Diversitas Journal
ISSN 2525-5215
Volume 8, Number 2 (apr./jun. 2023) p. 672 – 685
https://diversitasjournal.com.br/diversitas_journal

Leaf plasticity of species under different light intensities in an urban rainforest

Plasticidade foliar de especies sob diferentes intensidades de luz em uma floresta urbana

LEITE, Maria José de Holanda(1)

(1) 0000-0003-4154-3901; Universidade Federal de Alagoas, Campus de Engenharias e Ciências Agrárias. Rio Largo, Alagoas (AL), Brasil. maryholanda@gmail.com

ABSTRACT

Leaf characteristics of plants are useful to understand vegetation changes under different environmental pressures because species deal with variations in the levels of luminosity during the process of ecological succession. Assuming that the light availability is a good predictor of the variation of the leaf characteristics, we hypothesized that in environments with a higher light incidence, there will be a greater variation on leaf characteristics (mean and standard deviation) in an urban rainforest fragment. After confirming that geographic distances did not influence the values of the leaf variability indices, Linear Mixed Models (LMMs) were constructed to verify the influence of light intensity on leaf characteristics. All the evaluated leaf characteristics (LA = leaf area, LSMC = leaf dry matter content, SLA = specific leaf area and Cc_mass = chlorophyll content) presented smaller variability in A4<AB. The area with the highest light incidence (A4<AB) showed less variation in the standard deviation, which may indicate that plants in this environment are under the influence of disturbances, which leads to reduced variability. The light was not a good indicator of leaf variability. The LA, SLA, LSMC and Cc_mass, although widely variable in morphological and physiological terms, shown to have less variation in the area with a higher incidence of light and greater disturbances, indicating that more disturbed environments influence on the leaf variability decrease.

RESUME

As características foliares das plantas são úteis para entender as mudanças na vegetação sob diferentes pressões ambientais, pois as espécies lidam com variações nos níveis de luminosidade durante o processo de sucessão ecológica. Assumindo que a disponibilidade de luz é um bom preditor da variação das características foliares, hipotetizamos que em ambientes com maior incidência luminosa, haverá maior variação nas características foliares (média e desvio padrão) em um fragmento de floresta tropical urbana. Após confirmar que as distâncias geográficas não influenciaram os valores dos índices de variabilidade foliar, foram construídos Modelos Lineares Mistos (LMMs) para verificar a influência da intensidade luminosa nas características foliares. Todas as características foliares avaliadas (AF = área foliar, TMSF = teor de matéria seca foliar, AFE = área foliar específica e Cc_massa = teor de clorofila) apresentaram menor variabilidade em A4<AB. A área com maior incidência de luz (A4<AB) apresentou menor variação no desvio padrão, o que pode indicar que as plantas neste ambiente estão sob influência de distúrbios, o que leva à redução da variabilidade. A luz não foi um bom indicador da variabilidade foliar. O AF, AFE, TMSF e Cc_mass, embora amplamente variáveis em termos morfológicos e fisiológicos, mostraram ter menor variação na área com maior incidência de luz e maiores perturbações, indicando que ambientes mais perturbados influenciam na diminuição da variabilidade foliar.

ARTICLE INFORMATION

Article process:
Submitted: 25/10/2022
Approved: 24/03/2023
Published: 10/04/2023

Keywords:
Foliar characteristics, luminosity, functional characteristic, environmental stress.

Keywords:
Características foliares, luminosidade, característica functional, estresse ambiental

DOI: 10.48017/dj.v8i2.2465

Introduction

Functional characteristics of plants can respond in different ways to the availability of resources (i.e., water and light) (Lohbeck et al., 2013; Boukili and Chadzon, 2017); these responses are revealed in the different survival patterns as a result of their potential of acquisition and use of the resource in question (Pérez-Harguindeguy et al., 2013; Lasky et al., 2013; Menge and Chandon, 2016). Understanding the functional characteristics of species in a community can help to recognize plant responses to resource availability (Lebrija-Trejos et al., 2010; Kraft and Ackerly, 2014).

In forest environments, where light is the primary resource, it is known that at the beginning of succession, there is higher luminosity and lower values of basal area (Letcher and Chadzon, 2009; Boukili and Chadzon, 2017). In these habitats, high values of leaf area, specific leaf area and chlorophyll content (Pérez-Harguindeguy et al., 2013), low stem and root wood density, high water content in the stem and root point to strategies linked to resources acquisition (Slik et al., 2010; Réjou-Méchain et al., 2015; Boukili and Chadzon, 2017). As the succession progresses, the canopy closes, which leads to less light reaching the forest floor, leading to a higher plant survival with strategies more related to the conservation of light (Cornelissen et al., 2006).

It is also worth noting that plants respond to environmental changes through adjustments (ecological response) or adaptations (evolutionary response) (Schlichting and Wund, 2013). The variability within populations is a reflection of the adjustment value of a given trait from a access, according to changes in the environment within the individual life span (Valladares et al., 2014). On the other hand, adaptations result from selective pressure variations over the evolutionary time, capable of producing genetic differences among species through the evolution process (Lusk et al., 2008; Nicotra et al., 2010; Ramirez-Valiente et al., 2015). Besides, the leaf is the organ that best adjusts to light variations, especially at the beginning of the succession, when there is a higher light incidence (Valladares et al., 2000; Rozendaal et al., 2006; Laurans et al., 2012).

Assuming that the light availability is a good predictor of the variation in the leaf characteristics, we hypothesized that in environments where there is a higher incidence of light, there would be a more considerable variation on leaf characteristics (mean and standard deviation). If this is true, a higher standard deviation is expected in leaf dry matter content, specific leaf area, leaf area and chlorophyll content in these environments.

Material and methods

Study area

The study was carried out in a fragment of Ombrophylous Dense Lowland Forest (IBGE, 2012), in the Dois Irmãos *State Park*, located northwest of the municipality of Recife, State of Pernambuco, Brazil (between coordinates 7° 57' 21'' and 8° 00' 54'' S; 34° 55' 53'' and

34° 58' 38" W). In the area, the geological formation Barreiras and soils of the Podzolic type predominate, with subordinate Latosols, in general sandy-clayey, ranging from deep to very deep (Pernambuco, 2014). The soil acidity varies from medium to high, which is within the range expected for regions with high precipitation (Pernambuco, 2014). The local climate is As' type (tropical humid or tropical coastal), with an average monthly temperatures above 23°C, annual mean rainfall of 2460 mm and rainy season in the autumn-winter period (Coutinho et al., 1998).

Sample design, inclusion criterion and floristic list

A module of the Biodiversity Research Program (PPBio), Atlantic Forest Network, is set up in the PEDI area, which uses the RAPELD method, which is a combination of rapid inventories (RAP) with long term ecological research (Magnusson et al., 2005). The method consists of the opening of two straight trails of 5000 m of extension, distant 1000 m from each other. Along each trail, one-hectare plots were installed according to standard protocol (Magnusson et al., 2005). For this study, we selected one trail and four plots (250 × 40 m each), 1000 m apart from each other. For each plot, a 250 m corridor was installed, following the ground contour lines, according to the protocol defined by Freitas et al. (2011).

Within each hectare, 20 plots of 10 × 20 m without overlap were set up, from which botanical samples and functional characteristics were collected from all plants with a diameter of the stem at breast height (DBH) ≥ 5 cm, with at least five individuals in all four areas (Table 1). If the species was present in more than one area, the functional characteristics were collected in all areas.

Table 1.

List of species analyzed in the four areas in an urban rainforest fragment, Dois Irmãos State Park, Pernambuco, Brazil.

Family	Species	A1$_{>AB}$	A2$_{ABI}$	A3$_{ABI}$	A4$_{<AB}$
Anacardiaceae	*Anacardium occidentale* L.		X		
	Tapirira guianensis Aubl.	X	X	X	X
	Thyrsodium spruceanum Benth.	X	X	X	
Apocynaceae	*Himatanthus phagedaenicus* (Mart.) Woodson		X		
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	X	X		
Boraginaceae	*Cordia superba* Cham.		X		
Burseraceae	*Protium giganteum* Engl.	X			
	Protium heptaphyllum (Aubl.) Marchand	X			
Clusiaceae	*Clusia nemorosa* G. Mey.		X		
Elaeocarpaceae	*Sloanea guianensis* (Aubl.) Benth.	X			

Euphorbiaceae	*Pera ferruginea* (Schott) Müll. Arg.		X	X	X
	Pogonophora schomburgkiana Miers ex Benth.	X	X	X	X
Fabaceae	*Albizia pedicellaris* (DC.) L. Rico	X		X	
	Bowdichia virgilioides Kunth	X	X		
	Chamaecrista ensiformis (Vell.)			X	X
	Dialium guianense (Aubl.) Sandwith	X			
	Inga capitata Desv.		X		
	Inga thibaudiana DC.	X	X	X	
	Parkia pendula (Willd.) Benth. ex Walp.	X			
	Plathymenia reticulata Benth.		X	X	X
	Pterocarpus violaceus DC.	X	X		
	Tachigali densiflora (Benth.) L.G.Silva & H.C.Lima	X			
Lauraceae	*Ocotea glomerata* (Nees) Mez	X		X	
Lecythidaceae	*Eschweilera ovata* (Cambess.) Mart. ex Miers	X	X	X	
	Lecythis pisonis Cambess.		X	X	
Malvaceae	*Apeiba albiflora* Ducke			X	
	Luehea ochrophylla Mart.		X	X	
Malpighiaceae	*Byrsonima sericea DC.*		X	X	X
Melastomataceae	*Miconia prasina* (Sw.) DC.	X	X		
Moraceae	*Brosimum guianense* (Aubl.) Huber	X	X		
	Helicostylis tomentosa (Poepp. & Endl.) Rusby	X			
Myrtaceae	*Campomanesia dichotoma* (O. Berg)	X	X		X
	Myrcia splendens (Sw.) DC.		X		
	Myrcia sylvatica (G.Mey.) DC.	X	X	X	X
Nyctaginaceae	*Guapira laxa* (Netto) Furlan		X	X	
Ochnaceae	*Ouratea castaneifolia* (DC.) Engl.			X	
Polygonaceae	*Coccoloba mollis* Casar.	X	X	X	
Rubiaceae	*Alseis pickelii* Pilger & Schmale		X		
Sapotaceae	*Pouteria bangii* (Rusby) T.D. Penn.	X			
Urticaceae	*Cecropia pachystachya* Trécul		X	X	
Sapindaceae	*Talisia macrophylla* (Mart.) Radlk.	X			

$A1_{>AB}$ *(Area with higher basal area),* $A2_{ABI}$ *(intermediate basal area),* $A3_{ABI}$ *(basal intermediate area) and* $A4_{<AB}$ *(area with lower basal area).*

The floristic list was organized using the APG IV classification system (2016). All material was deposited in the Vasconcelos Sobrinho herbarium at the Federal Rural University of Pernambuco (UFRPE).

Leaf characteristics

Measurement of leaf characteristics followed the protocol of Pérez-Harguindeguy et al. (2013). Four leaf characteristics were measured (Table 2), and only characteristics present in five or more species were collected in the four areas (250 × 40 m plots). We sampled five individuals per species; from each individual, ten mature leaves were collected at the middle of the crown (exposed to the sun), with no evident symptoms of pathogen or herbivore attack. After being collected, samples were wrapped in wet paper, placed in closed plastic bags and stored in styrofoam with ice. In the laboratory, leaves (without petiole) were rehydrated and placed in deionized water in the dark for at least six hours. The chlorophyll content was measured at four points of each leaf with the aid of a SPAD chlorophyll meter (Minolta SPAD 502 D Sprectrum Technologies Inc., Plainfield, II, USA). We determined chlorophyll content by mass [Cmass = Chlorophyll content * (AFE / 10000), Poorter, 2009]. After rehydration, the leaves were weighed on an analytical scale to obtain the saturated weight. They were then scanned for leaf area measurement using the computer program "Image-Tool" (O'neal et al., 2002) and then placed in an oven at 60°C for 72 hours to obtain dry weight.

Table 2.

List of leaf characteristics analyzed in an urban rainforest fragment, Dois Irmãos State Park, Pernambuco, Brazil, adapted from Malhi et al. (2016).

Functional Characteristic	**Description**
SLA	Specific leaf area (LA/PS)
LSMC	Leaf dry matter content (PUF–PSF)
LA	Leaf area (Limbo area)
Cc_mass	concentration of chlorophyll (C_{massa}; chlorophyll content *(SLA/10000)

SLA - specific leaf area ($cm^2.mg^{-1}$); LSMC - leaf dry matter content ($mg.g^{-1}$); LA - leaf area (cm^2); $CC_{\_mass}$– chlorophyll content ($\mu mol.g^{-1}$).

2.4 Collection of light data

The total radiation (luminosity) was obtained in each of the 80 plots of 10 × 20 m (20 per area). Initially, hemispheric photos were taken in the center of each plot with the aid of a Nikon D50 camera with hemispherical lens (Nikon DX 18-105 mm lens adapted fisheye 67-58 mm) on a tripod adjustable one meter above the ground, horizontally leveled, positioned with the upper part aligned with the magnetic north by means of a compass. The photographs were taken between August and December 2015, between 8:30 and 11:00 am, to avoid the direct incidence of solar rays (Venturoli et al., 2012). In order to obtain the total radiation that passes through the canopy (luminosity) in each plot, the treatment of the images was done with the aid of GLA (Gap Light Analyzer) software version 2.0 (Frazer et al., 1999).

In order to verify if the light availability varies in the four studied areas (4000 m^2 each), as the basal area data did not present normal distribution, a Kruskal-Wallis non-parametric analysis of variance was performed, complemented by the Student-Newman-Keuls mean test. According to Table 3, it is observed that the light values reduced from area $A1_{>AB}$ to $A4_{<AB}$.

Table 3.

Light intensity average in the four areas studied in a fragment of urban rainforest, Dois Irmãos State Park, Pernambuco, Brazil.

Areas	**Light (%)**
$A1_{>AB}$	06.09c
$A2_{ABI}$	12.94c
$A3_{ABI}$	31.75b
$A4_{<AB}$	46.97a

$A1_{>AB}$ (area with greater basal area); $A2_{ABI}$ (intermediate basal area); $A3_{ABI}$ (intermediate basal area) and $A4_{<AB}$ (area with lower basal area). Means followed by equal letters do not differ by the Student-Newman Keuls test ($p < 0.05$).

Data analysis

Four leaf characteristics were analyzed, for their high variability: specific leaf area, leaf area, chlorophyll content and leaf dry matter content (Valladares et al., 2000; Rozendaal et al., 2006; Laurans et al., 2012). We calculate the weighted mean and standard deviation of the above characteristics, through which it is possible to evaluate the data variability.

The mean light intensity, weighted average and the standard deviation of the leaf characteristics in each area were submitted to the Shapiro-Wilk normality test. As the data did not present a normal distribution ($p < 0.05$), we performed a Kruskal-Wallis non-parametric analysis of variance, supplemented by the Student-Newman-Keuls mean test to verify if there were differences between light intensity variations and standard deviation in the four areas; to perform these tests we used the SPSS software (IBM Corp. Released 2011. IBM SPSS Statistics for Windows, Version 20.0).

In order to analyze if the geographical distances influence the standard deviation of leaf characteristics in each area, the Bray-Curtis index was applied in the data matrix, followed by the partial Mantel test (Mc Cune and Mefford, 2011). The significance of the correlations was tested using 999 permutations (Legendre and Fortin, 1989), using the nortest, vegan and APE packages in R version 3.3.1 (R Core Team, 2016).

To test the hypothesis that where there is a higher light availability, the values of leaf characteristics would present a higher variability, Mixed Linear Models (LMMs) were constructed, in order to verify the influence of the light intensity on leaf characteristics. The light was used as an independent variable (fixed effect) and species leaf characteristics (values of each characteristic per plot and area) were used as dependent variables (random effects). As a result of this analysis, the minimum explanatory model was obtained by removing the fixed-effect variables one by one, followed by deviation analysis (Crawley, 2007). All LMMs were made using the lme4 package in R version 3.3.1 (R Core Team, 2016).

Results and discussion

Analysis of the mean ($\underline{X}$) and the standard deviation (SD) of the characteristics in each environment revealed two patterns (Table 4). In general, areas with the lowest light intensity (Table 4, $A1_{>AB}$ and $A2_{ABI}$) did not differ from each other and presented higher average and standard deviation, since $A3_{ABI}$ and $A4_{<AB}$ were different.

Table 4.

Mean ($\underline{X}$) and standard deviation (SD) of leaf characteristics in the four areas of an urban rainforest fragment, Dois Irmãos State Park, Pernambuco, Brazil.

Areas	**LA** ($\underline{X}$) ± SD	**LSMC** ($\underline{X}$) ± SD	**SLA** ($\underline{X}$) ± SD	**Cc_mass** ($\underline{X}$) ± SD
$A1_{>AB}$	943.07 ± 5,75 a	5.98 ± 5,47 a	1214.84± 6,15 a	6.13 ± 4,00 a
$A2_{ABI}$	996.87 ± 6,04 a	4.86 ± 5,80 a	1293.34± 5,08 a	5.76± 2,48 a
$A3_{ABI}$	404.17 ± 3,50 b	2.71 ± 3,76 b	509.14± 3,50 b	2.44± 1,44 b
$A4_{<AB}$	37.09 ± 1,74 c	1.13 ± 1,60 c	165.04± 1,59 a	0.75± 1,00 c

LA - leaf area (cm^2), LSMC - leaf dry matter content ($mg.g^{-1}$), SLA - specific leaf area ($cm^2.mg^{-1}$), Cc_mass - chlorophyll content ($\mu mol.g^{-1}$). $A1_{AB}$ (area with greater basal area), $A2_{ABI}$ (intermediate basal area), $A3_{ABI}$ (basal intermediate area) and $A4_{<AB}$ (area with lower basal area); $\underline{M}$ - Weighted mean of leaf characteristics by area; $\underline{M}$ – weighted mean, SD - community standard deviation by area. Means followed by equal letters do not differ by the Student-Newman-Keuls test ($p < 0.05$).

The prediction that there would be higher variation in the mean and standard deviation in the four characteristics (LA, LSMC, SLA and Cc_mass) in the environment with higher light intensity ($A4_{<AB}$), was not confirmed, since all characteristics exhibited low mean values and standard deviation. The hypothesis that in environments with higher light intensity, the values of the standard deviation of leaf characteristics would be higher was not confirmed, since the

area $A4_{<AB}$ (higher availability of light; Table 4) presented the smallest standard deviation (Table 5).

To test the hypothesis that under a higher light intensity, there would be higher values of the standard deviation of leaf characteristics, mixed linear models (LMMs) were constructed (Table 6). All four analyzed characteristics (LA, LSMC, SLA and Cc_mass) were affected by light intensity, but not as expected, since in the environment with a higher light intensity (A4<AB; Table 4) smaller values of the standard deviation of those characteristics were recorded (Table 5).

Table 5.

Mixed linear models of the standard deviation of leaf characteristics in function of light intensity in a fragment of an urban rainforest, Dois Irmãos State Park, Pernambuco, Brazil.

Light intensity (%)					
	D	**Df**	**P**	**E**	**EP**
DP_LA (cm^2)	254.65	1	**0,00****	-1.84^{e-02}	$3,71^{e-02}$
DP_SLA ($cm^2.mg^{-1}$)	250.32	1	**0,00****	-1.22^{e-01}	$4,25^{e-02}$
DP_Cc_mass ($micromol.g^{-1}$)	174.24	1	**0,00****	-0.13^{e-01}	$0,23^{e-01}$
DP_LSMC ($mg.g^{-1}$)	300.46	1	**0,00****	-2.96^{e-01}	$1,24^{e-02}$

*SD = standard deviation, D = difference residue after removal of variable; Df = Degrees of freedom; P = associated p value; E = estimate; EP = standard error of the mean. DP_LA - leaf area; SLA - specific leaf area; Cc_mass - chlorophyll concentration; LSMC - leaf dry matter content; (Area with lower basal area), $A2_{ABI}$ (intermediate basal area), $A3_{ABI}$ (basal intermediate area) and $A4_{<AB}$ (area with lower basal area). Bold values are those that present statistical significance (** = $p < 0.01$).*

It is worth noting that when we performed the partial Mantel test to verify the effect of the geographical distance on the standard deviation values of the leaf characteristics, the results indicated that the distance did not affect the standard deviation ($r = -0.0577$; $p < 0.001$).

The fact that the lowest standard deviation of leaf characteristics have occurred in the environment with higher light availability (A4<AB, 46.97%; Table 4), contrarily to our hypothesis, may reveal that other factors such as environmental stress, disturbances and degradation are possibly influencing leaf variability (Dorn et al., 2000; Van Kleunen and Fischer, 2005). It is important to note that the area A4<AB is the most disturbed among the four studied areas. Taking that into consideration, fast-growing species (less investment in structural carbon), typical of open areas at the beginning of succession, with higher mortality, are perhaps more susceptible to extensive modifications. In this way, we infer that these environmental characteristics also cooperate for the lower leaf variability in the A4<AB (Bazzaz and Carlson, 1982; Strauss-Debenedetti and Bazzaz, 1994; Veneklaas and Poorter, 1998; Valladares et al., 2006; Valladares et al., 2014).

The fact that the three areas with less light (A1>AB, A2ABI and A3ABI) presented more considerable variation in the values of LA, LSMC, SLA and Cc_mass, contrarily to expectations, may suggest that this increased variability occurred because species that grow on shaded environments experienced ontogenetic changes in relation to low irradiance during the life cycle and, therefore, may demonstrate more significant variability (Rozendaal et al., 2006; Gratani, 2014).

It is valid to report that although leaf characteristics have been reported with higher variability in environments with higher light intensity (Straus-Debenedetti and Berlyn, 1994; Laurans et al., 2012), physiological characteristics are even more variable because they present rapid responses in the short term (Valladares, 2003; Valladares et al., 2000; Gratani, 2014). Such physiological constraints could explain the lower value of chlorophyll content in the area with more light (A4<AB). In this way, we conclude that lower leaf variability in the environment with more light probably occurred due to the disturbed condition that may have led to a decrease in characteristics of leaf plasticity.

Conclusões

The hypothesis of this work was not confirmed, since the four evaluated leaf characteristics (LA, LSMC, SLA and Cc_mass) presented smaller variability in the area with higher light intensity. This finding led us to the conclusion that plants in this environment were instead influenced by environmental disturbances, which made its variability to be reduced.

Leaf characteristics (A1>AB, A2ABI and A3ABI) showed higher variation in environments with less light incidence, because species that grow in environments with less incidence of light deal with several ontogenetic changes about light intensities during the life cycle and therefore may present more considerable variability.

The light did not show to be a good indicator of leaf variability of trees in this urban rainforest. Probably, this is a result of the constant exposition to frequent disturbances in such environments, which determines that leaf characteristics present a distinct variation from those areas in which succession occurs without disturbances. Leaf characteristics chosen in this study (LA, LSMC, SLA and Cc_mass) are widely variable in both morphological and physiological terms. Despite that, they showed lesser variation in the area with higher light incidence and significant disturbances. This unexpected pattern shed light on the fact that more disturbed environments can decrease leaf variability.

REFERENCES

APG IV (2016) The Angiosperm Phylogeny Group. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181. https://doi.org/10.1111/boj.12385

Bazzaz FA, Carlson RW. Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia. 1982;54(3):313-316.https://doi.org/10.1007/BF00379999

Boukili VK, Chazdon, RL (2017) Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. Perspectives in Perspect. Plant Ecol. Syst. 24:37–47. https://doi.org/10.1016/j.ppees.2016.11.003

Cornelissen JHC, Quested H, van Logtestijn R (2006). Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? Oecologia 147:315–326. https://doi.org/10.1007/s00442-005-0269-z

Coutinho RQ (1998) Características climáticas, geológicas, geomorfológicas e geotécnicas da Reserva Ecológica de Dois Irmãos. Recife Pernambuco-Brasil pp. 21–50.

Crawley MJ (2007) The R Book. New York: Wiley.

Dorn LA, Pyle EH, Schmitt J. (2000) Plasticity to light cues and resources in Arabidopsis thaliana: testing for adaptive value and costs. Evolution 54:1982-1994. https://doi.org/10.1111/j.0014-3820.2000.tb01242.x

Frazer GW, Canham CD, Lertzman KP (1999). Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, user’s manual and program documentation. New York.

Freitas MA, Costa F, Morais A (2011) Manual de Instalação Parcelas RAPELD: Protocolo de Instalação de Parcelas Terrestres. INPA. Available in: http://ppbio.inpa.gov.br/manuais. Accessed: 19 September 2014.

Gratani L (2014) Plant phenotypic plasticity in response to environmental factors. Adv. Bot. Res. Article ID 208747, 17 p. http://dx.doi.org/10.1155/2014/208747

Ibge (2012) Instituto Brasileiro de Geografia e Estatística. Manuais Técnicos em Geociências: Manual Técnico da Vegetação Brasileira, Rio de Janeiro.

IBM Corp. Released (2011) IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp.

Kraft N, Ackerly DD (2014) The assembly of plant communities. In: R. Monson (editor). The Plant Sciences - ecology and the environment. Berlin: Springer-Verlag. p. 67-88.

Lasky JR, Sun, IF, Su SH, Chen, ZS, Keitt, TH (2013) Trait-mediated effects of environmental filtering on tree community dynamics. J. Ecol. 101:722–733.doi: 10.1111/1365-2745.12065

Laurans M, Martin O, Nicolini E, Vincent G (2012). Functional traits and their plasticity predict tropical trees regeneration niche even among species with intermediate light requirements. J. Ecology 100:1440–1452. https://doi.org/10.1111/j.1365-2745.2012.02007.x

Lebrija-Trejos E, Meave JA, Poorter L, Perez-Garcia A, Bongers FE (2010) Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. Perspect. Plant Ecol. 12:267–275. https://doi.org/10.1016/j.ppees.2010.09.002

Legendre P, Fortin MJ (1989) Spatial pattern and ecological analysis. Vegetatio 80:107–138. https://doi.org/10.1007/BF00048036

Letcher SG, Chazdon RL (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in Northeastern Costa Rica. Biotropica 41:608-617. https://doi.org/10.1111/j.1744-7429.2009.00517.x

Letcher SG, Chazdon RL (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica 41:608-617.https://doi.org/10.1111/j.1744-7429.2009.00517.x

Lohbeck M, Poorter L, Lebrija-Trejos E, Martínez-Ramos M, Meave JA, Paz H, Pérez-García EA, Romero-Pérez IE, Tauro A, Bongers F (2013) Successional changes in functional composition contrast for dry and wet tropical forest. Ecol. 94:1211–1216. https://doi.org/10.1890/12-1850.1

Lusk CH, Falster DS, Jara-Vergara CK, Jimenez-Castillo M, Saldaña-Mendoza A (2008) Blackwell Publishing Ltd Ontogenetic variation in light requirements of juvenile rainforest evergreens. Funct. Ecol. 22:454–459. https://doi.org/10.1111/j.1365-2435.2008.01384.x

Magnusson WE, Lima AP, Luizão R, Luizão F, Costa FRC, Castilho CV, Kinupp VF (2005) RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotrop. 2:1–6. http://dx.doi.org/10.1590/S1676-06032005000300002

Malhi Y, Girardin CA, Goldsmith GR, Doughty CE, Salinas N, Metcalfe DB, ... & Aragão LE (2016) The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. New Phytol. 214:1019–1032. http://doi: 10.1111/nph.14189

Mc-cune MJ, Mefford (2011) PC-ORD. Multivariate Analysis of ecological data. Version 6 MJM Software, Gleneden Beach, U.S.A.

Menge DNL, Chazdon RL (2016) Higher survival drives the success of nitrogen-fixing trees through succession in Costa Rican rainforests. New Phytol. 209:965-977. http://doi: 10.1111/nph.13734

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. Trends Plant Sci. 15:684–692. https://doi.org/10.1016/j.tplants.2010.09.008

O'neal ME, Landis D, Isaacs R (2002) An inexpensive, accurate method for measuring leaf area and defoliation through digital image analysis. J. Econ. Entomol. 95:1190-1194. https://doi.org/10.1603/0022-0493-95.6.1190

Pérez-Harguindeguy N, Diaz S, Gamier E, Lavorel S, Poorter H, Jaureguiberry P, ... & Urcelay C (2013) New handbook for standardized measurement of plant functional traits worldwide. Aust. J. Bot. 61:167–234. https://doi.org/10.1071/BT12225_CO

Pernambuco (2014) Decreto nº 40.547, de 28 de março de 2014. Amplia os limites da unidade de conservação Parque Estadual de Dois Irmãos. Diário Oficial do Estado de Pernambuco.

Poorter L (2009) Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. New Phytol. 181:890–900. https://doi.org/10.1111/j.1469-8137.2008.02715.x

R Core Team (2016) R, A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org

Ramírez-Valiente JA, Valladares F, Delgado A, Nicotra AB, Aranda I (2015) Understanding the importance of intrapopulation functional variability and phenotypic plasticity in Quercus suber. Tree Genet. Genomes 11:1-11. https://doi: 10.1007/s11295-015-0856-z

Réjou-Méchain M, Blaise T, Lilian, B, Sophie F, Ted RF, Monteagudo A, Phillips OL, Chave J (2015) Using repeated small-footprint lidar acquisitions to infer spatial and temporal variations of a high-biomass Neotropical forest. Remote Sens. Environ. 169:93–101. https://doi.org/10.1016/j.rse.2015.08.001

Rôças G, Barros CF, Scarano FR (1997) Leaf anatomy plasticity of Alchornea triplinervia (Euphorbiaceae) under distinct light regimes in a Brazilian montane Atlantic rain forest. Trees Structure and Function 11:469-473. https://doi.org/10.1007/PL00009688

Rozendaal DMA, Hurtado VH, Poorter L (2006) Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Funct. Ecol. 20:207–216. https://doi.org/10.1111/j.1365-2435.2006.01105.

Schlichting CD, Wund MA (2014) Phenotypic plasticity and epigenetic marking: an assessment of evidence for genetic accommodation. Evol. 68:656-672. https://doi.org/10.1111/evo.12348

Slik JWF, Aiba SI, Brearley FQ, Cannon C H, Forshed O, Kitayama K, ... & Poulsen AD (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. Glob. Ecol. Biogeogr. 19:50–60. https://doi.org/10.1111/j.1466-8238.2009.00489.x

Strauss-Debenedetti S, Berlyn, GP (1994) Leaf anatomical responses to light in five tropical Moraceae of different successional status. Am. J. Bot. 81:1582-1591. https://doi.org/10.1002/j.1537-2197.1994.tb11470.x

Valladares F (2003) Light heterogeneity and plants: from ecophysiology to species coexistence and biodiversity. Progr. Bot. 64:439– 471.https://doi.org/10.1007/978-3-642-55819-1_17

Valladares F, Matesanz S, Guilhaumon F, Miguel B. Araújo MB, Balaguer L, Benito-Garzon M, Cornwell W, Gianoli E, Kleunen MV, Naya DE, Nicotra BA, Poorter H, Ramírez-Valiente JA (2015) Understanding the importance of intrapopulation functional variability and phenotypic plasticity in Quercus suber. Tree Genet. Genomes 11:1-11. http://doi.org/10.1007/s11295-015-0856-z

Valladares F, Sánchez-Gómez D, Zavala MA (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. J. Ecol. 94:1103-1116. https://doi.org/10.1111/j.1365-2745.2006.01176.x

Valladares F, Wright SJ, Lasso E, Kitajima K, Pearcy RW (2000) Plastic phenotypic response to light of 16 congeneric shrubs from a panamanian rainforest. Ecol. 81:1925–1936. https://doi.org/10.1016/j.rse.2015.08.001

van Kleunen M and Fischer M (2005) Constraints on the evolution of adaptive phenotypic plasticity in plants. New Phytol. 166:49-60. http//doi.org/10.1111/j.1469-8137.2004.01296.x

Veneklaas EJ, Poorter L (1998) Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. In: Lambers H, Poorter H, Van Vuuren MMI. (Ed.) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Leiden: Backhuys, pp.337-361.

Venturoli, F, Franco AC, Fagg CW, Felfili JM (2012) Regime de luz em uma floresta estacional semidecídua sob manejo, em pirenópolis, goiás. Rev. Arv. 36:1135-1144.