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## EFFECTS OF SEASONAL AIR TEMPERATURES AND LIGHT ON LEAF TRAITS AT ATLANTIC MONTANE FOREST, BRAZILIAN SOUTHEAST

MARCHIORI, N. M.; SILVA, J. G.; SANTOS, F. C.; DOMINGUES, L. M.; FREITAS, H. C.; ROCHA, H. R.; CAMARGO, P. B.; AIDAR, M. P. M. Effects of seasonal air temperatures and light on leaf traits at atlantic montane forest, brazilian southeast. **CERNE**, v. 25, n. 3, p.263-272, 2019.

### HIGHLIGHTS

Seasonal changes influence physiological metabolism in plants of Montane Rainforest in Brazil and it could be assessed and scaled up by photosynthesis and pigments contents.

The results obtained at montane tropical rain forest are interesting and the conclusions about the relationship between air temperature, albedo and some physiological leaf traits are probably new

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### ABSTRACT

Seasonal variation of temperature could place physiological constraints on the distribution and performance of tropical forest plants, associated with light and water availability. A simple way to assess the relationship between temperature and plant physiology is through the characterization of leaf traits. The main aim of this study was to evaluate, through foliar parameters, the responses of plants to inherent seasonality. A 0.09 ha plot was installed near the flux tower and albedo sensors at Montane Ombrophilous Dense Forest (MODF) - Santa Virgínia Nucleus. At the peak of the dry and wet seasons, the electron transport rate (ETR) and photosynthetic pigments were measured. The results indicated that in MODF, cold and light availability are the main factors that could be influencing the physiology of species, demonstrated by high ETR in the wet season ( $197.4 \mu\text{mol e-m}^{-2}\text{s}^{-1}$ ) compared to the dry season ( $87.4 \mu\text{mol e-m}^{-2}\text{s}^{-1}$ ). Photosynthetic pigments varied between seasons, we observed higher chlorophyll b content ( $p < 0.05$ ), and lower content of carotenoids and xanthophylls ( $p < 0.01$ ) and Chl a/b ( $p < 0.01$ ) in the dry season. The low temperatures and irradiance influenced metabolic activity.

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## INTRODUCTION

In Brazilian Atlantic Rainforest one of the key factors that drives community structure and composition between forest physiognomies is the altitude (Oliveira-Filho and Gomes, 2000; Sanchez et al., 2013), associated with environmental conditions, such as temperature, irradiance (Scudeller et al., 2001), cloud level and fog formation (Rosado et al., 2010, 2012; Vieira et al., 2011; Joly et al., 2012). The functionality of these ecosystems can also vary between sites and seasons. Seasonal changes influence physiological metabolism of many forest plants and, the understanding of these variations is important to predict ecosystem balance and their responses to climate change in nutrient, carbon and water balances (Guan et al., 2015).

An approach to understand ecosystem functionality can be assessed through characterization of foliar parameters (Ollinger et al., 2008, 2010; Hollinger et al., 2009), since processes that modulate responses at the leaf level could be extrapolated to ecosystem process. Thus, the leaf functionality is directly related to its composition, morphology and energy balance (Roderick et al., 1999; Reich et al., 1992; Hikosaka and Osone, 2009).

Photosynthetically active radiation (PAR) was shown to be a relevant element driving the forest productivity, as plants use this radiation on photosynthesis. A percentage of the radiation is reflected back to the atmosphere, which is called albedo. Freitas (2012) defined albedo as the measure of diffusive reflection of solar radiation out of the total solar radiation received by a body, important for the radiation budget of an ecosystem and for the exchange of heat, matter and water between land and the atmosphere. Forest albedo is spatially variable and temporally dynamic, influenced by plant and canopy traits and surface reflectivity, including forest composition and leaf phenology (Leonardi et al., 2015).

The determination of photosynthetic pigments is one of the most frequently carried out analyses in plant ecology and physiology, as pigments can provide valuable insight into the physiological performance of leaves and ecosystem productivity (Peñuelas et al., 1995). Chlorophyll fluorescence measurements have become a widely adapted method to quantify photosynthetic performance of plants under various conditions (Maxwell and Johnson, 2000), as it is strongly sensitive to stress caused by high (Li et al., 2013; Slot and Winter, 2017) or low temperatures (Tsonev et al., 2003).

Tropical montane forests are among the most endangered tropical forests (França and Stehmann, 2004), especially due to the high deforestation caused by logging, agriculture and anthropogenic pressures. They

are also very sensitive to variations in the environment, particularly temperature, in fact, evidence of biodiversity loss already exists (Colwell et al., 2008) in consequence of global climate change. The importance of these forests is well recognized by the scientific community, because of their high biodiversity, endemism and structural complexity (Joly et al., 2014).

Understanding how photosynthesis of the tropical trees could adapt to variation in temperature and others environmental factors that change along elevation gradients is not precisely known. In addition, studies that emphasize the effects of low temperatures in photosynthetic characteristics in tropical montane forest are rare (Wittich et al., 2012). Based on that, the aim of this study was to characterize the relationship between leaf physiology, including photosynthesis, and seasonal surface albedo in tree species in the Montane Tropical Forest at “Serra do Mar” State Park, São Paulo State, Brazil.

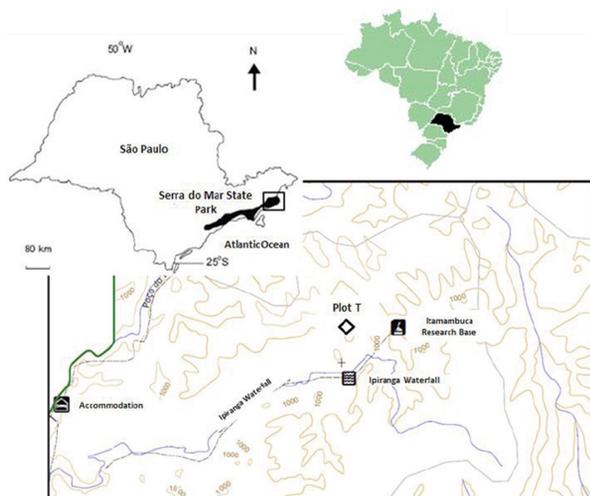
## MATERIAL AND METHODS

### Study Area

This study was carried out in Ribeirão da Casa de Pedra watershed –Santa Virgínia Nucleus, Serra do Mar State Park, southeastern Brazilian Atlantic Tropical Forest – Ubatuba, SP – Brazil (Figure 1). Specifically in the eddy Covariance Flux tower installed in 2007 (23°17'-23°24'S and 45°03'- 45°11'W; 1,020 m of altitude; <http://www.fluxdata.org:8080/SitePages/siteInfo.aspx?BR-Afs>).

According to Köppen (1948), the regional climate is classified as Cfa or Cfb (Cfa = Humid subtropical climate and Cfb = Temperate oceanic climate), with higher rainfall in wet season (Joly et al., 2012). The soil is shallow and shows more carbon, nitrogen and phosphorus contents than in lowland forests (Vieira et al., 2011; Joly et al., 2012). The Atlantic Forest physiognomy sampled was Montane Ombrophilous Dense Forest (Veloso et al., 1991) and the community is characterized by Marchiori et al. (2016) as in a secondary successional stage due to the past land occupation and logging activities up to 1977, when the Serra do Mar State Park was implemented.

The micro-meteorological variables measured by the tower indicated moist month average (q) between 8.0 and 13.5 g.kg<sup>-1</sup>, solar irradiance (Ki) - 120 and 200 W.m<sup>-2</sup> and air temperature (Tar) between 12 and 19°C, respectively in the dry and wet season. The albedo of the photosynthetically active radiation (albedo PAR) was measured between July 2010 and July 2011 (Freitas, 2012).



**FIGURE 1** Maps showing the location of the study site in Serra do Mar State Park São Paulo State, Brazil. The symbol (◊) indicates the forest plot sampled (Plot T).

### Vegetation sampling

The study included two plots, both in the surrounding area of flux tower. The first plot (Plot T) has 1.0 ha (100 x 10m) and was located near the flux tower, approximately 300m apart, in an area inside the forest. In this plot we measured the litterfall productivity, phytosociology and species composition (details of species composition in Marchiori et al., 2016).

The second plot had 0.09 ha (30 x 30m) and was installed just below the flux tower footprint. The plot area had been chosen to relate data obtained by plant physiology and albedo sensors (Kipp-Zonen CM 3 Kipp and Zonen PAR-Lite), installed 60 m high at the flux and meteorological tower. The individuals with diameter at breast height (DBH)  $\geq 4,8$  cm were identified and had leaf traits sampled. Twenty two tree individuals belonging to 11 different species reached the previous criteria and were included in the sample. The species selected to the present study show different successional strategies (Aidar et al., 2003). Pioneer species (PSS) included *Vernonia puberula* Less. (1 individual); Early secondary species (ESS) – *Alchornea triplinervia* (Spr.) Muell. Arg (4 individuals), *Cyathea* sp. (1 individual), *Guarea kunthiana* A. Juss. (1 individual), *Inga marginata* Willd. (5 individuals), *Inga sessilis* (Vell.) Mart. (1 individual), *Phytolacca dioica* L. (2 individuals), Fabaceae not identified (1 individual), *Tibouchina pulchra* Cogn. (1 individual); and Late secondary species (LSS) – *Euterpe edulis* Mart. (1 individual) and *Ocotea dispersa* Mez (4 individuals). Samples from north face of the upper canopy were taken in winter ('dry' season; July 2011) and summer ('wet' season; December 2011).

Meteorological data were provided by the Climate and Biosphere Lab team - IAG / USP and Fapesp Thematic project "Carbon tracker and water availability: controls of land use and climate changes" (FAPESP 08/ 58120-3).

### Estimation of electron transport rate

Photosynthetic activity was estimated using a modulated chlorophyll fluorometer (PAM 2100, Walz, Effeltrich, Germany) in three detached leaves for each individual, once per season. The modulated red light ( $0.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) was turned on to obtain complete re-oxidation of the primary electron acceptor of PSII and determine minimal fluorescence ( $F_0$ ), when all PS II reaction centers are open. The apparent electron transport rate (ETR) was calculated using the following equation:  $\text{ETR} = \text{PAR} \times \Delta F / F'_m \times 0.5 \times 0.84$  (Genty et al., 1989; Krall and Edwards, 1992). For ETR calculation, 0.5 was used as the fraction of excitation energy distributed to PSII, and 0.84 was a factor of photons absorbed by chlorophyll molecules. All measurements were taken between 8 – 12 a.m. under natural light conditions. Leaf temperatures and PAR incident at leaf were measured with the leaf clip holder of the PAM-2000 system.

### Content of photosynthetic pigments, specific leaf area and Nitrogen/Carbon content measurements

Chlorophyll and carotenoids were determined using a spectrophotometric method. Nine discs with  $0.79 \text{ cm}^2$  each were taken from the same leaves used for chlorophyll a fluorescence analyses. Three discs were placed in plastic tubes in the dark with 2 mL of 96% ethanol (Oliveira 2011). After 4 days, 1 ml of extract was diluted in 5 ml 96% ethanol and determined their optical density in a spectrophotometer (DU®-65, Beckman, USA) at absorbance wavelengths of 470, 649 and 665 nm. The photosynthetic pigments were quantified according to Lichtenthaler and Wellburn (1983) and Wellburn (1994) for chlorophyll a (Chl a), chlorophyll b (Chl b), chlorophyll a/ chlorophyll b ratio (Chl a/b), carotenoids + xantophylls. The values were estimated in  $\text{mg}\cdot\text{g}^{-1}$  dry weight.

For the same individuals and leaves from fluorescence analysis, three circular disks from the leaves ( $0.79 \text{ cm}^2$  area) were oven-dried at  $70^\circ\text{C}$  for at least 72 h and weighed to determine Specific Leaf Area (SLA) ( $\text{cm}^2\cdot\text{LA}\cdot\text{g}^{-1}$  LDW). In addition, total content of Nitrogen (N), Carbon (C) and C/N ration,  $^{15}\text{N}$  and  $^{13}\text{C}$  isotopes were measured at Isotopic Ecology Laboratory of CENA/ ESALQ / USP - Brazil. We measured mass based foliar N concentration (N mass, g of N per 100 g of dry leaf matter) and, then we determined N per unit leaf area (N area) by multiplying N mass by the LMA (g leaf per  $\text{cm}^2$  leaf) of the sample (N area = N mass \* LMA).

## Litter sampling

The litterfall traps were randomly distributed in a 1 ha plot (Plot T), which covered a major area with 1,704 tree species (Marchiori et al. 2016). This plot was divided in 25 subplots of 20 x 20 m and allocated 5 litterfall traps in each one. The litter traps were made with PVC pipes and screens nylon, whose total area was 0.25 m<sup>2</sup> (0.5m x 0.5m) and opening of 3 mm screen to prevent the loss of small leaves. The litter was collected every month and the samples were dried at 60°C for 3 days, then they were weighed (g.0.25cm<sup>-2</sup>) and transformed in ton.ha<sup>-1</sup>. The data given here includes the litter from 27<sup>st</sup> July 2010 to 30<sup>st</sup> June 2011.

## Data Analysis

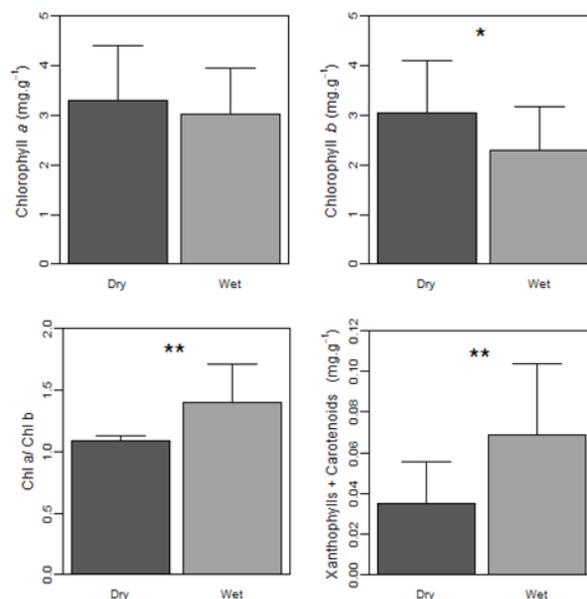
We had a total of three different leaves for each tree individual (22 individuals). For each parameter, the normal distribution and homogeneity of the data was determined with the Shapiro-Wilk and Levene test. We used a logarithmic transformation in those variables that did not follow a normal distribution. To evaluate the influence of variables in the species physiology between seasons, a Student t-test was performed ( $p < 0.05$ ), to normal distribution, or a Mann-Whitney test ( $p < 0.05$ ), when non-normal distribution was found. In addition, Pearson correlation coefficients were used to check the relationship between variables.

Data was analyzed by principal component analysis (PCA) to separate the species in different groups and seasons taking into account Chl b, Chl a/b, carotenoids + xanthophylls, N/area, CN ratio and  $\delta^{13}\text{C}$ . PCA is a linear dimensionality reduction technique that identifies orthogonal directions of maximum variance in the original data and projects the data into a lower-dimensionality space made of a sub-set of the highest-variance components (Manly, 2008). In this study, a space of two dimensions (two principal components), which was demarcated by two axes labeled PC1 and PC2, was suitable to our analysis. The methodologies applied are described in Zar (1999). For statistical analysis and figures we used the R Development Core Team (2011).

## RESULTS

The leaf photosynthetic pigments content were different among seasons, with higher Chl b content ( $p < 0.05$ ), and lower content of carotenoids + xanthophylls ( $p < 0.01$ ) and Chl a/b ( $p < 0.01$ ) in the dry season (Figure 2). The mean values were: Chl b, 3.038 mg.g<sup>-1</sup> in the dry season and 2.28 mg.g<sup>-1</sup> in the wet season. Concentration

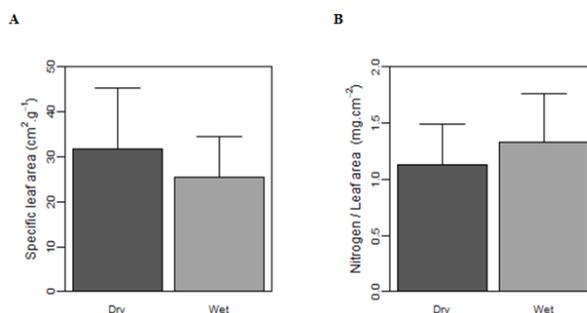
of carotenoids and xanthophyll in the leaves were 0.069 mg.g<sup>-1</sup> in the wet season and 0.035 mg.g<sup>-1</sup> in the dry season. Chlorophyll a and b were positively correlated ( $r = 0.89$ ,  $p < 0.01$ ), as well as Chl a/b ratio and xanthophyll + carotenoids contents ( $r = 0.48$ ,  $p < 0.01$ ).



**FIGURE 2** Concentrations of pigments (mean  $\pm$  sd) between dry and wet seasons: A. Chlorophyll a; B. Chlorophyll b; C. Chlorophyll a/b ratio; D. Xanthophylls + Carotenoids. \* and \*\* indicate significant differences between seasons ( $p \leq 0.05$  and  $p \leq 0.01$ , respectively).

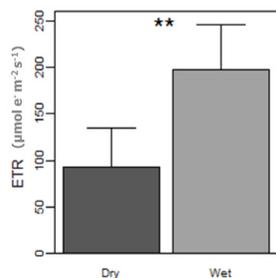
The nitrogen content per leaf area (N/Area) showed no statistical difference between seasons, although it tends to be higher in wet than in dry seasons (Figure 3). SLA had a tendency to increase in dry season and was negatively correlated to the concentration of carotenoids and xanthophylls ( $r = -0.6$   $p < 0.01$ ) and N/Leaf Area was positively correlated with the concentration of carotenoids and xanthophylls ( $r = 0.61$ ,  $p < 0.01$ ). Isotopic ratio of N, C and C/N ratio were statistically similar between seasons (data not shown).

The average values of ETR for all sampled individuals were higher in the wet season (197.4  $\mu\text{mol}$



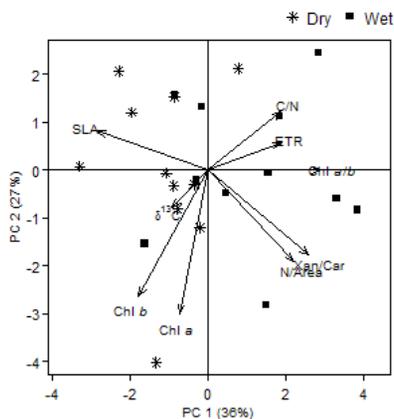
**FIGURE 3** A. Specific leaf area; B. nitrogen/leaf area (mean  $\pm$  sd) between dry and wet seasons..

e-m<sup>-2</sup>·s<sup>-1</sup>) compared to the dry season (87.4 μmol e-m<sup>-2</sup>·s<sup>-1</sup>; Figure 4), even with wide variance within species (Figure 4). There was a relationship between the ETR and the concentration of carotenoids and xanthophylls ( $r = 0.42$ ,  $p < 0.01$ ) and the Chl a/b ratio ( $r = 0.48$ ,  $p < 0.01$ ).



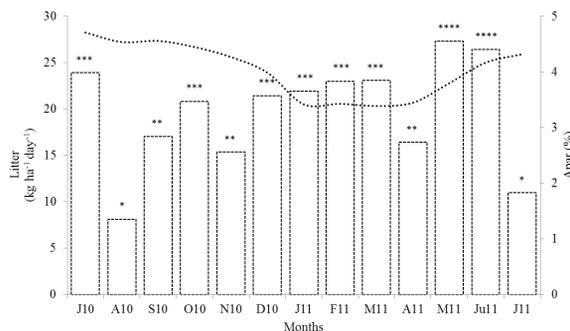
**FIGURE 4** Electron transport rate (mean ± sd) between dry and wet seasons. \*\* indicate significant differences between seasons ( $p \leq 0.01$ ).

The PCA explained 59% of total data variation in the first two axis (Figure 5). The principal component 1 (PC1) summarized 33% of variability and the main variables related to axis 1 were SLA (ev= -0.466), Chl a/b ratio (ev=0.447), xanthophylls + carotenoids (ev=0.427) and N/Leaf Area (ev=0.383). The main correlations with PC2 were Chl a (ev= -0.571) and Chl b (ev= -0.526). Most wet season samples were on the right side of PCA and they were correlated with high values of chlorophyll a/b ratio, xanthophylls + carotenoids and N/Leaf Area and low levels of SLA. While most dry season samples were on the left side and they were related in reverse way with this variables. There is no strong distinction between seasons in axis 2 and symbols in the negative side of PC2 were related with high values of Chl a and Chl b.



**FIGURE 5** Principal component analysis (PCA) according to leaf parameters in dry (\*) and wet (■) seasons. Each symbol represent mean for specie. Length of the arrow lines corresponds to the strength of correlation. SLA – Specific Leaf Area, C/N – carbon and nitrogen ratio, ETR – Electron Transport Rate, Chl a/b – Chlorophyll a and chlorophyll b ratio, Xan/Car – xanthophyll and carotenoids ratio, N/area – quantity of nitrogen per leaf area, Chl a – Chlorophyll a, Chl b – Chlorophyll b,  $\delta^{13}C$  – carbon isotope 13.

The albedo PAR evaluation at the study site indicated clear seasonality in light reflectance, showing higher values during the dry season (Figure 5). The litter production (Figure 6) showed no patterns among seasons and months and did not correlate with albedo values.



**FIGURE 6** Albedo PAR (Apar %; dotted line) and Litter production (Kg ha<sup>-1</sup> day<sup>-1</sup>; bars) in the study site. T test and ANOVA ( $p < 0.05$ ). \* and \*\* indicate significant differences between seasons ( $p \leq 0.05$  and  $p \leq 0.01$ , respectively).

## DISCUSSION

Chlorophyll and carotenoid concentrations are indicators of plant use and response to light intensity, as they can be synthesized and degraded (photooxidation) by it (Strauss-DeBenedetti and Bazzaz, 1991; Gonçalves et al., 2001). Chlorophyll is responsible for the photochemical phase in photosynthesis, and it is the most abundant in the reaction centers of the photosystems I and II (Streit et al., 2005). However, in elevated light conditions, the degradation rate overtakes the synthesis, and a reduction was seen in chlorophyll concentration in the reaction centers (Gonçalves et al., 2001), as well as we obtained in this study, especially for Chl b.

Carotenoid pigments content, which are important to dissipate the excessive energy and responsible for the photosynthetic apparatus protection (Streit et al., 2005), had higher values in wet season, consistent with elevated photosynthetic activity. Studies indicate that sun leaves are able to absorb only 10% of the incident radiation, with the remainder considered excess and removed by carotenoids to prevent damage to the photosynthetic apparatus (Demmig-Adams and Adams, 1996).

The increase of Chl b, the decline of Chl a/b and xanthophyll + carotenoids during the dry season could be understood as a decrease in the antenna of photosystems and accessory pigments to light-harvesting apparatus, resulting in low transference of energy to the reaction centers (Streit et al., 2005; Walters, 2005) compatible to lessening in photosynthetic activity. The ratio between the concentrations of Chl a/b is an indicator for the

functionality of pigments and adaptation/ acclimatization of the photosynthetic apparatus (Gonçalves et al., 2001), suggesting that reduction in air temperature during the winter impairs photosynthetic activity by constraining the pigment production and functionality. However, more studies should be done to make it clearer.

The decrease of chlorophyll a/ xanthophyll+carotenoid in the wet season highlighted this ratio as an important descriptor of photooxidative damage and relevance of carotenoids as a light filter (Hendry and Price, 1993). Similar result was obtained by Gonçalves et al. (2001) with mahogany and tonka bean at Amazon forest. Freitas (2012) demonstrated that irradiance level is considerably higher in the wet season compared to dry season in montane forest site. Therefore, to avoid photoinhibition caused by the excessive light incidence and a fall in photosynthesis rates (Barber and Andersson, 1992; Krause and Weis, 1991), some species may present increased photosynthetic assimilation (Lichtenthaler and Burkart, 1999) and higher contents of carotenoids (Demmig-Adams et al., 1989).

The sampled plants showed low SLA average ( $28.5 \text{ cm}^2\cdot\text{g}^{-1}$ ) when compared to other studies realized in Atlantic lowland forest with an approximate average of  $70.0 \text{ cm}^2\cdot\text{g}^{-1}$  (Boeger and Wisniewski, 2003), probably due to reduction of temperatures and high irradiances, typical in Montane dense rain forest (Rosado et al., 2015). The lower SLA values are common in dry habitats, where leaf construction costs are normally higher (Boeger and Wisniewski, 2003; Westoby et al., 2002; Wright et al., 2002). The leaf area in tropical forests is negatively related to latitude, altitude and positively to temperature (Boeger and Wisniewski, 2003).

Rosado et al. (2015) verified low specific leaf area and leaf water content at montane forest and suggested the importance of fog events to natural functionality of the ecosystem and reinforced the vulnerability to climate change (Eller et al., 2013; Ponce-Reyes et al., 2012). According to Freitas (2012), the net ecosystem exchange evaluated by "eddy covariance" flux tower demonstrated that fog events influenced the seasonal signal, as it is usually decrease during dry season.

Rosado et al. (2015) found that in Montane Atlantic forest, leaves invest more in density than in thickness when compared to lower altitudes. This suggest that species in montane rainforest have more water tolerance and leaf longevity (Brujinzeel and Veneklaas, 1998), probably due to an increase in fiber and sclereids that promote tissues durability (Ryser, 1996; Witkowski and Lamont, 1991). In conditions of absence of fog and high irradiance, the parenchyma can act as sunscreen to reflect excess uptake,

similar function performed by carotenoid pigments and xanthophylls (Lee et al., 1990), and this is a plausible explanation for the negative correlation between SLA and carotenoid pigments and xanthophylls.

A greater N/Leaf Area value for wet season is due to the higher content of chlorophyll in this season. Primary light-harvesting molecules comprises 6.5% (by weight) of nitrogen and protein ribulose-1,5 bisphosphate carboxylase-oxygenase (Rubisco) allocate 30–50% of green leaf N (Wicklein et al., 2012). Approximately 70% of leaf nitrogen is invested in compounds that support carbon fixation (Evans, 1989). There are a wide range of studies with different species and places associating leaf N status with net photosynthetic capacity (Amax) (Evans, 1989; Reich et al., 1992, 1997, 1999; Wright et al., 2004; Wicklein et al., 2012). Based on that, Hollinger et al. (2010) hypothesized that leaf N concentration (Nmass) and canopy albedo covariate between N-containing photosynthetic enzymes and internal leaf structures necessary to support different rates of photosynthesis.

The comparison between species demonstrated a great variation in pigments content and photosynthesis potential, as each species has its own characteristics and are controlled by endogenous (nutrition demand, hormones) and exogenous (light,  $\text{CO}_2$ , temperature and water tension) factors (Marenco and Lopes, 2007). Distinction of species between seasons were observed mainly for SLA, Chl a/b ratio, xanthophylls + carotenoids and N/Area, traits related to attenuation of excessive light to photosynthesis apparatus.

The photosynthetically active radiation (PAR) is almost completely absorbed, while a small fraction is reflected back into the atmosphere and this albedo is especially driven by the intrinsic characteristics of the plant and the surface. This variation of albedo PAR between seasons may result from solar incidence, rainfall rates, availability of nutrients and temperature (Culf et al., 1995; Ollinger et al., 2010). In the summer, the environmental conditions are better for growth, including the higher soil moisture and temperature. In contrast, during the dry season, the air temperatures lower, as well as the irradiance and could cause plant physiological and structural changes, like lower metabolic rate, leaf nitrogen and pigments content (Lichtenthaler et al., 2007; Ponzoni and Disperati, 1995). Those leaf changes could have a negative relationship to photosynthetic process, decreasing the ETR ratio and, consequently, causing an increase in the albedo PAR rates.

Ollinger (2011) assumed that albedo could vary in accordance to internal leaf structures, tree crowns and whole plant canopies. In addition, the variation in

reflectance at both leaf and canopy levels is mostly in the NIR region since there are few compounds that absorb this radiation (Gates et al., 1965; Ollinger, 2011). Considering the leaf, reflectance in the visible part of the spectrum (400–700 nm) is mainly guided by the photosynthetic pigments, near infrared radiation (NIR: 700–1,350 nm) by leaf structure and water is increasingly important with wavelength in the mid-infrared (Mid IR, 1,350–2,500 nm) (Gates et al., 1965; Slaton et al., 2001). At the stem and canopy level, scattering or photons absorption is influenced by structural traits such as shoot architecture, leaf angle distribution, and crown geometry (Ollinger, 2011; Wicklein et al., 2012). In addition, the variation of the solar albedo (RFA + NIR) can be related to the complexity of the mesophyll. According to Ollinger et al. (2010) and Hollinger et al. (2009), a thicker mesophyll supports large intercellular spaces and, if structural changes that occur within or between leaves covariate with foliar N, they could explain the nature of the canopy-level N–albedo relationship, especially infrared radiation (NIR), and culminate in higher rates of solar albedo.

Indications of long leaf longevity at the Montane site are supported by the fact that, despite the higher aboveground biomass (Alves et al., 2010), litter production is lower and not associated with a particular season at the Montane site (Marchiori et al., 2016, Wittich et al., 2010) which, therefore, may be associated with lower rates of leaf death. The litter production in the study area shows no influence of seasonality.

## CONCLUSIONS

We conclude that the lower electron transport rate and higher values of Albedo PAR during the dry season in the Montane Ombrophilous Dense Forest were probably due the lower air temperatures and radiation, which impaired plant metabolic activity resulting in lower leaf photosynthetic pigment content and photosynthetic capacity. Key results indicate that low temperature and high light decrease ETR, carotenoids and xanthophylls and Chl a/b ratio, but increase Chl b concentration in the winter/dry season compared with summer. The variation in these physiological leaf traits has been explained with changing irradiance (albedo) and air temperature.

## REFERENCES

- AIDAR, M.P.M.; SCHMIDT, S.; MOSS, G.; STEWART, G.R.; JOLY, C.A. Nitrogen use strategies of neotropical rainforest trees in threatened Atlantic Forest. **Plant, Cell and Environment**, v. 26, n.3, p. 389-399, 2003.
- ALVES, L.F.; VIEIRA, S.; SCARANIELLO, M.A.; CAMARGO, P.B.; SANTOS, F.A.; JOLY, C.A.; MARTINELLI, L.A. Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). **Forest Ecology and Management**, v. 260, n. 5, p. 679–691, 2010.
- BARBER, J.; ANDERSSON, B. Too much of a good thing: light can be bad for photosynthesis. **Trends in Biochemical Sciences**, v.17, p. 61-66, 1992
- BARRADAS, V.L.; ADEM, J. Albedo model for a tropical dry deciduous forest in western Mexico. **International Journal of Biometeorology**, v. 36, n. 2, p. 113-117, 1992
- BAKER, I.T.; HARPER, A.B.; DA ROCHA, H.R.; DENNING, A.S.; ARAÚJO, A.C.; BORMA, L.S.; FREITAS, H.C. et al. Surface ecophysiological behavior across vegetation and moisture gradients in tropical South America. **Agricultural and Forest Meteorology**, v. 182–183, p.177–188, 2013.
- BOEGER, M.R.T.; WISNIEWSKI, C. Comparação da morfologia foliar de espécies arbóreas de três estádios sucessionais distintos de Floresta Ombrófila Densa (Floresta Atlântica) no Sul do Brasil. **Revista Brasileira de Botânica**, v.26, n.1, p. 61-72, 2003.
- BONGERS, F.; POPMA, J. Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico. **Botanical Gazette**, v. 151, n. 3, p. 354-365, 1990.
- BRUIJNZEEL, L.A.; VENEKLAAS, E.J. Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. **Ecology**, v. 79, p. 3-9, 1998.
- CHAZDON, R.L.; PEARCY, R.W.; LEE, D.W.; FETCHER, N. Photosynthetic responses of tropical forest plants to contrasting light environments. In: MULKEY, S.S.; CHAZDON, R.L.; SMITH, A.P. (eds.) **Tropical forest plant ecophysiology**. Chapman & Hall, New York, 1996, p.5-55.
- CULF, A.D.; FISCH, G.; HODNETT, M.G. The albedo of Amazonian forest and ranch land. **Journal of Climate**, v. 8, n.6, p.1544-1554, 1995.
- COLWELL, R.K.; BREHM, G.; CARDELIS, C.L.; GILMAN, A.C.; LONGINO, J.T. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. **Science**, v. 322, n. 5899, p. 258-261, 2008.
- CUNNINGHAM, S.C.; READ, J. Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature. **Oecologia**, v. 133, p.112–119, 2002.
- DEMMIG-ADAMS, B.; WINTER, K.; KRUGER, A.; CZYGAN, F.C. Light response of CO<sub>2</sub> assimilation, dissipation of excess excitation energy, and zeaxanthin content of sun and shade leaves. **Plant Physiology**, v. 90, n.3, p. 881-886, 1989.
- DEMMIG-ADAMS, B.; ADAMS, W.W. The role of xanthophyll cycle carotenoids in the protection of photosynthesis. **Trends in Plant Science**, v. 1, p. 21-26, 1996.

- EVANS, J.R. Photosynthesis and nitrogen relationships in leaves of C3 plants. **Oecologia**, v. 78, p. 9–19, 1989.
- FINNIGAN, J. The footprint concept in complex terrain. **Agricultural and Forest Meteorology**, v. 127, n. 3-4, p. 117-129, 2004.
- FRANÇA, G.S.; STEHMANN, J.R. Composição florística e estrutura do componente arbóreo de uma floresta altimontana no município de Camanducaia, Minas Gerais, Brasil. **Revista Brasileira de Botânica**, v. 27, n. 1, p. 19-30, 2004.
- HARRIS, P.P.; HUNTINGFORD, C.; COX, P.M. Amazon Basin climate under global warming: the role of the sea surface temperature. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 363, p. 1753–1759, 2008.
- FIELD, C.; MOONEY, H.A. The photosynthesis-nitrogen relationship in wild plants. In: GIVINSH, T.I. (ed) **On the economy of form and function**. Cambridge University Press, Cambridge, 1986, p. 25–55.
- FREITAS, H.C. **A influência dos transportes advectivos na estimativa do fluxo líquido do ecossistema: um estudo de caso para a mata atlântica com uso de técnicas micrometeorológicas**. 2012. 84 p. PhD Thesis – Escola Superior de Agricultura “Luiz de Queiroz”, USP.
- GATES, D.M.; KEEGAN, H.J.; SCHLETER, J.C.; WEIDNER, V.R. Spectral properties of plants. **Applied Optics**, v. 4, p. 11–20, 1965
- GENTY, B.; BRIANTAIS, J.V.; BAKER, N.R. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. **Biochim Biophys Acta**, v. 990, p. 87-92, 1989.
- GONÇALVES, J.F.C.; MARENCO, R.A.; VIEIRA, G. Concentration of photosynthetic pigments and chlorophyll fluorescence of mahogany and tonka bean under two light environments. **Revista Brasileira de Fisiologia Vegetal**, v. 13, n. 2, p. 149-157, 2001.
- GUAN, K.; PAN, M.; LI, H.; WOLF, A.; WU, J.; MEDVIGY, D.; CAYLOR, K.K.; SHEFFIELD, J.; WOOD, E.F.; MALHI, Y.; LIANG, M.; KIMBALL, J.S.; SALESKA, S.; BERRY, J.; JOINER, J.; LYAPUSTIN, A.I. Photosynthetic seasonality of global tropical forests constrained by hydroclimate. **Nature Geoscience**, v. 8, n. 4, p. 284-289, 2015.
- HENDRY, G.A.F.; PRICE, A.H. Stress indicators: chlorophylls and carotenoids. In: HENDRY, G.A.F.; GRIME J.P. (Eds.) **Methods in comparative plant ecology**. Chapman & Hall, London, 1993, 148-152p.
- HIKOSAKA, K.; OSONE, Y. A paradox of leaf-trait convergence: why is leaf nitrogen concentration higher in species with higher photosynthetic capacity? **Journal of Plant Research**, v. 122, n. 3, p. 245-251, 2009.
- HISCOX, J.D.; ISRAELSTAM, G.F. A method for the extraction of chlorophyll from leaf tissue without maceration. **Canadian Journal of Botany**, v. 57, p. 1332-1334, 1979.
- HOLLINGER, D.Y.; OLLINGER, S.V.; RICHARDSON, A.D.; MEYERS, T.P.; DAIL, D.B.; MARTIN, M.E.; SCOTT, N.A.; ARKEBAUER, T.J.; BALDOCCHI, D.D.; CLARK, K.L. et al. Albedo estimates for land surface models and support for a new paradigm based on foliage nitrogen concentration. **Global Change Biology**, v. 16, p. 696–710, 2009.
- IPCC - Intergovernmental Panel on Climate Change. Climate Change 2013: **The Physical Science Basis**. Cambridge University Press, 2013.
- JOLY, C. et al. Florística e fitossociologia em parcelas permanentes da Mata Atlântica do sudeste do Brasil ao longo de um gradiente altitudinal. **Biota Neotropica**, v. 12, n. 1, p. 125-145, 2012.
- JOLY, C.; METZGER, J.; TABARELLI, M. Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. **New Phytologist**, v. 204, n. 3, p. 459-473, 2014.
- KÖPPEN, W. **Climatologia: con un estudio de los climas de la tierra**. México: Fondo de Cultura Economica, 478p, 1948.
- KRALL, J.P.; EDWARDS, G.E. Relationship between photosystem II activity and CO<sub>2</sub> fixation in leaves. **Physiol. Plant.**, v. 86, n. 1, p. 180-187, 1992.
- LEONARDI, S.; MAGNANI, F.; NOLE, A.; NOIJE, T.V.; BORGHETTI, M. A global assessment of forest surface albedo and its relationships with climate and atmospheric nitrogen deposition. **Global Change Biology**, v. 21, p. 287–298, 2015.
- KRAUSE, G.; WEIS, E. Chlorophyll Fluorescence and Photosynthesis: The Basics. **Annual Review of Plant Physiology and Plant Molecular Biology**, v. 42, n. 1, p. 313-349, 1991.
- LEE, D.W.; BONE, R.A.; TARSIS, S.L.; STORCH, D. Correlates of Leaf Optical Properties in Tropical Forest Sun and Extreme-Shade Plants. **American Journal of Botany**, v. 77, n. 3, p. 370-380, 1990.
- LI, J.; YANG, L.; JIN, D.; NEZAMES, C.D.; TERZAGHI, W.; DENG, X.W. UV-B-induced photomorphogenesis in Arabidopsis. **Protein Cell**, v. 4, p. 485–492, 2013.
- LICHTENTHALER, H.K.; WELLBURN, A.R. Determination of total carotenoids and chlorophylls a and b of leaf extracts in different solvents. **Biochemical Society Transactions**, v. 11, p. 591-592, 1983.
- LICHTENTHALER, H.K.; BURKART, S. Photosynthesis and high light stress. **Bulg. J. Plant Physiol.**, v. 25, p. 3-16, 1999.

- LICHTENTHALER, H.K.; BUSCHMANN, C. Chlorophylls and Carotenoids: Measurement and Characterization by UV-VIS Spectroscopy. **Current Protocols in Food Analytical Chemistry**, p. 1-8, 2001
- LICHTENTHALER, H.K.; AC, A.; MAREK, M.V.; KALINA, J.; URBAN, O. Differences in pigment composition photosynthetic rates and chlorophyll fluorescence images of sun and shade leaves of four tree species. **Plant Physiol Biochem**, v. 45, p. 577-588, 2007.
- MANLY, B.F.J. Multivariate statistical methods. Chapman & Hall, London, 2008.
- MARCHIORI, N.M.; ROCHA, H.R. DA; TAMASHIRO, J.Y.; AIDAR, M.P.M. Tree community composition and aboveground biomass in a Secondary Atlantic Forest, Serra do Mar State Park, São Paulo, Brazil. **Cerne**, v. 22, n. 4, p. 501-514, 2016.
- MARENCO, R.A.; LOPES, N.F. **Fisiologia vegetal: fotossíntese, respiração, relações hídricas e nutrição mineral**. 2 ed. Editora UFV, Viçosa, MG., 2007. 469 p.
- MARTINS, S.C.; NETO, E.S.; PICCOLO, M.C.; ALMEIDA, D.Q.A.; CAMARGO, P.B.; CARMO, J.B.; PORDER, S.; LINS, S.R.M.; MARTINELLI, L.A. Soil texture and chemical characteristic along an elevation range in the coastal Atlantic Forest of Southeast Brazil. **Geoderma Regional**, v. 5, p. 106-116, 2015.
- MAXWELL, K.; JOHNSON, G.N. Chlorophyll fluorescence – a practical guide. **J. Exp. Bot.**, v. 51, p. 659-668, 2000.
- MIYAZAWA, Y.; KIKUZAWA, K. Winter photosynthesis by saplings of evergreen broadleaved trees in a deciduous temperate forest. **New Phytol.**, v. 165, p. 857-866, 2005.
- NOTTINGHAM, A.; WHITAKER, J.; TURNER, B.L.; SALINAS REVILLA, N.; ZIMMERMANN, M.; MALHI, Y.; PATRICK, M. Climate Warming and Soil Carbon in Tropical Forests: Insights from an Elevation Gradient in the Peruvian Andes. **BioScience**, v. 65, n. 9, p. 906-921, 2015.
- OLIVEIRA, V.C. **Sobrevivência, morfo-anatomia, crescimento e assimilação de carbono de seis espécies arbóreas neotropicais submetidas à saturação hídrica do solo**. 2011, 136p. PhD Thesis Universidade Estadual de Campinas, Campinas.
- OLIVEIRA-FILHO, A.T.; FONTES, M.A.L. Patterns of floristic differentiation among Atlantic Forests in southeastern Brazil and the influence of climate. **Biotropica**, v. 32, n. 4b, p. 793-810, 2000.
- OLLINGER, S.V.; RICHARDSON, A.D.; MARTIN, M.E. et al. Canopy nitrogen, carbon assimilation and albedo in temperate and boreal forests: functional relations and potential climate feedbacks. **PNAS**, v. 105, p. 19335-19340, 2008.
- OLLINGER, S.V. Sources of variability in canopy reflectance and the convergent properties of plants. **New Phytol.**, v. 189, p. 375-394, 2011.
- OTTO, J.; BERVEILLER, D.; BRÉON, F.M.; DELPIERRE, N.; GEPPERT, G.; GRANIER, A.; JANS, W.; KNOHL, A.; KUUSK, A.; LONGDOZ, B.; MOORS, E.; MUND, M.; PINTY, B.; SCHELHAAS, M.J.; LUYSSAERT, S. Forest summer albedo is sensitive to species and thinning: how should we account for this in Earth system models? **Biogeosciences**, v. 11, p. 2411-2427, 2014.
- PEÑUELAS, J.; FILELLA, I.; GAMON, J.A. Assessment of photosynthetic radiation-use efficiency with spectral reflectance. **New Phytol.**, v. 131, p. 291-296, 1995.
- PONCE-REYES, R.; REYNOSO-ROSALES, V.H.; WATSON, J.; VANDERWAL, J.; FULLER, R.A.; PRESSEY, R.L.; POSSINGHAM, H.P. Vulnerability of cloud forest reserves in Mexico to climate change. **Nat. Clim. Change.**, v. 2, p. 448-452, 2012.
- PONZONI, F.J.; DISPERATI, A.A. **Comportamento espectral da vegetação**. INPE (INPE 5619 pud/065), 1995.
- R DEVELOPMENT CORE TEAM. R: **A language and environment for statistical computing**. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>, 2011
- RAICH, J.W.; RUSSELL, A.E.; KITAYAMA, K.; PARTON, W.J.; VITOUSEK, P.M. Temperature influences carbon accumulation in moist tropical forests. **Ecology**, v. 87, p. 76-87, 2006.
- REICH, P.B.; WALTERS, M.B.; ELLSWORTH, D.S. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. **Ecol Monogr.**, v. 62, p. 365-392, 1992.
- REICH, P.B.; WALTERS, M.B.; ELLSWORTH, D.S. From tropics to tundra: global convergence in plant functioning. **Proc Natl Acad Sci**, v. 94, p. 13730-13734, 1997.
- REICH, P.B.; ELLSWORTH, D.S.; WALTERS, M.B.; VOSE, J.M.; GRESHAM, C.; VOLIN, J.C.; BOWMAN, W.D. Generality of leaf trait relationships: a test across six biomes. **Ecology**, v. 80, p. 1955-1969, 1999.
- RESTREPO-COUBE, N.; ROCHA, H.R.; DA HUTYRA, L.R.; ARAUJO, A.C. DA, BORMA, L.S.; CHRISTOFFERSEN, B.; CABRAL, O.M.R.; CAMARGO, P.B. DE; et al. What drives the seasonality of photosynthesis across the Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux network. **Agric For Meteorol.**, v. 182-183, p. 128-144, 2013.
- RODERICK, M.L.; BERRY, S.L.; NOBLE, I.R.; FARQUHAR, G.D. A theoretical approach to linking the composition and morphology with the function of leaves. **Funct Ecol**, v. 13, p. 683-695, 1999.

- ROSADO, B.H.P.; OLIVEIRA, R.; AIDAR, M.P.M. Is leaf water repellency related to vapor pressure deficit and crown exposure in tropical forests? **Acta Oecol.**, v. 36, p. 645-649, 2010.
- ROSADO, B.H.P.; OLIVEIRA, R.S.; JOLY, C.A.; AIDAR, M.P.M.; BURGESS, S.S.O. Diversity in nighttime transpiration behavior of woody species of the Atlantic Rain Forest, Brazil. **Agric. For. Meteorol.**, v. 158, p. 13-20, 2012.
- ROSADO, B.H.P.; JOLY, C.A.; BURGESS, S.S.O.; OLIVEIRA, R.S.; AIDAR, M.P.M. Changes in plant functional traits and water use in Atlantic rainforest: evidence of conservative water use in spatio-temporal scales. **Trees**, v. 30, p. 47-61, 2015.
- RYSER, P. The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. **Funct Ecol**, v.10, p. 717-723, 1996.
- SANCHEZ, M.; PEDRONIA, F.; EISENLOHR, P.V.; OLIVEIRA-FILHO, A.T. Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, southeastern Brazil, from near sea level to 1000 m of altitude. **Flora**, v. 208, p. 184-196, 2013.
- SCUDELLER, V.V.; MARTINS, F.R.; SHEPHERD, G.J. Distribution and abundance of arboreal species in the Atlantic Ombrophilous Dense forest in Southeastern Brazil. **Plant Ecol**, v. 152, p. 185-199, 2001.
- SERBIN, S.P.; DILLAWAY, D.N.; KRUGER, E.L.; TOWNSEND, A.P. Leaf optical properties reflect variation in photosynthetic metabolism and its sensitivity to temperature. **J. Exp. Bot.**, v. 63, n. 1, p. 489-502, 2012.
- SLATON, M.R.; HUNT, E.R.; SMITH, W.K. Estimating near-infrared leaf reflectance from leaf structural characteristics. **Am. J. Bot.**, v. 88, p. 278-284, 2001.
- SLOT, M.; WINTER, K. Photosynthetic acclimation to warming in tropical forest tree seedlings. **J. Exp. Bot.**, v. 68, p. 2275-2284, 2017.
- STRAUSS-DEBENEDETTI, S.; BAZZAZ, F.A. Plasticity acclimation to light in tropical Moraceae of different successional positions. **Oecologia**, v. 87, p. 377-387, 1991.
- STREIT, N.M.; CANTERLE, L.P.; CANTO, M.W.; HECKTHEUER, L.H.H. As clorofilas. **Ciênc. rural.**, v. 35, n. 3, p. 748-755, 2005.
- TSONEV, T.; VELIKOVA, V.; GEORGIEVA, K.; HYDE, P.F.; JONES, H.G. Low temperature enhances photosynthetic down-regulation in French bean (*Phaseolus vulgaris* L.) plants. **Ann. Bot.**, v. 91, p. 343-352, 2003.
- VELOSO, H.P.; RANGEL-FILHO, A.L.R.; LIMA, J.C.A. **Classificação da vegetação brasileira, adaptada a um sistema universal**. Rio de Janeiro, IBGE, 1991.
- VIEIRA, A.S.; ALVES, L.F.; DUARTE-NETO, P.J.; MARTINS, S.C.; VEIGA, L.G.; SCARANELLO, M.A.; PICOLLO, M.C.; CAMARGO, P.B.; CARMO, J.B.; SOUSA NETO, E.; SANTOS, F.A.M.; JOLY, C.A.; MARTINELLI, L.A. Stocks of carbon and nitrogen and partitioning between above- and belowground pools in the Brazilian coastal Atlantic Forest elevation range. **Ecol. Evol.**, v. 1, p. 421-434, 2011.
- WALTERS, R.G. Towards an understanding of photosynthetic acclimation. **J. Exp. Bot.**, v. 56, n. 411, p. 435-447, 2005
- WELLBURN, A.R. The spectral determination of chlorophylls a and b, as well as total carotenoids using various solvents with spectrophotometer of different resolution. **J. Plant Physiol.**, v. 144, p. 307-313, 1994.
- WESTOBY, M.; FALSTER, D.S.; MOLES, A.T.; VESK, P.A.; WRIGHT, I.J. Plant ecological strategies: some leading dimensions of variation between species. **Annu. Rev. Ecol. Syst.**, v. 33, p. 125-159, 2002.
- WICKLEIN, H.F.; OLLINGER, S.V.; MARTIN, M.E.; HOLLINGER, D.Y.; LEPINE, L.C.; DAY, M.C.; BARTLETT, M.K.; RICHARDSON, A.D.; NORBY, R.J. Variation in foliar nitrogen and albedo in response to nitrogen fertilization and elevated CO<sub>2</sub>. **Oecologia**, v. 169, p. 915-925, 2012
- WITKOWSKI, E.T.F.; LAMONT, B.B. Leaf specific mass confounds leaf density and thickness. **Oecologia**, v. 88, p. 486-493, 1991.
- WITTICH, B.; HORNA, V.; HOMEIER, J.; LEUSCHNER, C. Altitudinal Change in the Photosynthetic Capacity of Tropical Trees: A Case Study from Ecuador and a Pantropical Literature Analysis. **Ecosystems**, v. 15, n. 6, p. 958-97, 2012.
- WRIGHT, I.J.; REICH, P.B.; WESTOBY, M.; ACKERLY, D.D.; BARUCH, Z.; BONGERS, F.; CAVENDER-BARES, J. et al. The worldwide leaf economics spectrum. **Nature**, v. 428, p. 821-827, 2004
- WRIGHT, I.J.; WESTOBY, M.; REICH, P.B. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. **J. Ecol.**, v. 90, p. 534-543, 2002.
- ZAR, J.H. **Biostatistical analysis**. 4<sup>ed</sup>. New Jersey, Prentice-Hall, Inc., 663p +212App, 1999