



Leaf architecture and symmetry of understory tree species of an Araucaria forest

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ABSTRACT. Shade plants of ombrophilous forests are subjected to light-limiting conditions and need to invest in architectural structures associated with leaf symmetry to increase light capture. This study investigated the leaf architecture of six Araucaria forest tree species with distinct symmetry: *Cupania vernalis*, *Casearia sylvestris*, *Schinus terebinthifolius*, *Piper gaudichaudianum*, *Roupala brasiliensis* and *Cedrela fissilis*. We hypothesized that symmetry, associated with other traits, minimizes self-shading. Asymmetry index, petiole length, total leaf area, leaf angle, internode length and stem diameter were measured. The asymmetry index did not indicate a clear distinction between asymmetric and symmetric leaves. Leaves classified as asymmetric had higher values for the asymmetry index in the median and basal regions of the leaf, while symmetrical leaves had higher values in the apical region. The results also indicated an adjustment among structural leaf traits that facilitated a three-dimensional organization that produced an advantageous arrangement for light capture, which seems to be a response to selective pressure by the heterogeneous light conditions of the ombrophilous forest understory.

Keywords: ombrophilous forest; asymmetry index; leaf morphology; shade leaves; light efficiency.

Arquitetura foliar e simetria de espécies do sub-bosque da floresta com Araucária

RESUMO. Nas florestas ombrófilas, as plantas de sombra estão sujeitas a condições limitantes de luz e necessitam investir em atributos estruturais associados à simetria foliar para maximizar a captura da luz. Esse estudo investigou a arquitetura foliar de seis espécies arbóreas (*Cupania vernalis*, *Casearia sylvestris*, *Schinus terebinthifolius*, *Piper gaudichaudianum*, *Roupala brasiliensis* e *Cedrela fissilis*) da Floresta com Araucária. Nossa hipótese é que a simetria foliar, associada a outros atributos foliares, minimiza o auto-sombreamento. Foram mensurados o índice de assimetria, o comprimento do pecíolo, a área foliar total, ângulo foliar, o comprimento do internó e o diâmetro do caule. O índice de assimetria não indicou uma distinção clara entre folhas assimétricas e simétricas. Folhas classificadas como assimétricas apresentaram maior índice na região mediana e basal da folha, enquanto as folhas simétricas apresentaram maior índice na região apical. Os resultados também indicaram um ajuste entre os atributos estruturais que permitiram um arranjo tridimensional das folhas vantajoso para a captura de luz, o que parece ser uma resposta à pressão seletiva pelas condições heterogêneas de luz do sub-bosque de floresta ombrófila.

Palavras-chave: índice de assimetria; eficiência de luz; floresta ombrófila; folhas de sombra; morfologia foliar.

Introduction

Small amounts of diffuse radiation punctuated by sun flecks of short duration (Valladares & Niinemets, 2008) results in less than 2% of active photosynthetic radiation reaching the understory stratum of ombrophilous forests. In such limiting light conditions forest and, especially, understory plants need to maximize light capture by investing in structures with low construction and maintenance costs (Givnish, 1988).

Shaded leaves tend to be thinner and larger than sun leaves. Other traits associated with lamina expansion have been related to the process of light

capture such as leaf angle, petiole length and specific leaf mass, as well as leaf shape and phyllotaxis (Valladares & Brites, 2004; Boeger, Garcia, & Soffiatti, 2009). The organization of these traits defines leaf architecture and optimizes carbon gain by individual leaves, thus contributing to the total performance of the plant (Ackerly, 1999). The combination of these traits can influence the degree of self-shading and minimizing leaf overlap, which in turn can cause an increase in photosynthetic rates (Givnish, 1984), especially in ombrophilous forests.

In addition to the aforementioned traits, self-shading can be reduced by leaf asymmetry (Givnish,

1984), especially in leaves with asymmetric bases. Leaves with total or partial asymmetry occur in some plant species of the genera *Begonia* (Begoniaceae), *Columnnea* (Gesneriaceae) and *Tilia* (Tiliaceae), and in species with compound leaves in ombrophilous forests (Givnish, 1984; Boeger, Alves, & Negrelle, 2004). According to Chitwood et al. (2012), asymmetry can be due to the asymmetric transport of auxin to different leaves of the same branch, thereby forming leaves with distinct sides.

As a functional attribute, however, asymmetry is poorly studied. Asymmetry can lead to a reduction in leaf area of one side of a leaf and consequently influence photosynthetic rates (Givnish, 1984). On the other hand, if asymmetry occurs at the base of the lamina it minimizes auto-shading, and may be compensated for by the greater area of the other side of the leaf. A similar phenomenon is observed with anisophyllous leaves, with the leaf area of the smaller leaves being compensated for by the leaf area of the larger leaves (Muelbert, Varassin, Boeger, & Goldenberg, 2010).

Leaf area, shape, size, length and width are often used as ecological functional traits for measuring functional diversity in ecosystem dynamics (Pérez-Harguindeguy et al., 2013). Variation in a certain functional trait can influence species fitness, with less variation in the trait indicating less functional diversity in a given community (Rosenfeld, 2002). However, as a functional trait leaf symmetry is still poorly understood, as well as its relationships with other functional traits.

This study investigated the leaf architecture of six understory species with distinct symmetry of an Araucaria forest. We hypothesized that asymmetry, associated with other traits such as leaf angle, leaf shape and petiole and internode length, minimizes self-shading without compromising leaf surface. These traits are important for increasing light capture and maintaining photosynthetic rates, especially in understory plants.

Material and methods

Study area

Plant material was collected from a 2.5 ha remnant of Araucaria forest in Curitiba, State of Paraná, Brazil (25°25'S, 49°17'W; 900 m) (Hirai, Yano, & Ribas, 1998). The climate is classified as Cfb (Köppen): humid subtropical, mesothermal, with no dry season, mild summers, and winters with frosts. For the year 2015, the mean temperature was 18°C, relative humidity was 81.4% and the annual rainfall was 1426.7 mm (SIMEPAR-Sistema Meteorológico do Paraná, Curitiba, Parana State). The

soils are hydromorphic close to drainage channels, with cambisols and podsols predominating in more drained areas. The relief is smooth and undulating (Neto et al., 2002). The forest comprises two well-defined strata with a heavily shaded understory where photosynthetically active radiation (PAR) varies from 36.21 ± 32.4 to $73.6 \pm 22.8 \mu\text{mol m}^{-2} \text{s}^{-1}$, which represents 1.60 to 3.25% of the canopy radiation, respectively (Vieira, Boeger, Cosmo, & Coan, 2014).

Studied species

Six understory species were selected based on their importance value as determined by a phytosociological survey (Neto et al., 2002) and based on the presence of least ten individuals in the forest (Table 1). The limited number of chosen species is due to the low number of species with asymmetrical leaves in the study area (Silveira, Boeger, Maranhão, Melo, & Soffiatti, 2015). The chosen species are as follows:

Roupala brasiliensis Klotzsch (Proteaceae) is a native tree species of forests in South Brazil, and is commonly known as *carvalho* or *carvalho-brasileiro*. The leaves are compound, odd-pinnate, and alternate with elliptical and asymmetrical leaflets with an acuminate apex (Lorenzi, 1992).

Casearia sylvestris Swartz (Salicaceae), commonly known as *guaçatunga*, is a perennial species with symmetrical, simple and alternate leaves. The lamina is elliptical and has an acuminate apex, a cuneate base and crenate margins (Lorenzi, 1992).

Cupania vernalis Cambess (Sapindaceae) is a native tree species known as *camboatá* or *camboatá-vermelho*. It is found from the state of Minas Gerais to the State of Rio Grande do Sul. It occurs in different strata of secondary forests as well as the understory. Its leaves are alternate, compound and even-pinnate. The leaflets are symmetric and oblong, with an obtuse apex, an acute base and serrate margins (Lorenzi, 1992).

Cedrela fissilis Vellozo (Meliaceae) is known as *cedro rosa* and is widely distributed in all tropical vegetation except the *Cerrado*. Its leaves are compound with asymmetrical and oblong leaflets, with an obtuse base and an acute apex (Carvalho, 2006).

Schinus terebinthifolius Raddi (Anacardiaceae) is known as *aroeira vermelha* or *pimenta rosa*. It is widely distributed throughout South America and occurs from the State of Rio Grande do Norte to the State of Rio Grande do Sul in Brazil. It occurs in many forest types including Araucaria forest, Atlantic forest, deciduous forest and mangroves (Lorenzi, 1992). It possesses compound leaves with

asymmetrical and elliptical leaflets with an acute apex and a decurrent base.

Piper gaudichaudianum Kunth (Piperaceae) is a native shrub that is very common in montane Atlantic forest where it occupies forest edges. It is commonly known as *jaborandi*. Its leaves are simple, alternate and elliptical with an asymmetric base, an acuminate apex and entire margins (Albiero, Souza, Mourão, Almeida, & Lopes, 2005).

Methodological procedures

Ten individuals of each species were selected for study. The median branches were marked and removed with pruning shears and three leaves between the 3rd and 6th nodes from the apex were selected. For compound leaves, median leaflets were selected and treated as simple leaves (Bongers & Popma, 1990). According to some authors, leaflets can be functionally similar to single leaves when they are in the same size class because of their origin, patterns of differentiation (Sinha, 1997) and function (Bongers & Popma, 1990).

The following measurements were made: internode length (between 3rd and 6th nodes); petiole length; median leaflet angle; and the width of each side of the leaflet from the central midrib to the margin of lamina in three points (Figure 1-I): apical region (one cm from the base; Figure 1-I a and b); median region (Figure 1-I c and d) and basal region (one cm from the apex; Figure 1-I e and f). Linear measurements were made with a digital caliper and leaf angles with a protractor.

Total leaflet area (cm²) was calculated from a digital image obtained using a flatbed scanner and Sigma Scan software (version 4.0, SPSS Inc., Chicago, IL, USA). Asymmetry of median leaflets was calculated by an asymmetry index (Palmer & Strobeck, 1986). The asymmetry index (AI) was calculated for each leaflet region [apical (a-b), median (c-d) and basal (e-f)], (Figure 1-I), using mean values as: $AI = (\Sigma [Ai - Bi]) / N$, where *Ai* indicates the larger side and *Bi* the smaller side for the three regions of the leaflet (Figure 1-II), and *N* is the number of the total individuals measured per species.

Statistical analysis

Mean values and respective standard deviations were calculated for all quantitative variables. Leaf sides were compared using the *T-test* ($\alpha = 0.05$) and Person correlations among leaf traits were performed using Past version 1.34 (Hammer, Harper, & Ryan, 2001).

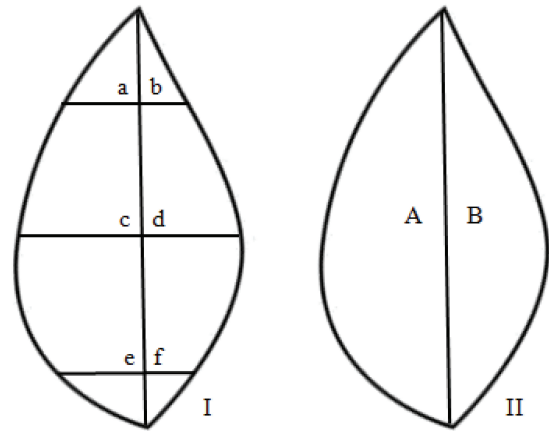


Figure 1. Figure 1. Schematic drawing indicating leaf/leaflet measurements. I. Measurements between midrib and leaf/leaflet margin in apical region (a and b); median region (c and d) and basal region (e and f). II. Letter A indicates the larger side of the leaf and B the smaller side, as used for calculating leaf area.

Results

The asymmetry index varied among regions of the studied leaves (Table 1). The leaves of *Roupala brasiliensis* and *Piper gaudichaudianum* had the highest leaf asymmetry indexes, while *Cedrela fissilis* and *Schinus terebinthifolius* had the lowest (Table 1). For asymmetrical leaves, the asymmetry was greater in the median and basal regions of the leaves; for *P. gaudichaudianum* the asymmetry was greater in the basal region of the leaf (Table 1) and for *R. brasiliensis* it was greater in the median region of the leaf (Table 1). The asymmetry of *P. gaudichaudianum* was significant ($p < 0.001$) and represented a difference of 15% between the areas of the two sides of the leaf, while in *R. brasiliensis* the difference was greater, around 35% ($p < 0.001$). The differences between the areas of the two sides for *C. fissilis*, *S. terebinthifolius*, *C. vernalis* and *C. sylvestris* were 3, 7 and 7% and 12%, respectively (Figure 2), but these values were not significant ($p > 0.05$).

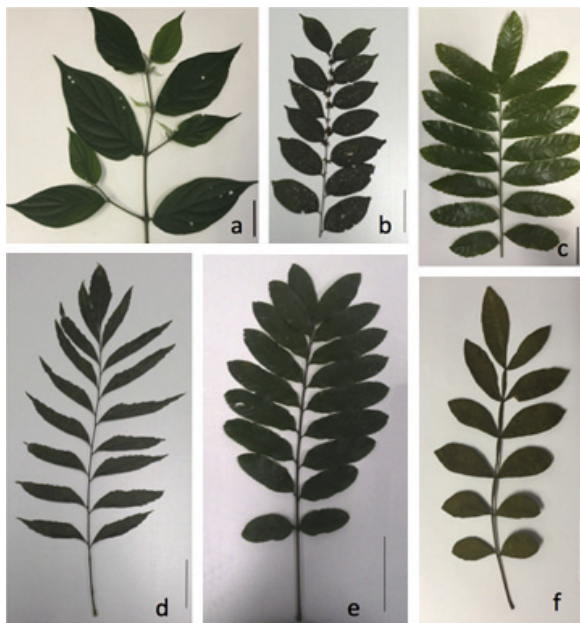
The leaves of *S. terebinthifolius* had the smallest total leaf area while *P. gaudichaudianum* and *C. fissilis* had the largest; however, leaves with larger areas (*P. gaudichaudianum*, *C. fissilis* and *C. vernalis*) also had greater standard deviations (Table 1). *Roupala brasiliensis* and *P. gaudichaudianum* had the greatest difference between side A and B indicated, as indicated by the A/B ratio (Table 1). The A/B ratio was lower and similar among the other species, independently of the leaf symmetry (Table 1).

Table 1. Asymmetry index and leaf areas for leaves of the studied species. Different letters represent significantly different means according to the *T-test* ($p < 0.05$).

Traits	<i>Cedrela fissilis</i>	<i>Roupala brasiliensis</i>	<i>Cupania vernalis</i>	<i>Casearia sylvestris</i>	<i>Piper gaudichaudianum</i>	<i>Schinus terebinthifolius</i>
Asymmetry index						
Leaf side (AB)	0.46	4.88	1.50	0.90	4.29	0.39
Apical region (ab)	0.15	1.06	0.40	0.45	0.07	0.13
Median region (cd)	0.61	2.68	0.29	0.11	4.23	0.16
Basal region (ef)	0.06	2.14	0.23	0.04	6.63	0.26
Leaf area (cm ²)						
Total	50.5 (9.9)	22.7(3.9)	40.1 (13.5)	12.4 (5.9)	44.9 (14.0)	5.2 (1.2)
Side A	25.8 (5.3)a	13.8 (2.6)a	20.8 (7.1)a	6.6 (3.1)a	24.3 (8.0)a	2.7 (0.6)a
Side B	25.0 (4.7)a	8.9 (1.4)b	19.3 (6.5)a	5.8 (2.8)a	20.0 (6.2)b	2.5 (0.6)a
A/B area ratio	1.1	1.3	1.1	1.1	1.2	1.1

Table 2. Leaf traits and means and standard deviations for stem diameter, internode/rachis length, leaf angle and petiole/petiolule length for the studied species.

Traits	<i>Cedrela fissilis</i>	<i>Roupala brasiliensis</i>	<i>Cupania vernalis</i>	<i>Casearia sylvestris</i>	<i>Piper gaudichaudianum</i>	<i>Schinus terebinthifolius</i>
Lamina type	compound	compound	simple	compound	simple	compound
Lamina symmetry	asymmetric	asymmetric	symmetric	symmetric	asymmetric	asymmetric
Phyllotaxis/leaflet phyllotaxis	alternate/opposite	alternate/opposite	alternate	alternate/opposite	alternate	alternate/opposite
Lamina shape	oblong	elliptical	oblong	elliptical	elliptical	elliptical
Apex shape	acute	acuminate	obtuse	acuminate	acuminate	acute
Stem diameter	15.3 (4.0)	10.7(3.5)	14.3 (4.3)	37.7 (12.2)	6.0 (1.6)	18.4 (11.6)
Internode/rachis length	3.66 (3.8)	3.65(5.2)	3.52 (6.2)	2.03 (4.1)	6.37 (1.78)	2.2 (0.2)
Leaf angle	67.6 (4.0)	53.4 (8.4)	64.3 (9.8)	65.6 (8.7)	63.7 (17.8)	66.2 (6.1)
Petiole/Petiolule length	2.6 (0.9)	2.7 (1.0)	3.1 (1.3)	5.0 (0.8)	3.9 (0.9)	3.3 (2.7)

**Figure 2.** General view of studied leaves. a. *Piper gaudichaudianum*; b. *Casearia sylvestris*; c. *Cedrela fissilis*; d. *Roupala brasiliensis*; e. *Cupania vernalis*; f. *Schinus terebinthifolius*. Bar = 5 cm.

The longest petioles/petiolules occurred in leaves of *C. sylvestris* and the shortest in *R. brasiliensis* and *C. fissilis* (Table 2). The internode/rachis lengths did not vary among species, except in *P. gaudichaudianum*, which had the highest mean value (Table 2). The leaf angles also exhibited little variation, except for *R. brasiliensis*, which had the lowest mean (Table 2).

For asymmetric leaves, leaf angle was negatively correlated with leaf area ($r = -0.42$, $p < 0.005$) and

positively correlated with the asymmetry index ($r = 0.51$, $p < 0.005$); leaf area was positively correlated with petiole length ($r = 0.55$; $p < 0.005$) and negatively correlated with the asymmetry index ($r = -0.51$; $p < 0.005$); petiole length was weakly and negatively correlated with the asymmetry index ($r = -0.37$; $p < 0.05$). For symmetric leaves, leaf area was negatively correlated with internode length ($r = -0.62$; $p < 0.005$) and positively correlated with petiole length ($r = 0.58$; $p < 0.005$); internode length was weakly and negatively correlated with petiole length ($r = -0.35$; $p < 0.05$).

Discussion

As expected, the highest asymmetry indexes were for *P. gaudichaudianum* and *R. brasiliensis*, with the highest values being at the leaf base. This high degree of asymmetry is further supported by differences between absolute measurements of the major and minor sides of the leaves of these species. This difference represents a reduction of area (Figure 2) in *P. gaudichaudianum* (17%) and in *R. brasiliensis* (35%). The highest leaf area reduction in the median and basal regions of the leaves in species with asymmetric leaves (Figure 2) indicates that asymmetry contributes to self-shading avoidance in the leaf below and subsequent leaves or leaflets, which minimizes the negative effect of leaf area loss. Furthermore, overlapping is a respiratory drag for shaded leaves and a potential source of abrasion for all leaves. Plants that avoid this overlap have an additional advantage for light competition (Givnish, 1984).

Asymmetry is also a function of hormonal action on primordial leaves due to biased auxin distribution during phyllotactic patterns. In spiral systems, the peak of auxin concentration is displaced towards the descending side of the center of mass of leaf primordia and is influenced by architecture of the shoot apical meristem, as observed in tomato (D  b, Marti, Frenz, K  hlemeier, & Reinhardt, 2015). Studies on *Vitis* spp and *Hedera helix* showed that the asymmetric flux of auxin in the shoot apical meristem accentuates differences along the left-right axis and is influenced by phyllotaxis (Martinez, Chitwood, Smith, & Sinha, 2016).

The results presented here also indicated an adjustment between structural characteristics, such as asymmetry, leaf area, petiole length, internode length, foliar angle, phyllotaxis and leaf shape, that allowed a three-dimensional arrangement of the leaves for each species, as suggested by the correlation analysis.

The architecture of branches and leaves is influenced by several characteristics that are important in maximizing light capture in heterogeneous environments and/or artificial environments such as crop fields (Yuan, Yong, & Peng, 2015). The combination of leaf architectural features seems to be the main element for success in capturing light in these environments, because these architectural traits are very plastic, and plants usually adapt leaves to their environment (Valladares, Gialoni & G  mez, 2007). The entire light-harvesting component of the ecosystem seems to be based on relationships between specific leaf traits despite extensive intraspecific variation in these traits (Xu, Guo, Xu, Wei & Wang, 2009).

The set of processes that enable a plant to avoid shading by neighboring plants is known as shade avoidance syndrome (Smith & Whitelam, 1997) and it confers higher fitness in dense stands of plants (Franklin & Whitelam, 2005). Shade avoidance syndrome is one the most important competitive strategies for shaded plants and its effectiveness depends the combination of multiple responses they develop, such as internode and petiole elongation, leaf angle, leaf size and shape, phyllotaxis and asymmetry (Smith & Whitelam, 1997; Valladares & Niinemets, 2008).

Leaf area is a very plastic and highly variable attribute among species (Boeger et al., 2006) and among individuals of the same species (Vieira, Boeger, Cosmo & Coan, 2014). In the study area, species occurring in the understory varied from 9.7 cm² (*Myrcia rostrata*) to 43.7 cm² (*Luehea divaricata*) (Boeger et al., 2006; Vieira et al., 2014). The average

values for leaf area of the studied species, both those with asymmetrical and symmetrical leaves, are similar to the values for other species occurring in this area, except for *S. terebinthifolius*. Additionally, all the studied species were classified as notophylls, which is the most common size class in shaded environments, as well as a response to light conditions, humidity and temperature (Boeger, Alves & Negrelle, 2004).

Leaves with larger surfaces are expected in shaded environments because they favor the capture of light (Givnish, 1984), as observed in *Cupania vernalis* and *P. gaudichaudianum* (> 40 cm²). Furthermore, diffuse light in shaded environments represents 10% of the total sun radiation, and can be important for shade leaves, since this light may be harvested from both sides of the leaf (Valladares & Brites, 2004).

The angle formed by two subsequent leaves varied from 106.8   to 135.2   (Table 2), which are close to the Golden Angle (136.7  ). The Golden Angle is considered the best angle for allowing several leaves to be arranged around the stem without a complete overlap (Valladares & Brites, 2004), thus improving light capture efficiency (Sarlikioti, de Visser, Buck-Sorlin & Marcelis, 2011) with minimal cost of investment and tissue maintenance (Givnish, 1987). Leaf angles can vary within an individual plant, with those in the upper canopy being more vertical, while those in the lower canopy and low light habitats being more horizontal. This variation in leaf angle can result in a more uniform distribution of light (Niinemets, 2010). Leaf angle is also influenced by phyllotaxis. Spiral/alternate phyllotaxis is considered selectively favorable for light interception in light-limiting environments (Valladares et al., 2002; Valladares & Niinemets, 2008). Spiral/alternate phyllotaxis facilitates a more efficient use of space near the branch (Givnish, 1984), and ensures greater photosynthetic activity and thus maximal carbon gain (King, Beck, & L  ttge, 2004).

The combination of internode length, petiole length and leaf area also favor light capture, since arrangements of these attributes can maintain a greater distance between subsequent leaves. Internode length can compensate for inefficient leaf angles and types of phyllotaxis (Brites & Valladares, 2005) by increasing the distance between leaves. Because leaves with smaller areas require a smaller investment in structural tissues for leaf support, the investment in longer petioles is considered an effective way to avoid shading by neighboring leaves (Brites & Valladares, 2005). Investment in larger

internodes is related to larger leaf areas (e.g. *P. gaudichaudianum*, *R. brasiliensis* and *C. vernalis*), while leaves with smaller areas, such as in *C. Sylvestris*, invest more in the length of the petiole and less in internodes.

Elliptically-shaped leaves are considered the most efficient blade type for avoiding self-shading. An elliptical shape, as with the studied leaves, diminishes the area of overlap between subsequent leaves, mainly in the basal region, and represents an additional advantage in heterogeneous light environments (Givnish, 1984).

Leaf asymmetry, petiole and internode length, leaf shape, leaf angle and leaf area were correlated and form an architectural organization of leaves. This architecture facilitates an advantageous spatial arrangement for light capture and appears to be a response to selective pressure from the heterogeneous conditions of ombrophilous forests. The elements that influenced leaf architecture did not vary between asymmetric and symmetric leaves, when analyzed individually. However, when they occur in different combinations they result in species-specific architecture that increases light capture throughout the growth and development of individual plants. Furthermore, this architectural organization is adjusted by the growth dynamics of individual trees that occupy multiple different forest strata with distinct light conditions.

Conclusion

All the species studied presented some degree of asymmetry, based on the asymmetry index, including the species described morphologically as symmetric. The asymmetry in asymmetric leaves, such as those of *P. gaudichaudianum* and *R. brasiliensis*, is striking in the median and basal regions of the blade, which is associated with self-shading avoidance. Besides asymmetry, leaves can adjust certain leaf traits, such as petiole length, leaf angle and leaf form, in different spatial arrangements. These distinct architectural organizations allow shade species to increase light capture and occupy multiple different forest strata. Thus, this architecture seems to be a response to selective pressure.

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References

- Ackerly, D. (1999). Self-shading, carbon gain and leaf dynamics: a test of alternative optimality models. *Oecologia*, 119(3), 300-310. doi: 10.1007/s004420050790
- Albiero, A. L. M., Souza, L. A., Mourão, K. S. M., Almeida, O. J. G., & Lopes, W. A. L. (2005). Morfo-anatomia do caule e da folha de *Piper gaudichaudianum* Kuntze (Piperaceae). *Acta Farmacêutica Bonaerense*, 24(4), 550-554.
- Brites, D., & Valladares, F. (2005). Implications of opposite phyllotaxis for light interception efficiency of Mediterranean woody plants. *Trees*, 19(6), 671-679. doi: 10.1007/s00468-005-0431-6
- Boeger, M. R. T., Alves, L. C., & Negrelle, R. R. B. (2004). Leaf morphology of 89 tree species from a lowland Tropical rain forest (Atlantic Forest) in South Brazil. *Brazilian Archives of Biology and Technology*, 47(6), 933-943. doi: 10.1590/S1516-89132004000600013
- Boeger, M. R. T., Kaehler, M., Melo Júnior, J. C. F., Gomes, M. Z., Chaves, C. R. M., & Schottz, E. S. (2006). Estrutura foliar de seis espécies do subosque de um remanescente de Floresta Ombrófila Mista. *Hoehnea*, 33(4), 521-531.
- Boeger, M. R. T., Garcia, S. F. P., & Soffiatti, P. (2009). Arquitetura foliar de *Impatiens walleriana* Hook. f. (Balsaminaceae) Hook. f. (Balsaminaceae). *Acta Scientiarum, Biological Sciences*, 31(1), 29-34. doi: 10.4025/actasciobiolsci.v31i1.935.
- Bongers, F., & Popma, J. (1990). Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico. *Botanical Gazette*, 151(3), 354-365. doi:10.1086/337836
- Carvalho, P. E. R. (2006). *Espécies Arbóreas Brasileiras* (v. 2). Colombo, PR: Embrapa Florestas.
- Chitwood, D. H., Naylor, D. T., Thammaphichai, P., Weeger, A. C. S., Headland, L. R., & Sinha, N. R. (2012). Conflict between intrinsic leaf asymmetry and phyllotaxis in the resupinate leaves of *Alstroemeria psittacina* Front. *Plant Science*, 3, 182. doi: 10.3389/fpls.2012.00182
- Déb, Y., Marti, D., Frenz, M., Kuhlemeier, C., & Reinhardt, D. (2015). Phyllotaxis involves auxin drainage through leaf primordia. *Development*, 142(11), 1992-2001. doi: 10.1242/dev.121244.
- Franklin, K. A., & Whitelam, G. C. (2005). Phytochromes and shade-avoidance responses in plants. *Annals of Botany*, 96(2), 169-175. doi: 10.1093/aob/mci165
- Givnish, T. J. (1984). Leaf and canopy adaptations in tropical forests. In E. Medina, H. A. Mooney, & C. Vazquez-Yanes (Eds.). *Physiological ecology of plants in the wet tropics* (p. 51-84). The Hague, NL: Dr.W. Junk publishers.
- Givnish, T. J. (1987). Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist*, 106(1), 131-160. doi: 10.1111/j.1469-8137.1987.tb04687.x
- Givnish, T. J. (1988). Adaptation to sun and shade: a whole plant perspective. *Australian Journal of Plant Physiology*, 15(2), 63-92.

- Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). Past: Paleontological Statistics Software Package for Education and Data Analysis. *Paleontologia Electronica*, 4(1), 1-9.
- Hirai, R. Y., Yano O., & Ribas, M. E. G. (1998). Musgos da mata residual do Centro Politécnico (Capão da Ed. Física), Curitiba, Paraná, Brasil. *Boletim do Instituto de Botânica*, 11(1), 81-118.
- King, S., Beck, F., & Lüttge, U. (2004). On the mystery of the Golden angle in phyllotaxis. *Plant, Cell and Environment*, 27(6), 685-695. doi: 10.1111/j.1365-3040.2004.01185.x
- Lorenzi, H. (1992). *Árvores Brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil* (v. 2). Nova Odessa, SP: Editora Plantarum.
- Martinez, C. C., Chitwood, D. H., Smith, R. S., & Sinha, N. R. (2016). Left-right leaf asymmetry in decussate and distichous phyllotactic systems. *Philosophical Transactions of the Royal Society B*, 371(1710), 20150412. doi: 10.1098/rstb.2015.0412
- Muelbert, A. E., Varassin, I. G., Boeger, M. R. T., & Goldenberg, R. (2010). Incomplete lateral anisophyly in *Miconia* and *Leandra* (Melastomataceae): inter- and intraspecific patterns of variation in leaf dimensions. *The Journal of the Torrey Botanical Society*, 137(2/3), 214-219.
- Neto, R. M. R., Kozera, C., Andrade, R. R., Cecy, A. T., Hummes, A. P., Fritzsons, E., ... Souza, M. K. F. (2002). Caracterização florística e estrutural de um fragmento de Floresta Ombrófila Mista, em Curitiba, PR-Brasil. *Floresta*, 32(1), 3-16. doi: 10.53 80/rf.v32i1.2366
- Niinemets, Ü. (2010). A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecological Research*, 25(4), 693-714. doi: 10.1007/s11284-010-0712-4
- Palmer, A. R., & Strobeck, C. (1986). Fluctuating asymmetry: measurement, analysis, patterns. *Annual Review of Ecology and Systematics*, 17(1), 391-421. doi: 10.1146/annurev.es.17.110186.002135
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... Cornelissen, J. H. C. (2013). New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3), 167-234. doi: 10.1071/BT12225
- Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos*, 98(1), 156-162. doi: 10.1034/j.1600-0706.2002.980116.x
- Sarlikioti, V., Visser, P. H., Buck-Sorlin, G. H., & Marcelis, L. F. (2011). How plant architecture affects light absorption and photosynthesis in tomato: towards an ideotype for plant architecture using a functional – structural plant model V. *Annals of Botany*, 108(6), 1065-1073. doi: 10.1093/aob/mcr221.
- Silveira, T. I., Boeger, M. R. T., Maranhão, L. T., Melo Jr., J. C. F., & Soffiatti, P. (2015). Functional leaf traits of 57 woody species of the Araucaria Forest, Southern Brazil. *Brazilian Journal of Botany*, 38(2), 357-366. doi: 10.1007/s40415-014-0111-0
- Sinha, N. (1997). Simple and compound leaves: reduction or multiplication? *Trends in Plant Science*, 2(10), 396-402. doi: 10.1016/S1360-1385(97)90055-8.
- Smith, H., & Whitelam, G. C. (1997). The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant, Cell, and Environment*, 20(6), 840-844. doi: 10.1046/j.1365-3040.1997.d01-104.x
- Valladares, F., Chico, J. M., Aranda, I., Balaguer, L., Dizengremel, P., & Manrique, E. (2002). The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. *Trees*, 16(6), 395-403. doi: 10.1007/s00468-002-0184-4
- Valladares, F., & Brites, D. (2004). Leaf phyllotaxis: Does it really affect light capture? *Plant Ecology*, 174(1), 11-17. doi: 10.1023/B:VEGE.0000046053.23576.6b
- Valladares, F., Gialoni, E., & Gómez, J. M. 2007. Ecological limits to phenotypic plasticity. *New Phytologist*, 176(4), 749-763. doi: 10.1111/j.1469-8137.2007.02275.x
- Valladares, F., & Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution and Systematics*, 39(1), 237-257. doi: 10.1146/annurev.ecolsys.39.110707.173506.
- Vieira, W. L., Boeger, M. R. T., Cosmo, N. L., & Coan, A. I. (2014). Leaf morphological plasticity of tree species from two developmental stages in Araucaria Forest. *Brazilian Archives of Biology and Technology*, 57(4), 476-485. doi: 10.1590/S151689132014005000010
- Yuan, S., Yong, L., & Peng, S. (2015). Leaf lateral asymmetry in morphological and physiological traits of rice plant. *Plos One*, 10(6), e0129832. doi: 10.1371/journal.pone.0129832.
- Xu, F., Guo, W., Xu, W., Wei, Y., & Wang, R. (2009). Leaf morphology correlates with water and light availability: What consequences for simple and compound leaves? *Progress in Natural Science*, 19(12), 1789-1798. doi: 10.1016/j.pnsc.2009.10.001.

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