Functional leaf traits of understory species: strategies to different disturbance severities

Prado Júnior, J.[a], Schiavini, I.[a], Vale, V.[a], Lopes, S.[b], Arantes, C.[a] and Oliveira, AP.[a]*

[a]Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais, Laboratório de Ecologia Vegetal, Instituto de Biologia, Universidade Federal de Uberlândia – UFU, Rua Ceara, Umuarama, CEP 38400-902, Uberlândia, MG, Brazil

[b]Programa de Pós-Graduação em Ecologia e Conservação, Laboratório de Ecologia Vegetal, Departamento de Biologia, Universidade Estadual da Paraiba – UEPB, Rua Baraunas, Universitario, CEP 58429-500, Campina Grande, PB, Brazil

*e-mail: jamirpradojunior@gmail.com

Received: July 16, 2013 – Accepted: January 21, 2014 – Distributed: May 31, 2015
(With 1 figure)

Abstract

The specific leaf area (SLA) has been related to environmental disturbances, showing a positive correlation between the disturbances intensities and SLA in a plant community. These studies, however, assessed the responses of plant community as a whole, neglecting species attributes, such as the position in the vertical stratum of forests. Considering the importance of SLA to understand forest ecological processes, this study aimed to determine the influence of the disturbance regime on the SLA of understory species, considering that, unlike for communities as a whole, an increase in the disturbance intensity implies a decrease in SLA of understory species. This study was conducted in nine understories of seasonal forests in Brazil. The most abundant species were selected and their SLA were evaluated. The variability of SLA among populations in different forests was analyzed by Student's t-tests. The SLA of the understories (SLA_U) was also compared by an adaptation of the Community-weighted mean index. The comparison of species SLA showed significant differences among the populations of understories under different disturbance regime, showing a decrease in SLA with an increase in the disturbance intensity. Similar results were found for the SLA of understories communities (SLA_U), corroborating our hypothesis. The correlation between a reduction in species SLA and in SLA of understory with an increase in disturbance intensity, contradicted the trend observed in the literature for the community as a whole. This study highlights the importance of the evaluation of SLA in understories, as an indicator of the successional stage of communities.

Keywords: community-weighted mean index, conservation, intraspecific variability, semideciduous seasonal forests, specific leaf area.

Traços funcionais foliares de espécies de sub-bosque: estratégias às diferentes intensidades de perturbação

Resumo

A área foliar específica (SLA) tem sido relacionada a distúrbios ambientais, apresentando uma correlação positiva entre a intensidade de perturbação e a SLA da comunidade vegetal. Estes estudos, no entanto, avaliaram as respostas da comunidade vegetal como um todo, negligenciando os atributos por espécies, tais como a posição vertical no estrato florestal. Considerando a importância da SLA para entender os processos ecológicos das florestas, este estudo teve como objetivo determinar a influência do regime de perturbação na SLA de espécies de sub-bosque, cuja hipótese é que, ao contrário de comunidades como um todo, um aumento na intensidade de perturbação implica na diminuição da SLA de espécies de sub-bosque. Este estudo foi realizado em nove sub-bosque de florestas estacionais no Brasil. As espécies mais abundantes foram selecionados e suas SLA foram avaliadas. A variabilidade de SLA entre as populações em diferentes florestas foi analisada pelo teste t de Student. O SLA dos sub-bosque (SLAu) também foi comparado por uma adaptação do índice de média ponderada da comunidade. A comparação de SLA das espécies mostraram diferenças significativas entre as populações de sub-bosque sob um regime de distúrbios diferentes, mostrando um decréscimo na SLA com um aumento na intensidade de perturbação. Resultados semelhantes foram encontrados para o SLA dos sub-bosque (SLAu), corroborando nossa hipótese. A correlação entre a redução no SLA espécies e SLA do sub-bosque com um aumento na intensidade de perturbação contradiz a tendência observada na literatura para a comunidade como um todo. Este estudo destaca a importância da avaliação de SLA em sub-bosque, como um indicador do estágio sucessional das comunidades.

Palavras-chave: índice de média ponderada da comunidade, conservação, variabilidade intra-específica, florestas estacionais semideciduais, área foliar específica.

1. Introduction

A functional trait is an attribute with a potential influence on the establishment, survival or fitness of a species in a natural environment (Reich et al., 2003). Quantifying changes in these traits is important to understand the patterns of species distribution and to predict vegetation responses to environmental changes (Silva and Batalha, 2009; Freitas et al., 2012).

Variations in leaf functional traits, especially in specific leaf area (SLA), have guided many studies of functional ecology, which have addressed important ecological correlations, such as relative growth rate and the photosynthetic efficiency of a species (Reich et al., 2003; Zhang et al., 2012). Of all the environmental factors affecting leaf functional leaf traits, light is perhaps one of the most studied in the literature (Pearcy, 2007; Hulshof and Swenson, 2010; Mallik et al., 2013). Plants growing under high light exposure generally show thicker leaves with a lower SLA (Cornelissen et al., 2003). Shade leaves show a low foliar construction cost, since they are less thick and with lower concentrations of photosynthetic enzymes per area, which increases their SLA (Westoby et al., 2002).

Recently, the SLA has been related to another important environmental factor: the disturbance intensity. Most studies show a positive correlation between the intensity or frequency of disturbances and SLA in a plant community (Reich et al., 2003; Garnier et al., 2004; Wright et al., 2004; Fortunel et al., 2009). However, most of these studies focus on responses to grass, herbs and shrubs and are concentrated in temperate environments (Fortunel et al., 2009). Moreover, the studies assessed the responses of the plant community as a whole, neglecting species attributes, such as the position in the vertical stratum of forests.

In tropical forest understories, an environment that is typically shaded, the irradiance available to plants might represent only 1-2% of the total incoming radiation to the canopy (Poorter et al., 2006), and then, the plant species might exhibit different responses. Thus, the increase in irradiance on understories, caused by disturbances, can result in distinct functional leaf responses compared to those in the entire community, with a selection pressure towards an increase in the SLA (Schieving and Poorter, 1999; Cornelissen et al., 2003).

Evaluate the patterns of responses of functional traits for each stratum of vegetation can assist in understanding responses of forest communities to environmental changes related to the disturbance. The understory, especially, is the most sensitive stratum to environmental perturbations (Mulkey and Pearcy, 1992). This, considering the importance of SLA as a guide to understanding forest changes, this paper aimed to determine the influence of the disturbance regime in the study areas on the SLA of understory species, considering that, unlike the communities as a whole, the increase in the intensity of disturbance implies a decrease in SLA in species from this stratum.

2. Methods

2.1. Research areas and species selection

This study used the database from previous phytosociological tree community studies (DBH ≥ 5 cm) in ten areas of seasonal semideciduous forests in Central Brazil, totaling a sample of 10 ha (Table 1) (Lopes et al., 2012). These studies evaluated the structure and floristic diversity of the areas comparing density, basal area and frequency of community species from methodology of sample plots (25 plots per area). The botanical classification of these studies was based on the Angiosperm Phylogenetic Group (APG III, 2009). Species sampled from the ten areas used in this study were classified by Lopes et al. (2014) according to their position in the stratum community: canopy species, intermediary stratum species (under-canopy) and understory species, using a nonparametric methodology of quartiles and medians of heights of community and species. For this study, we used just the species classified as understory species (Prado Junior et al., 2014). Since this paper aimed to study tree community, with DBH ≥ 5 cm standardized for seasonal semidecidual forests (Felfili et al., 2011), herbaceous and shrubby species that are present in understory "*lato sensu*" were not included in sample. Thus, tested hypothesis are applicable just for tree community in understory.

Lopes et al. (2013) classified the areas according to disturbance severity (Table 2) from an impact matrix, in which were considered structural parameters such as abundance of pioneer species, canopy height, presence of large gaps or internal trails and selective logging, among others. Areas under lower disturbance severity have forests in advanced succession stages, fragments higher than 70 ha, with lower edge effect, absence of cattle and selective

Table 1. Classification and description of nine sites of seasonal semideciduous forests according to disturbance intensity (adapted from Lopes et al., 2013).

Areas	Disturbance intensity	Description
1,2	Low	Low number of pioneer species, many individuals with large basal area, high canopy, large fragments without internal trails or logging
3,4,5,6	Medium	Low number of pioneer species, few individuals with large basal area, high canopy, small fragments, presence of internal trails with surrounding disturbed matrix
7,8,9	High	High number of pioneer species, few individuals with large basal area, low canopy, presence of internal trails with surrounding disturbed matrix

Table 2. Comparison between the mean SLA of species that occurred in at least two areas under different disturbance intensities.

Species	Disturbance intensity			T	P
	Low	Medium	High		
Ardisia ambigua	14.62	-	13.49	3.61	< 0.01
Cheiloclinium cognatum	-	13.12	11.72	11.70	< 0.01
Chrysophyllum gonocarpum	12.90	-	14.25	4.47	< 0.01
*Cordiera sessilis**	-	11.86	12.06	1.50	0.17
Siparuna guianensis	-	18.88	18.10	3.09	< 0.01
Siphoneugena densiflora	-	9.90	8.79	9.22	< 0.01
Trichilia catigua	14.59	-	12.84	6.25	< 0.01

*No significant difference was found in the SLA of this species. SLA = specific leaf area; *T* = value of the Student's t-test; *P* = probability value of the Student's t-test.

logging (Lopes et al., 2013). It present low number of pioneer species (below 10% of trees), high canopy (trees commonly higher than 25 m). Areas under intermediary disturbance, as well as the lower impact areas, present high canopy and low number of pioneer species, but are small fragments (lower than 30 ha), under a matrix strongly disturbed, have internal trails and livestock, which increases the trampling and grazing in the area, increasing its degradation (Lopes et al., 2013). Areas under higher disturbance severity are under a matrix strongly disturbed, presenting a large edge effect. They present the lowers canopies (lower than 17 m), higher number of pioneer species (near 25% of trees), have many internal trails and presence of cattle and selective logging (Lopes et al., 2013). For more details on sampling methodology and impact matrix description of ten areas can be found in Lopes et al. (2013).

Only the understory species with higher absolute densities were selected, until they comprised at least 70% of the total density of this stratum. According to Cornelissen et al. (2003), the most representative species can be considered as those that summarize about 70-80% of the total abundance in the community.

2.2. Functional leaf traits

Fully expanded leaves were harvested from adults with no obvious symptoms of pathogen or herbivore attack. Twenty leaves were collected from each of 10 individuals by species in each study area. Leaves were packed in sealed plastic bags to remain turgid until the measurement of leaf traits in the laboratory. Leaves were scanned with a metric scale and subsequently, the leaf area (LA) was calculated using the program ImageJ (NIH, 2014). The leaves were placed in an oven at 60 °C for 72 h before measurement of leaf dry mass (DM). The SLA was calculated as the ratio LA (mm^2)/DM (mg).

For species with compound leaves, leaf traits were calculated for the leaf as a whole, and not for the leaflets. According to Hulshof and Swenson (2010), the variability among leaflets is much greater than that for whole leaves and, therefore, should be evaluated for the leaf as a whole.

2.3. Influence of disturbance intensity in specific leaf area (SLA)

The SLA of species collected in at least two understories under different disturbance intensities were compared by Student's t-tests. To evaluate the influence of disturbance intensity on the SLA of the understory community (SLA_U) was used an adaptation from the Community-weighted mean index (Garnier et al., 2004). This index evaluates not only the mean of the species functional traits, but also the relative contribution (abundance) of each species. The SLA_U was obtained using the Formula 1:

$$SLA_U = \sum_{i=1}^{n} p_i \times SLA_i \quad (1)$$

Where: p_i = relative contribution of species *i* to the maximum abundance of the community; n = number of species evaluated; SLA_i = SLA value of species *i*.

3. Results

3.1. The influence of disturbance intensity on specific leaf area (SLA)

For intraspecific analyses, from seven species sampled in at least two understories under different disturbance intensities, five species (*Ardisia ambigua*, *Cheiloclinium cognatum*, *Siparuna guianensis*, *Siphoneugena densiflora* and *Trichilia catigua*) differed significantly with a decrease in SLA on more disturbed understories (Table 2). *Chrysophyllum gonocarpum* had a higher SLA, with an increase of disturbance and *Cordiera sessilis* not differ significantly with the disturbance intensity (Table 2).

For interspecific analyses, there was a trend towards a reduction in the mean with an increase in disturbance intensity, particularly among understories under low and high disturbance (Figure 1 and Appendix 1). The SLA_U values obtained by the functional traits index ranged from 20.18 $mm^2.mg^{-1}$ (SLA_{A4}, Area 4) to 11.85 $mm^2.mg^{-1}$ (SLA_{A5}, Area 5). The less disturbed understories had a mean SLA_U above 17 mm^2 .mg^{-1} and the most disturbed understory had a SLA_U below 15 $mm^2.mg^{-1}$. The greatest variation between the values of SLA_U was observed for understories under medium disturbance intensity, where

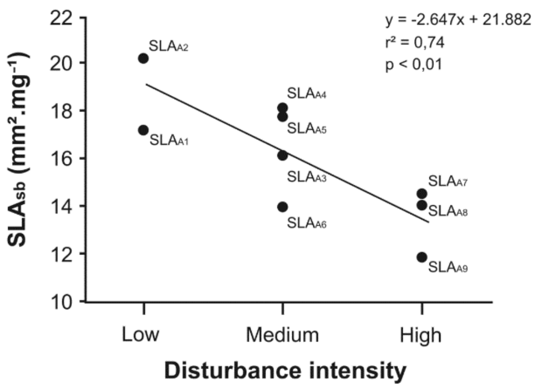

Figure 1. Functional traits index (SLA_U) of the nine areas of semideciduous forest sampled according to its classification as for disturbance intensity. Values correspond to values obtained in Appendix 1.

the highest was SLA_{A7} (18.09 $mm^2.mg^{-1}$) and the lowest, SLA_{A10} (13.94 $mm^2.mg^{-1}$).

The species *Siparuna guianensis* (mean SLA = 18.84 $mm^2.mg^{-1}$) in Area 6, 7, 9 and *Galipea jasminiflora* mean SLA = 22.71 $mm^2.mg^{-1}$) in Area 4, represent more than half of the individuals in these areas, increasing their SLA_U. In Area 1, from 13 species, six had a mean SLA greater than 18 $mm^2.mg^{-1}$ however, these represented only 31% of the relative density in this area. The high density (68%) of *Cheiloclinium cognatum* (mean SLA = 12.85 $mm^2.mg^{-1}$) was the main species responsible for the low SLA_{A10} in Area 10. In the three understories under a high intensity of disturbance ($SLA_{A3,5,8}$), the species *Cordiera sessilis* (mean SLA = 12.07 $mm^2.mg^{-1}$), *Cheiloclinium cognatum* and *Maytenus floribunda* (mean SLA = 10.56 $mm^2.mg^{-1}$) had the highest relative densities in these areas, and a low SLA_U. Although the values of SLA_U differed substantially among the understories, species co-occurring with low and high SLA were observed in all of them, independently of the disturbance intensity.

4. Discussion

Species-specific leaf area in all understories (SLA_U) and for the majority of all species, decreased with an increase in the disturbance intensity, corroborating our hypothesis. These results contradict those in the literature (Reich et al., 2003; Garnier et al., 2004; Wright et al., 2004; Fortunel et al., 2009) and indicate a positive correlation of the community SLA with disturbance intensity.

Interspecific studies comparing light-demanding pioneer and shade-tolerant species show a higher SLA for the former as a consequence of their higher relative growth, respiration rates and lower leaf longevity (Walters and Reich, 1999; Reich et al., 2003). Thus, increases in the disturbance intensity increase the number of forest pioneer species, probably the main cause for the increase in SLA in disturbed communities. However, as we found in this study, these generalized relationships might not be detected for understory species and should remain tentative.

The light availability in the understory can influence the species SLA, since there is a positive correlation between SLA and photosynthetic efficiency per leaf mass (Evans and Poorter, 2001). Thus, the increase in the SLA of understory species might favor their growth and reproduction under low irradiation conditions of tropical forests, mostly in the form of unstable beams of scattered light (sunflecks) (Chazdon and Pearcy, 1991).

Leaves of the understory tend to be thinner, with a low biomass per unit of leaf area, which increases the SLA, and therefore, the interception of light per unit leaf biomass invested (Valladares and Niinemets, 2008). This SLA increment in understory species is related to a restricted investment into structural tissues such as the epidermis, which acts as a protection mechanism for plants against photoinhibition (Pearcy, 2007).

Schieving and Poorter (1999) simulated the competition between plants of two similar genotypes in all traits, with the exception of the SLA, in light gradient environments. These authors observed that the genotype with the higher SLA also showed a higher carbon gain and replaced the lower SLA genotype whenever light was limiting in the system.

The increase in light availability in disturbed forests understories, as a consequence of the lower canopy height and gaps, causes physiological and morphological responses to the understory species (Ishii and Asano, 2010), which might involve a reduction in their SLA. The greatest exposure to light favors the development of extra layers of palisade tissue or the stretching of these layers, which results in an increase of biomass per leaf area, and therefore, a reduction in SLA (Pearcy, 2007).

When exposed to excessive light, damage to photosystem II, responsible for light absorption for photosynthesis, occurs for understory species (Pearcy, 2007). This process involves a dramatic reduction in net photosynthesis, which reduces their competitive power (Poorter and Arets, 2003; Pearcy, 2007). Thus, the increase of disturbance and consequently, in excessive light in understories, selects species with a thicker epidermis and higher content of pigments such as xanthophyll, which assists in dissipating the excess energy as heat (Koniger et al., 1995; Cornelissen et al., 2003), to reduce photoinhibition. This structural investment increases the biomass per unit leaf area and thereby reduces the SLA in understories with high light exposure.

The large range in understory SLA might indicate the different resource exploration in light capture (Reich et al., 2003). Even in less-disturbed understories, natural gaps occur (Pearson et al., 2003), which increase the gradient of light in the understory. This light gradient allows the occurrence of multiple strategies for light capture, and the coexistence of a large number of species in forests understories. Moreover, the occurrence of species with different functional traits promotes functional stability in understories and increases its resilience (Folke et al., 2004; Wright et al., 2004), which allows the maintainance of its ecological processes, even following changes in natural conditions.

The results of this study show that in communities under high disturbance intensity, the functional response observed in the understories is a decrease in SLA for most species and for the SLA of understory community. Thus, the evaluation of the SLA in the understory level (SLA_U) can be an important tool for the evaluation of the conservation of the plant community. As the disturbances regional and even global directly affect the functional traits of species (Craine et al., 2003), evaluate the distribution patterns of these traits in natural remnants may aid the understanding of ecological processes and vegetation responses to future disturbances.

Acknowledgements

The authors would like to thank *Fundo de Amparo a Pesquisa do Estado de Minas Gerais* for financial support for this project (FAPEMIG process nº APQ-00694-08).

References

Angiosperm Phylogeny Group - APG III, 2009. An update of the Angiosperm Phylogeny Group classification for the order and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, vol. 161, p. 105-121.

CHAZDON, RL. and PEARCY, RW., 1991. The importance of sunflecks for forest understory plants photosynthetic machinery appears adapted to brief, unpredictable periods of radiation. *Bioscience*, vol. 41, no. 11, p. 760-766. http://dx.doi.org/10.2307/1311725.

CORNELISSEN, JHC., LAVOREL, S., GARNIER, E., DÍAZ, S., BUCHMANN, N., GURVICH, DE., REICH, PB., STEEGE, H., MORGAN, HD., HEIJDEN, MGA., PAUSAS, JG. and POORTER, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, vol. 51, no. 4, p. 335-380. http://dx.doi.org/10.1071/BT02124.

CRAINE, JM., WEDIN, DA., CHAPIN, FS. and REICH, PB., 2003. Relationship between the structure of root systems and resource use for 11 North American grassland plants. *Plant Ecology*, vol. 165, no. 1, p. 85-100. http://dx.doi.org/10.1023/A:1021414615001.

EVANS, JR. and POORTER, H., 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant, Cell & Environment*, vol. 24, no. 8, p. 755-767. http://dx.doi.org/10.1046/j.1365-3040.2001.00724.x.

FELFILI, JM., EISENLORH, PV., MELO, MMRF., ANDRADE, LA., and MEIRA-NETO, JAA., 2011. *Fitossociologia no Brasil: métodos e estudos de casos*. Viçosa: Universidade Federal de Viçosa. 556 p. vol. 1.

FOLKE, C., CARPENTER, S., WALKER, B., SCHEFFER, M., ELMQVIST, T., GUNDERSON, L. and HOLLING, CS., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology Evolution and Systematics*, vol. 35, no. 1, p. 557-581. http://dx.doi.org/10.1146/annurev.ecolsys.35.021103.105711.

FORTUNEL, C., GARNIER, E., JOFFRE, R., KAZAKOU, E., QUESTED, H., GRIGULIS, K., LAVOREL, S., ANSQUER, P., CASTRO, H., CRUZ, P., DOLEZAL, J., ERIKSSON, O., FREITAS, H., GOLODETS, C., JOUANY, C., KIGEL, J., KLEYER, M., LEHSTEN, V., LEPS, J., MEIER, T., PAKEMAN, R., PAPADIMITRIOU, M., PAPANASTASIS, VP., QUÉTIER, F., ROBSON, M., STERNBERG, M., THEAU, JP., THÉBAULT, A. and ZAROVALI, M., 2009. Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology*, vol. 90, no. 3, p. 598-611. http://dx.doi.org/10.1890/08-0418.1. PMid:19341132

FREITAS, JR., CIANCIARUSO, MV. and BATALHA, MA., 2012. Functional diversity, soil features and community functioning: a test in a cerrado site. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 72, no. 3, p. 463-470. http://dx.doi.org/10.1590/S1519-69842012000300008. PMid:22990816

GARNIER, E., CORTEZ, J., BILLES, G., NAVAS, ML., ROUMET, C., DEBUSSCHE, M., LAURENT, G., BLANCHARD, A., AUBRY, D., BELLMANN, A., NEILL, C. and TOUSSAINT, JP., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, vol. 85, no. 9, p. 2630-2637. http://dx.doi.org/10.1890/03-0799.

HULSHOF, CM. and SWENSON, NG., 2010. Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Functional Ecology*, vol. 24, no. 1, p. 217-223. http://dx.doi.org/10.1111/j.1365-2435.2009.01614.x.

ISHII, H. and ASANO, S., 2010. The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests. *Ecological Research*, vol. 25, no. 4, p. 715-722. http://dx.doi.org/10.1007/s11284-009-0668-4.

KÖNIGER, M., HARRIS, GC., VIRGO, A. and WINTER, K., 1995. Xanthophyll-cycle pigments and photosynthetic capacity in tropical forest species - a comparative field-study on canopy, gap and understory plants. *Oecologia*, vol. 104, no. 3, p. 280-290. http://dx.doi.org/10.1007/BF00328362.

LOPES, SDF., SCHIAVINI, I., OLIVEIRA, AP. and VALE, VS., 2012. An Ecological Comparison of Floristic Composition in Seasonal Semideciduous Forest in Southeast Brazil: Implications for Conservation. *International Journal of Forestry Research*, vol. 2012, p. 1-14. http://dx.doi.org/10.1155/2012/537269.

LOPES, SF., PRADO JUNIOR, JA., VALE, VS., and SCHIAVINI, I., 2013. Impactos ambientais antrópicos como modificadores da estrutura e funcionalidade de florestas estacionais semideciduais no Triângulo Mineiro, Brasil. *Caminhos de Geografia*, vol. 14, no. 47, p. 233-242.

LOPES, SF., VALE, VS., SCHIAVINI, I., PRADO JUNIOR, JA., OLIVEIRA, AP., and ARANTES, CS., 2014. Canopy stratification in tropical seasonal forests: how the functional traits of community change among the layers. *Bioscience Journal*, vol. 30, no. 5, p. 1551-1562.

MALLIK, AU., KREUTZWEISER, DP., SPALVIERI, CM. and MACKERETH, RW., 2013. Understory plant community resilience to partial harvesting in riparian buffers of central Canadian boreal forests. *Forest Ecology and Management*, vol. 289, p. 209-218. http://dx.doi.org/10.1016/j.foreco.2012.09.039.

MULKEY, SS. and PEARCY, RW., 1992. Interactions between acclimation and photoinhibition of photosynthesis of a tropical forest understorey herb, Alocasia macrorrhiza, during simulated canopy gap formation. *Functional Ecology*, vol. 6, no. 6, p. 719-729. http://dx.doi.org/10.2307/2389969.

<soft>National Institutes of Health – NIH, *ImageJ. Version 1.34*. 2014. Available from: <http://imagej.nih.gov/ij/>.</soft>

PEARCY, RW., 2007. Responses of Plants to Heterogeneous Light Environments. In PUGNAIRE, F. and VALLADARES, F. (Eds.). *Functional plant ecology*. New York: Taylor & Francis Group. p. 213-258. http://dx.doi.org/10.1201/9781420007626.ch7.

PEARSON, TRH., BURSLEM, DF., GOERIZ, RE. and DALLING, JW., 2003. Regeneration niche partitioning in neotropical pioneers: effects of gap size, seasonal drought and herbivory on growth and survival. *Oecologia*, vol. 137, no. 3, p. 456-465. http://dx.doi.org/10.1007/s00442-003-1361-x. PMid:12920642

POORTER, L. and ARETS, E., 2003. Light environment and tree strategies in a Bolivian tropical moist forest: an evaluation of the light partitioning hypothesis. *Plant Ecology*, vol. 166, no. 2, p. 295-306. http://dx.doi.org/10.1023/A:1023295806147.

POORTER, L., BONGERS, L. and BONGERS, F., 2006. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology*, vol. 87, no. 5, p. 1289-1301. http://dx.doi.org/10.1890/0012-9658(2006)87[1289:AOMTST]2.0.CO;2. PMid:16761607

PRADO JUNIOR, JA., LOPES, SF., VALE, VS., ARANTES, CS., OLIVEIRA, AP., and SCHIAVINI, I., 2014. Floristic patterns in understoreys under different disturbance severities in seasonal forests. *Journal of Tropical Forest Science*, vol. 26, no. 4, p. 458-468.

REICH, PB., WRIGHT, IJ., CAVENDER-BARES, J., CRAINE, JM., OLEKSYN, J., WESTOBY, M. and WALTERS, MB., 2003. The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences*, vol. 164, no. S3, p. S143-S164. http://dx.doi.org/10.1086/374368.

SCHIEVING, F. and POORTER, H., 1999. Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. *The New Phytologist*, vol. 143, no. 1, p. 201-211. http://dx.doi.org/10.1046/j.1469-8137.1999.00431.x.

SILVA, IA. and BATALHA, MA., 2009. Phylogenetic overdispersion of plant species in southern Brazilian savannas. *Brazilian journal of biology = Revista brasileira de biologia*, vol. 69, no. 3, p. 843-849. http://dx.doi.org/10.1590/S1519-69842009000400011. PMid:19802443

VALLADARES, F. and NIINEMETS, U., 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology Evolution and Systematics*, vol. 39, no. 1, p. 237-257. http://dx.doi.org/10.1146/annurev.ecolsys.39.110707.173506.

WALTERS, MB. and REICH, PB., 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? *The New Phytologist*, vol. 143, no. 1, p. 143-154. http://dx.doi.org/10.1046/j.1469-8137.1999.00425.x.

WESTOBY, M., FALSTER, DS., MOLES, AT., VESK, PA. and WRIGHT, IJ., 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, vol. 33, no. 1, p. 125-159. http://dx.doi.org/10.1146/annurev.ecolsys.33.010802.150452.

WRIGHT, IJ., REICH, PB., WESTOBY, M., ACKERLY, DD., BARUCH, Z., BONGERS, F., CAVENDER-BARES, J., CHAPIN, T., CORNELISSEN, JHC., DIEMER, M., FLEXAS, J., GARNIER, E., GROOM, PK., GULIAS, J., HIKOSAKA, K., LAMONT, BB., LEE, T., LEE, W., LUSK, C., MIDGLEY, JJ., NAVAS, ML., NIINEMETS, U., OLEKSYN, J., OSADA, N., POORTER, H., POOT, P., PRIOR, L., PYANKOV, VI., ROUMET, C., THOMAS, SC., TJOELKER, MG., VENEKLAAS, EJ. and VILLAR, R., 2004. The worldwide leaf economics spectrum. *Nature*, vol. 428, no. 6985, p. 821-827. http://dx.doi.org/10.1038/nature02403. PMid:15103368

ZHANG, JL., POORTER, L. and CAO, KF., 2012. Productive leaf functional traits of Chinese savanna species. *Plant Ecology*, vol. 213, no. 9, p. 1449-1460. http://dx.doi.org/10.1007/s11258-012-0103-8.

Appendix 1. Values of SLA_{sb} of nine understories of semideciduous seasonal forests, obtained from the functional traits index. NI = number of individuals, NI/N = species relative density, SLA = specific leaf area ($mm^2.mg^{-1}$).

Understories	Species	NI	NI/N	SLA	NI/N × SLA
Area 1	*Chrysophyllum gonocarpum*	30	0.25	12.91	3.25
	Eugenia involucrata	28	0.24	16.52	3.89
	Ardisia ambigua	13	0.11	14.62	1.6
	Inga marginata	10	0.08	18.17	1.53
	Chomelia pohliana	7	0.06	35.05	2.06
	Allophylus racemosus	6	0.05	18.92	0.95
	Acalypha gracilis	6	0.05	24.28	1.22
	Quararibea turbinata	5	0.04	22.09	0.93
	Calyptranthes widgreniana	4	0.03	13.21	0.44
	*Cheiloclinium cognatum**	3	0.03	12.85	0.32
	*Trichilia pallida**	3	0.03	22.06	0.56
	*Cordiera sessilis**	2	0.02	12.07	0.2
	*Eugenia subterminalis**	2	0.02	13.19	0.22
	TOTAL	119			17.17
Area 2	*Galipea jasminiflora*	142	0.66	22.71	15.07
	Trichilia catigua	28	0.13	14.59	1.91
	Eugenia subterminalis	18	0.08	13.19	1.11
	Eugenia ligustrina	17	0.08	14.86	1.18
	*Calyptranthes widgreniana**	3	0.01	13.21	0.19
	*Chomelia pohliana**	3	0.01	35.05	0.49
	*Maytenus floribunda**	1	< 0.01	10.56	0.05
	*Hirtella gracilipes**	1	< 0.01	17.03	0.08
	*Trichilia pallida**	1	< 0.01	22.06	0.10
	TOTAL	214			20.18
Area 3	*Siparuna guianensis*	97	0.52	17.95	9.26
	Cheiloclinium cognatum	36	0.19	12.83	2.46
	Siphoneugena densiflora	18	0.10	10.39	0.99
	Trichilia pallida	17	0.09	22.06	1.99
	Cordiera sessilis	15	0.08	11.63	0.93
	*Trichilia catigua**	3	0.02	14.30	0.23
	*Campomanesia velutina**	2	0.01	23.03	0.25
	TOTAL	188			16.11
Area 4	*Siparuna guianensis*	106	0.65	20.01	13.01
	Cheiloclinium cognatum	32	0.20	13.68	2.69
	Cordiera sessilis	11	0.07	12.01	0.81
	Coussarea hydrangeifolia	11	0.07	19.6	1.32
	*Faramea hyacinthina**	2	0.01	12.66	0.16
	*Byrsonima laxiflora**	1	0.01	16.85	0.10
	TOTAL	163			18.09
Area 5	*Siparuna guianensis*	131	0.66	17.41	11.4
	Guapira opposita	29	0.15	24.36	3.53
	Cordiera sessilis	9	0.05	11.93	0.54
	Faramea hyacinthina	9	0.05	12.66	0.57
	*Cheiloclinium cognatum**	7	0.04	12.85	0.45
	*Trichilia catigua**	5	0.03	14.30	0.36

*Is used to indicate the type of SLAs, with data obtained from other areas.

Appendix 1. Continued...

Understories	Species	NI	NI/N	SLA	NI/N × SLA
	*Eugenia ligustrina**	3	0.02	14.86	0.22
	*Coussarea hydrangeifolia**	3	0.02	20.02	0.30
	*Campomanesia velutina**	3	0.02	23.03	0.35
	*Chrysophyllum gonocarpum**	1	0.01	13.56	0.07
	TOTAL	200			17.79
Area 6	*Cheiloclinium cognatum*	153	0.68	12.86	8.78
	Siparuna guianensis	40	0.18	18.01	3.22
	Siphoneugena densiflora	19	0.08	9.37	0.79
	*Cordiera sessilis**	3	0.01	12.07	0.16
	*Chomelia pohliana**	3	0.01	35.05	0.47
	*Trichilia catigua**	2	0.01	14.30	0.13
	*Trichilia pallida**	2	0.01	22.06	0.20
	*Allophylus sericeus**	1	< 0.01	18.92	0.08
	*Acalypha gracilis**	1	< 0.01	24.28	0.11
	TOTAL	224			13.94
Area 7	*Maytenus floribunda*	25	0.18	11.06	2.09
	Cordiera sessilis	25	0.18	11.51	2.09
	Chrysophyllum gonocarpum	21	0.15	14.25	2.17
	Hirtella gracilipes	21	0.15	17.03	2.59
	Siparuna guianensis	14	0.10	16.20	1.64
	Byrsonima laxiflora	8	0.06	16.85	0.98
	Trichilia catigua	7	0.05	12.84	0.65
	Ardisia ambigua	6	0.04	13.5	0.59
	*Eugenia involucrata**	3	0.02	16.52	0.36
	*Coussarea hydrangeifolia**	3	0.02	20.02	0.44
	*Campomanesia velutina**	2	0.01	23.03	0.33
	*Siphoneugena densiflora**	1	0.01	9.91	0.07
	*Trichilia pallida**	1	0.01	22.06	0.16
	*Chomelia pohliana**	1	0.01	35.05	0.25
	TOTAL	138			14.32
Area 8	*Cordiera sessilis*	173	0.68	12.86	8.72
	Campomanesia velutina	45	0.18	23.03	4.06
	Maytenus floribunda	28	0.11	9.83	1.08
	*Siparuna guianensis**	4	0.02	18.84	0.30
	*Coussarea hydrangeifolia**	2	0.01	20.02	0.16
	*Cheiloclinium cognatum**	1	< 0.01	12.85	0.05
	*Allophylus sericeus**	1	< 0.01	18.92	0.07
	*Trichilia pallida**	1	< 0.01	22.06	0.09
	TOTAL	225			14.53
Area 9	*Cordiera sessilis*	125	0.51	10.55	5.38
	Cheiloclinium cognatum	79	0.32	11.73	3.78
	Siphoneugena densiflora	13	0.05	8.79	0.47
	Siparuna guianensis	13	0.05	18.95	1.01
	*Coussarea hydrangeifolia**	11	0.04	20.02	0.9
	*Trichilia pallida**	3	0.01	22.06	0.27
	*Maytenus floribunda**	1	< 0.01	10.56	0.04
	TOTAL	245			11.85

*Is used to indicate the type of SLAs, with data obtained from other areas.