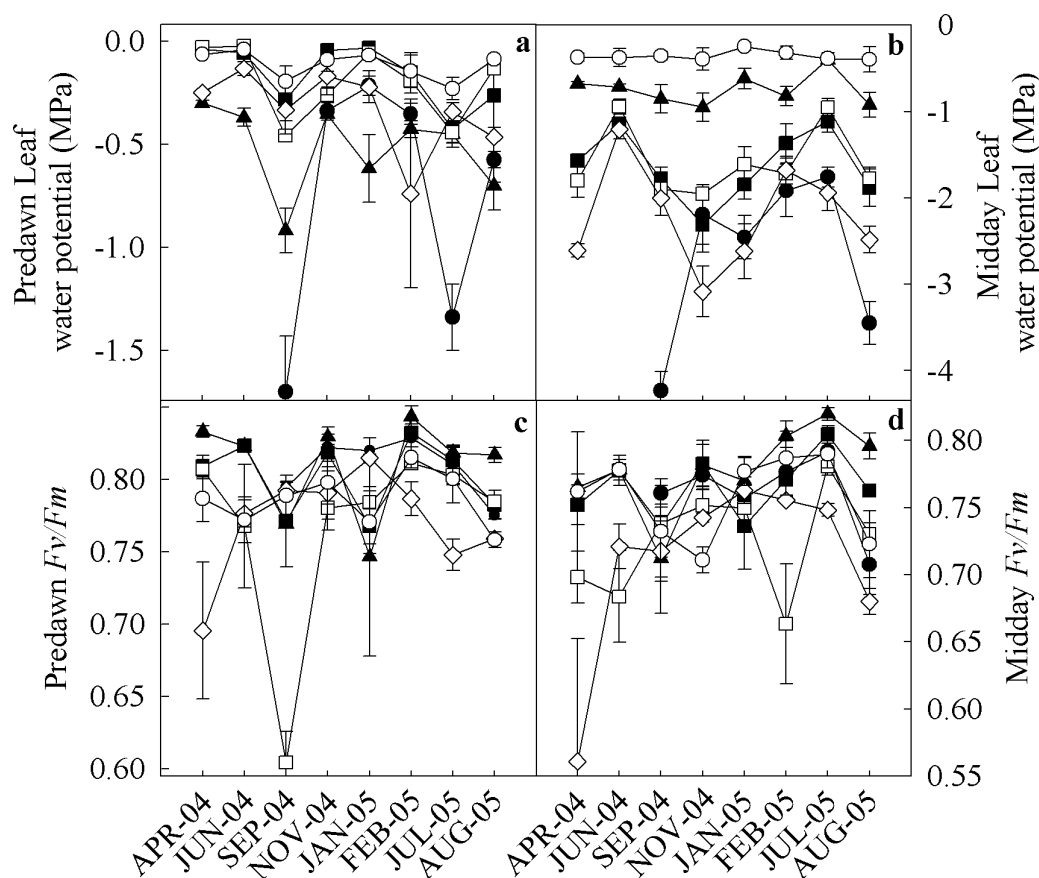


Figure 2 - Seasonal variation at predawn, midday in leaf water potential (panels **a** and **b**) and chlorophyll *a* fluorescence (panels **c** and **d**, respectively). Species are represented as follows: closed squares – *Byrsonima* (■); closed triangles – *Clusia* (▲); closed circles – *Erythroxylum* (●); open squares – *Eugenia* (□); open diamonds – *Ocotea* (◇) and open circles – *Protium* (○).

TABLE II

Midday leaf water potential (Ψ_{md}), predawn leaf water potential (Ψ_{pd}), potential quantum yield of photosystem II at midday (F_v/F_{mmd}), potential quantum yield of photosystem II at predawn (F_v/F_{mpd}), minimal fluorescence yield (F_{0pd}) and maximal fluorescence yield (F_{mpd}) during dry and wet seasons. In each column, different letters represent significant differences (two-way repeated-measures ANOVA, Tukey's test, $P < 0.05$).

| Species | Season | Ψ_{md} (MPa) | Ψ_{pd} (MPa) | F_v/F_{mmd} | F_v/F_{mpd} | F_{0pd} | F_{mpd} |
|---------------------|--------|-------------------|-------------------|---------------|---------------|-----------|-------------|
| <i>Byrsonima</i> | Dry | -1.78bc | -0.28c | 0.74ab | 0.77b | 342.50c | 1501.50bcd |
| | Wet | -1.37cd | -0.15c | 0.77 ab | 0.83d | 263.67a | 1577.00de |
| <i>Clusia</i> | Dry | -0.85de | -0.92b | 0.71ab | 0.77b | 335.00bc | 1482.50bcd |
| | Wet | -0.82de | -0.43c | 0.80b | 0.84d | 251.67a | 1617.50de |
| <i>Erythroxylum</i> | Dry | -4.23a | -1.70a | 0.76 ab | 0.79bc | 286.50abc | 1399.25bcde |
| | Wet | -1.92bc | -0.35c | 0.78 ab | 0.83d | 282.50abc | 1642.50de |
| <i>Eugenia</i> | Dry | -1.90bc | -0.46c | 0.74 ab | 0.60a | 459.00d | 1176.50a |
| | Wet | -1.72bc | -0.19c | 0.66a | 0.81cd | 349.33c | 1859.83e |
| <i>Ocotea</i> | Dry | -2.00b | -0.46c | 0.72 ab | 0.76b | 291.50abc | 1230.00abc |
| | Wet | -1.68bc | -0.22c | 0.76 ab | 0.82cd | 309.83abc | 1675.17cde |
| <i>Protium</i> | Dry | -0.36e | -0.20c | 0.73 ab | 0.79bc | 263.50a | 1257.50ab |
| | Wet | -0.32e | -0.15c | 0.79b | 0.82cd | 270.33ab | 1484.50bcd |

TABLE III

Results of two-way ANOVAs conducted to test the effects of species and seasons on the change in midday leaf water potential (Ψ_{mid}), predawn leaf water potential (Ψ_{pd}), potential quantum yield of photosystem II at midday (F_v/F_{mmd}), potential quantum yield of photosystem II at predawn (F_v/F_{mpd}), minimal fluorescence yield (F_{opd}) and maximal fluorescence yield (F_{mpd}). Significance levels are indicated as follows: **** – $P < 0.0001$; *** – $P < 0.001$; ** – $P < 0.01$; * – $P < 0.05$. Season is abbreviated to “Se” and species to “Sp”.

| Effects | df | Ψ_{mid} (MPa) | | | Ψ_{pd} (MPa) | | | F_v/F_{mmd} | | | F_v/F_{mpd} | | | F_{opd} | | | F_{mpd} | | |
|-----------|----|---------------------------|------|----------|--------------------------|------|----------|----------------------|--------|-------|----------------------|--------|----------|------------------|-------|----------|------------------|-------|--------|
| | | SS | MS | F | SS | MS | F | SS | MS | F | SS | MS | F | SS | MS | F | SS | MS | F |
| Se | 1 | 2.72 | 2.71 | 23.04*** | 1.37 | 1.27 | 28.39*** | 0.006 | 0.006 | 5.24* | 0.0526 | 0.0526 | 270.8*** | 15708 | 15708 | 20.97*** | 81834 | 81834 | 47.1** |
| Sp | 5 | 26.68 | 5.33 | 91.60*** | 3.24 | 0.64 | 22.86*** | 0.018 | 0.0036 | 1.52 | 0.0462 | 0.009 | 30.42*** | 70665 | 14133 | 9.66*** | 13985 | 27972 | 1.10 |
| Sp:Se | 5 | 5.77 | 1.15 | 9.80*** | 1.85 | 0.37 | 7.70** | 0.023 | 0.004 | 3.89* | 0.033 | 0.006 | 34.06*** | 22668 | 4533 | 6.05*** | 38126 | 76254 | 4.38* |
| Residuals | 12 | 1.41 | 0.11 | | 0.58 | 0.05 | | 0.014 | 0.0012 | | 0.002 | 0.0001 | | 8988 | 749 | | 20844 | 17371 | |

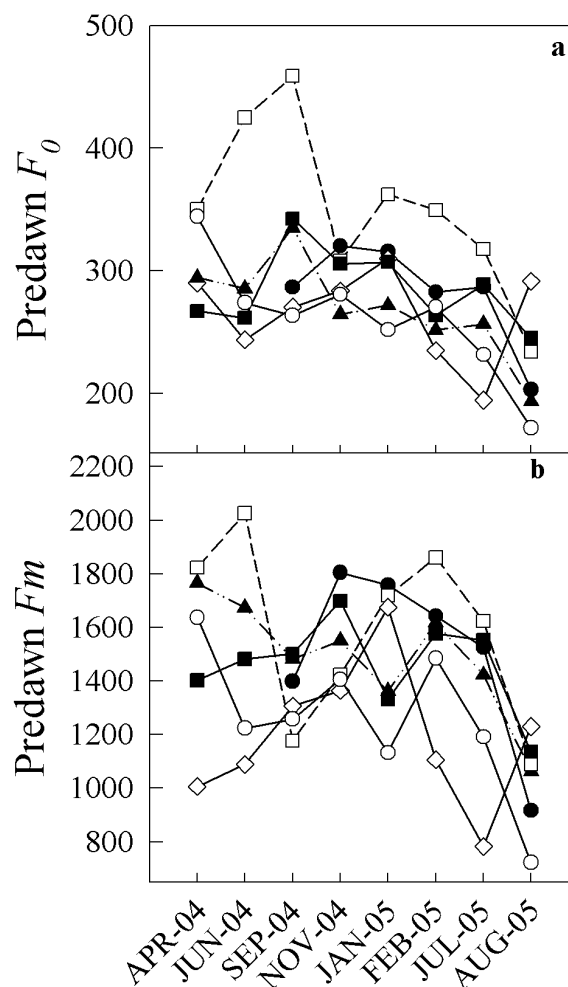


Figure 3 - Seasonal variation in predawn basal (a) and maximum fluorescence yield (b) (F_{opd} and F_{mpd} respectively). Species symbols as for Figure 2.

Multiple linear regressions indicated that only NRD showed a negative relationship with Ψ_{pd} and F_v/F_{mpd} in *Clusia*, *Erythroxylum* and *Eugenia*. Both parameters were affected in *Erythroxylum*, while only to Ψ_{pd} or F_v/F_{mpd} responded to NRD in *Clusia* and *Eugenia*, respectively (Table IV). For midday measurements, only *Ocotea* showed a significant negative relationship between F_v/F_{mmd} and VPD (Table V).

The first two axes of the PCA explained 41.89% and 26.90% of the variation observed in the six traits, respectively (Table VI). The first axis was most strongly associated with F_v/F_{mpd} , F_{mpd} and F_{opd} . The second axis was most strongly associated with

Ψ_{pd} and Ψ_{md} . From the wet to the dry season, all species showed responses associated with the first axis of variation, being positively associated with F_{0pd} and negatively with F_v/F_{mpd} , F_v/F_{mmd} and F_{mpd} .

For *Erythroxylum*, however, the response was more closely associated with the second axis, with the response from wet to dry season being negatively related to Ψ_{pd} and Ψ_{md} (Fig. 4).

TABLE IV

Coefficient of multiple regression between predawn leaf water potential (Ψ_{pd} , MPa), F_v/F_{mpd} , daily maximum air vapor pressure deficit (VPD, Pa KPa⁻¹) and the number of rainless days (NRD). We selected the greatest VPD for each day on which measurements were taken and the number of rainless days during the one, two, three or four weeks before that. Asterisks and bold values indicate $P < 0.05$.

| Species | Trait | Factor | Weeks | | | |
|---------------------|---------------|--------|---------------|-----------------|----------------|-----------------|
| | | | 1 | 2 | 3 | 4 |
| <i>Byrsonima</i> | Ψ_{pd} | VPD | -0.06 | 0.04 | -0.01 | 0.00 |
| | | NRD | -0.08 | -0.02 | -0.02 | -0.02 |
| | F_v/F_{mpd} | VPD | -0.06 | 0.04 | -0.01 | 0.00 |
| | | NRD | -0.08 | -0.02 | -0.02 | -0.02 |
| <i>Clusia</i> | Ψ_{pd} | VPD | 0.12 | -0.08 | -0.01 | -0.02 |
| | | NRD | -0.05 | -0.0995* | -0.04 | -0.04 |
| | F_v/F_{mpd} | VPD | 0.02 | 0.005 | 0.01 | 0.01 |
| | | NRD | 0.00 | -0.01 | -0.003 | -0.002 |
| <i>Protium</i> | Ψ_{pd} | VPD | -0.07 | -0.03 | -0.06 | -0.05 |
| | | NRD | -0.03 | -0.01 | -0.01 | -0.01 |
| | F_v/F_{mpd} | VPD | 0.03 | 0.03 | 0.03 | 0.03 |
| | | NRD | 0.00 | 0.00 | 0.00 | 0.00 |
| <i>Erythroxylum</i> | Ψ_{pd} | VPD | -0.46 | -0.27 | -0.56 | -0.45 |
| | | NRD | -0.36 | -0.21 | -0.24* | -0.12 |
| | F_v/F_{mpd} | VPD | 0.03 | 0.03* | 0.03 | 0.03 |
| | | NRD | -0.01* | -0.008* | 0.00 | -0.0034* |
| <i>Eugenia</i> | Ψ_{pd} | VPD | -0.13 | -0.08 | -0.17 | -0.12 |
| | | NRD | -0.07 | -0.03 | -0.04 | -0.02 |
| | F_v/F_{mpd} | VPD | -0.07 | -0.09 | -0.11 | -0.09 |
| | | NRD | -0.04 | -0.04* | -0.024* | -0.017* |
| <i>Ocotea</i> | Ψ_{pd} | VPD | 0.01 | 0.12 | 0.02 | 0.06 |
| | | NRD | -0.06 | 0.00 | -0.02 | -0.01 |
| | F_v/F_{mpd} | VPD | -0.03 | -0.03 | -0.02 | -0.03 |
| | | NRD | -0.01 | 0.00 | 0.00 | 0.00 |

TABLE V

Coefficient of multiple regression between temporal variation in midday leaf water potential (Ψ_{md} , MPa), F_v/F_{mmd} , daily maximum air vapor pressure deficit (VPD) and the number of rainless days (NRD). We selected the greatest VPD on each day on which measurements were taken and the number of rainless days during the one, two, three or four weeks before that. Asterisks and bold values indicate $P < 0.05$.

| Species | Trait | Factor | Weeks | | | |
|------------------|---------------|--------|-------|-------|-------|-------|
| | | | 1 | 2 | 3 | 4 |
| <i>Byrsonima</i> | Ψ_{md} | VPD | -0.64 | -0.31 | -0.29 | -0.35 |
| | | NRD | 0.18 | 0 | 0.03 | 0.02 |
| | F_v/F_{mmd} | VPD | -0.04 | -0.03 | -0.03 | -0.03 |
| | | NRD | 0 | 0 | 0 | 0 |

TABLE V (continuation)

| Species | Trait | Factor | Weeks | | | |
|---------------------|---------------|--------|-------|---------------|--------------|---------------|
| | | | 1 | 2 | 3 | 4 |
| <i>Clusia</i> | Ψ_{md} | VPD | -0.34 | -0.3 | -0.31 | -0.28 |
| | | NRD | 0.02 | -0.04 | -0.01 | -0.01 |
| | F_v/F_{mmd} | VPD | -0.05 | -0.05 | -0.07 | -0.04 |
| | | NRD | 0 | -0.01 | -0.01 | 0 |
| <i>Protium</i> | Ψ_{md} | VPD | 0.03 | 0.04 | 0.04 | 0.04 |
| | | NRD | -0.01 | 0 | 0 | 0 |
| | F_v/F_{mmd} | VPD | -0.02 | -0.02 | -0.02 | -0.02 |
| | | NRD | -0.01 | -0.01 | 0 | 0 |
| <i>Erythroxylum</i> | Ψ_{md} | VPD | -0.87 | -0.45 | -1.14 | -0.54 |
| | | NRD | -0.41 | -0.44 | -0.27 | -0.19 |
| | F_v/F_{mmd} | VPD | 0.01 | 0.02 | 0 | 0.01 |
| | | NRD | -0.01 | -0.01 | 0 | 0 |
| <i>Eugenia</i> | Ψ_{md} | VPD | -0.78 | -0.84 | -0.77 | -0.82 |
| | | NRD | 0 | -0.04 | 0 | -0.01 |
| | F_v/F_{mmd} | VPD | -0.78 | -0.84 | -0.77 | -0.05 |
| | | NRD | 0 | -0.04 | 0 | 0 |
| <i>Ocotea</i> | Ψ_{md} | VPD | -0.05 | -0.13 | 0.06 | -0.14 |
| | | NRD | 0.23 | 0.12 | 0.1 | 0.05 |
| | F_v/F_{mmd} | VPD | -0.12 | -0.12* | -0.12 | -0.12* |
| | | NRD | 0 | 0 | 0 | 0 |

TABLE VI

Eigen vector scores from a PCA of three axes obtained from a matrix of six traits and six species in two seasons. The six traits measured were midday leaf water potential (Ψ_{md}), predawn leaf water potential (Ψ_{pd}), potential quantum yield of photosystem II at midday (F_v/F_{mmd}), potential quantum yield of photosystem II at predawn (F_v/F_{mpd}), minimal fluorescence yield (F_{0pd}) and maximal fluorescence yield (F_{mpd}). Percentage values indicate the percentage of variation accounted for by each axis. Bold values indicate the highest values for each axis.

| | Axis 1 | Axis 2 | Axis 3 |
|----------------------|---------------|--------------|---------------|
| Physiological Traits | 41.89% | 26.90% | 18.92% |
| F_v/F_{mpd} | 0.928 | -0.270 | 0.218 |
| F_{0pd} | -0.838 | 0.347 | 0.224 |
| F_{mpd} | 0.618 | 0.013 | 0.705 |
| F_v/F_{mmd} | 0.462 | -0.321 | -0.677 |
| Ψ_{md} | 0.440 | 0.776 | -0.287 |
| Ψ_{pd} | 0.402 | 0.846 | -0.026 |

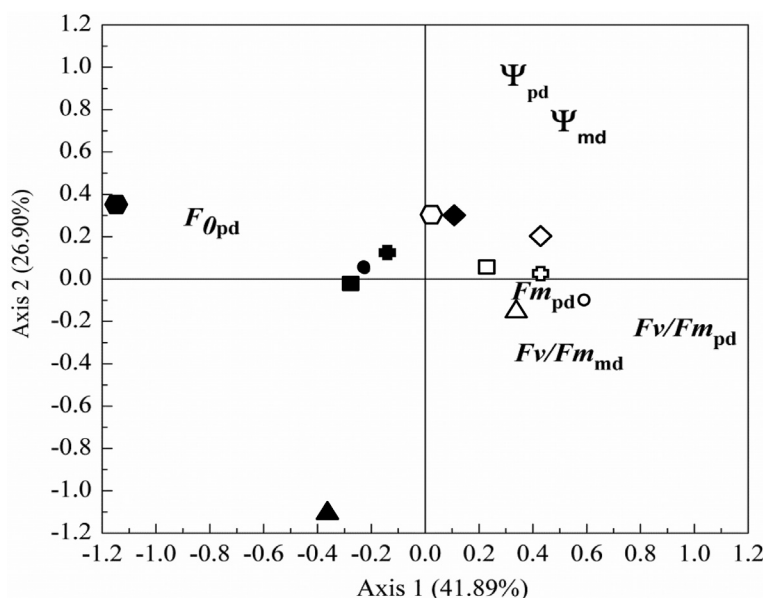


Figure 4 - PCA ordination of six species in two seasons on the basis of six traits: predawn (Ψ_{pd}) and midday leaf water potential (Ψ_{md}), predawn (F_v/F_{mpd}), midday chlorophyll fluorescence (F_v/F_{mmd}), predawn basal (F_{0pd}) and maximum fluorescence yield (F_{mpd}). Each species, in the wet and dry seasons (open and closed symbols, respectively) are represented as follows: *Byrsonima* (cross), *Clusia* (circles), *Eugenia* (hexagon), *Erythroxylum* (triangle), *Protium* (losangle) and *Ocotea* (square). Axis 1 and 2 represent 41.89% and 26.90% of total variance, respectively.

DISCUSSION

Most of the six species did not differ across seasons in their ability to maintain Ψ_{md} . Although the dominant species, *Clusia* and *Protium* had higher values of Ψ_{md} throughout, the other species, except for *Erythroxylum*, maintained similar values throughout the year, which were consistently lower than the dominant species. These values were maintained despite differences in leaf morphology and phenology. This agrees with reports indicating that the maintenance of Ψ_{md} occurs in a series of ways, in contrast with the maintenance of constant hydraulic conductance, which occurs through changes in architectural traits such as leaf area per sapwood area (Meinzer et al. 1999, Bucci et al. 2005, Maseda and Fernández 2006, Franks et al. 2007). In *Protium*, for instance, the ability to maintain a higher Ψ_{md} throughout the year might be mediated by a substantial reduction in leaf number

during the dry season (Rosado and de Mattos 2010). Regardless of the mechanisms involved, it is noteworthy that only the two dominant species exhibited higher and constant Ψ_{md} , which suggests a higher safety margin for embolism (Sperry et al. 2002). Our findings support that in drought-prone habitats most species are able to maintain similar Ψ_{md} between dry and wet seasons. However, only a small number of species are able to maintain a relatively high Ψ_{md} , which may be an important trait related to the ability of these species to achieve dominance in sandy, drought-prone environments.

ARE THE SEASONAL RESPONSES OF CHLOROPHYLL FLUORESCENCE VARIABLES RELATED TO THE SEASONAL VARIATION IN Ψ_L ?

F_v/F_{mpd} was lower in the restinga plants than the optimal value for most species, which indicates photoinhibition (Demmig-Adams and Adams 2006). However, this was less pronounced than

in plants from other harsh environments, where F_v/F_m may reach values below 0.5 (Bellot et al. 2004, Zunzunegui et al. 2005, Ogaya et al. 2011). Nevertheless, there is a positive linear relationship between F_v/F_{mpd} and the leaf turnover rate for restinga species, which suggests that there are ecophysiological implications of even small decreases in F_v/F_{mpd} (Rosado and de Mattos 2010). The greatest decreases in F_v/F_{mpd} and F_v/F_{mmd} occurred after a rainless period of 30 days in September 2004. These decreases were probably caused by low soil water potential and high radiation load, as observed for woody species in semi-arid Mediterranean shrubland in Spain (Bellot et al. 2004).

The reversible decline in F_v/F_m reflects the protective down-regulation of PS II, which may prevent damage to the reaction centers when there is excess excitation energy (Walker 1992, Demmig-Adams and Adams 2006). However, a comparison of changes in F_0 and F_m indicates whether species are exhibiting increased thermal dissipation of excitation energy or deactivation of the PSII reaction centers (Krause 1988, Porcar-Castell et al. 2008). Thermal dissipation is associated with decreases in F_{0pd} and F_{mpd} , as observed when the dry season of 2005 was approaching, whereas photodamage and deactivation only increase F_{0pd} , as observed in September 2004 in most species. For *Clusia*, *Byrsonima* and *Eugenia*, F_{0pd} increased to various degrees, yet always significantly during the dry season, with the highest values recorded for *Eugenia*. This indicates that these species were subjected to photodamage (Krause 1988), as could be expected for plants exhibiting constant Ψ_{md} , due to strong stomatal closure (McDowell et al. 2008). Photoinhibition may have been alleviated during the cloudy day in July 2005, when all species showed the highest F_v/F_{mmd} . Cloudy days may also have decreased the strength of the general declining trend in F_{0pd} throughout 2005, because the higher accumulated rainfall in 2005 (770 mm)

in comparison with 2004 (246 mm) suggests that there were more cloudy days, which would reduce average light intensity.

Irrespective of leaf succulence and leaf phenology, with the exception of *Erythroxylum*, physiological changes of species across seasons were more strongly captured by chlorophyll fluorescence variables than to Ψ_L . The multivariate analysis showed that the responses of all species across seasons were positively associated with F_{0pd} , which suggests the occurrence of photodamage during the dry season. However, the differential displacement of each species between seasons in the multivariate space indicates different degrees of susceptibility to photoinhibition, with *Eugenia* showing the strongest changes between seasons. The only species for which changes in fluorescence between seasons was also paralleled by changes in Ψ_{md} and Ψ_{pd} , was *Erythroxylum*. For *Erythroxylum*, the negative relationship between Ψ_{md} and Ψ_{pd} was expected because of this species' higher wood density, which may decrease water transport to leaves (Rosado and de Mattos 2010).

HOW DOES VARIATION IN Ψ_L DIFFER IN RESPONSE TO NRD AND VPD THROUGHOUT THE YEAR?

The less responsive behavior of *Byrsonima*, *Clusia* and *Protium* to NRD and VPD indicates that these species have the ability to decouple from the main factors that drive daily and seasonal variation in water availability. In fact, *Byrsonima* and *Protium* show a strong midday depression of stomatal conductance in both wet and dry seasons (Lignani 2008), and the CAM photosynthesis in *Clusia* (Franco et al. 1996) may explain the lack of a midday response to NRD and VPD. In *Clusia*, the negative relationship between Ψ_{pd} and NRD might reflect nocturnal transpiration, typical in CAM species, which may lead to more negative Ψ_{pd} as NRD increases. In addition, the unresponsiveness of Ψ_{md} and Ψ_{pd} to NRD and/or VPD in *Byrsonima* may be related to this species' higher leaf death rate

and Ψ_{TLP} (Rosado and de Mattos 2010). The less negative Ψ_{TLP} associated with a higher rate of leaf shedding may be an escape strategy for *Byrsonima*, allowing it to avoid the possible adverse effects of NRD and/or VPD on Ψ_{md} and/or Ψ_{pd} (Rosado and de Mattos 2010).

On the other hand, *Eugenia*, *Erythroxylum* and *Ocotea* responded strongly to NRD and/or VPD (Table IV). The negative relationship between NRD and Ψ_{pd} for *Erythroxylum* may indicate a lower capacity for xylem refilling during prolonged rainless periods because of the species' high wood density (Donovan et al. 2001, Rosado and de Mattos 2010). Interestingly, predawn and midday F_v/F_m showed significant negative relationships with VPD and NRD, indicating that chlorophyll fluorescence may be more descriptive of the response of a species to water availability than Ψ_L .

Plants growing on sandy soils have a higher Ψ_{pd} than those growing on clay soils (Sperry et al. 2002, Sperry and Hacke 2002). However, this is true only when the former have access to deeper soil water profiles and/or soil moisture is frequently replenished by rainfall (Fravolini et al. 2005, Hultine et al. 2005). The Ψ_{pd} of restinga species growing where mean annual rainfall was 1100–1300 mm was higher than for other species occurring in sandy environments where the mean annual rainfall was around 450 mm (-0.1 to -1.70 MPa compared with -1.0 to -5.0 MPa, respectively) (Zunzunegui et al. 2005, Fravolini et al. 2005, Hultine et al. 2005). In comparison with other seasonal environments, the variation in Ψ_{pd} observed in restinga plants, -0.1 to -0.43 MPa in the wet season and -0.19 to -1.70 MPa during the dry season, was not as marked. In Mediterranean plants, Ψ_{pd} varies from -0.1 to -0.86 MPa during spring and from -1.45 to -2.28 MPa during summer (Mediavilla and Escudero 2004, David et al. 2007). In the Brazilian savannas, woody species show a significant decline in Ψ_{pd} , from values close to 0 MPa in the wet season to around -0.5 to -1.0 MPa during the dry season (Bucci et

al. 2005). It must be remembered, however, that it is not only soil properties, root access to the water table and/or rainfall patterns that affect Ψ_{pd} (Sperry et al. 2002, Fravolini et al. 2005). Differences in Ψ_{pd} among species may also be related to processes such as hydraulic conductance and nocturnal transpiration (Donovan et al. 2001, Dawson et al. 2007). For *Clusia*, the CAM behavior of nocturnal stomatal opening, as also observed in C_3 plants that show nocturnal transpiration, could explain the low Ψ_{pd} (Donovan et al. 2001). On the other hand, in *Erythroxylum*, the only brevi-deciduous species in this study, a decrease in the rate of water delivery to the leaves because of the species' high wood density ($\sim 0.77 \text{ g cm}^{-3}$; Rosado and de Mattos 2010) could promote more negative Ψ_{pd} and Ψ_{md} , as described in other studies (Donovan et al. 2001, Meinzer 2003).

In conclusion, temporal variation in Ψ_L and chlorophyll fluorescence was found useful for differentiating between groups of sandy soil species that are responsive or unresponsive to water availability. However, chlorophyll fluorescence appeared to be a more sensitive descriptor of their seasonal and short-term responses to NRD. The use of plant traits as proxies for the responses of communities to environmental change is gaining importance (Sutherland et al. 2013). In this study we have demonstrated that a better comprehension of how tropical species from drought-prone habitats cope with changes in water availability can be based on measurements of seasonal variation in Ψ_L and chlorophyll fluorescence. These findings reinforce the importance of ecophysiological knowledge when selecting functional traits for predicting responses to climate change (Rosado et al. 2013), and open important avenues for models specifically concerning species from dry environments. In addition, because we focused on species from the Atlantic rain forest complex that are able to occupy coastal sandy plains environments, our results contribute to the understanding of the environ-

mental filtering that affects community assembly in resource-poor habitats.

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RESUMO

Entre os efeitos da mudança ambiental, a intensificação dos eventos de seca é notável e a vegetação tropical é apontada como altamente vulnerável a ela. No entanto, não está claro como plantas tropicais em habitats propensos à seca responderão a essa mudança. Em um ambiente de planície costeira arenosa, avaliamos a resposta de seis espécies vegetais à déficit de água ao longo das estações, a relação entre as suas características morfo-fisiológicas, e quais características seriam as melhores descritoras de resposta das plantas à seca. Independentemente de suculência foliar e fenologia, respostas entre as estações foram mais fortemente relacionadas a fluorescência da clorofila. Neste estudo demonstramos que a melhor compreensão de como espécies tropicais de habitats propensos a seca lidam com mudanças na disponibilidade de água pode ser baseada na variação sazonal de potencial hídrico e fluorescência da clorofila. Esta variação temporal de potencial hídrico e fluorescência da clorofila foram úteis para diferenciar grupos de espécies que são responsivas ou não responsivas à disponibilidade de água. Ressalta-se que a fluorescência da clorofila foi o descritor mais sensível de respostas das espécies tanto em termos sazonais quanto em curto prazo.

Palavras-chave: seca, característica funcional, relações hídricas em plantas, fotoinibição, habitats sazonais.

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