Article

Hoehnea 49: e452021, 1 tab., 3 fig., 2022 https://doi.org/10.1590/2236-8906-45/2021

Light conditions affect *Myrcia splendens* (Sw.) DC. functional traits in an Atlantic Forest, Southeast, Brazil

Lucas Deziderio Santana[1,4], Kelly Marianne Guimarães Pereira[2], Natielle Gomes Cordeiro[1], Ana Cristina Atala Alves[3], and Fabrício Alvim Carvalho[3]

How to cite: Santana, L.D., Pereira, K.M.G., Cordeiro, N.G., Alves, A.C.A. & Carvalho, F.A. 2021. Light conditions affect *Myrcia splendens* (Sw.) DC. functional traits in an Atlantic Forest, Southeast, Brazil. Hoehnea 49: e452021. https://doi.org/10.1590/2236-8906-45/2021

ABSTRACT - (Light conditions affect *Myrcia splendens* (Sw.) DC. functional traits in an Atlantic Forest, Southeast, Brazil). Solar radiation is one of the aspects which most influence species composition, so light is a limiting factor to tree growth in forests. This study aimed to evaluate the leaf morphological variations between individuals of the *Myrcia splendens* (Sw.) DC. species under different light conditions in an urban forest. The fragment is characterized by having an open canopy area and an advanced regeneration stage in which branches of five individuals were collected, totaling 100 leaves. The traits evaluated were leaf area, fresh biomass, dry biomass, water content, specific leaf area and leaf dry matter content. An analysis of variance showed that most of the morphological traits (dry biomass, specific leaf area, leaf dry matter content) varied significantly. Furthermore, variables such as dry biomass, water content and leaf area showed a high correlation with fresh biomass in both areas. The morphological variation found in *M. splendens* allows for creating growth and establishment strategies according to the environmental conditions.
Keywords: functional traits, leaf plasticity, light, shade, survival strategy

RESUMO - (As condições de luz afetam os atributos funcionais de *Myrcia splendens* (Sw.) DC. em um fragmento de Mata Atlântica, Sudeste, Brasil). A radiação é um dos aspectos que influenciam a composição de espécies, sendo assim, a luz é um fator limitante para o crescimento das árvores. O estudo objetivou avaliar as variações morfológicas foliares entre indivíduos de *Myrcia splendens* (Sw.) DC., sob diferentes condições de luminosidade, em uma floresta urbana. O fragmento caracteriza-se por possuir uma área sem formação de dossel e uma com regeneração mais avançada. Foram coletados ramos de cinco indivíduos, totalizando 100 folhas. Avaliou-se a área foliar, massa fresca, massa seca, conteúdo de água, área foliar específica e teor de matéria seca das folhas. A análise de variância mostrou que a maioria das características (massa seca, área foliar específica, teor de matéria seca das folhas) variaram significativamente. A massa seca, conteúdo de água e área foliar apresentaram alta correlação com a massa fresca em ambos os ambientes. A variação morfológica encontrada em *M. splendens* permite a criação de estratégias de crescimento e estabelecimento da espécie de acordo com as condições ambientais.
Palavras-chave: estratégia de sobrevivência, luz, plasticidade foliar, traços funcionais, sombra

Introduction

The great biodiversity in forest ecosystems, as well as the geographical distribution of plants, result from different aspects such as intrinsic species characteristics, slope, soil, climate, and water availability of each region (García-Palacios et al. 2018). However, solar radiation is one of the aspects that most influence species composition (Jagodzinski et al. 2016, Perot et al. 2017), so light is a limiting physical factor to the trees' establishment and growth in forests (Tang & Dubayah 2017, Chou et al. 2018).

Different environmental factors are decisive for the development of adaptive strategies by tree individuals and are represented by morphological, anatomical, and physiological characteristics, also known as functional traits (Sultan 2003, Violle et al. 2007). Thus, species coexistence in tree communities may be explained by functional trait diversity since these traits reflect the plant ecological strategies (Adler et al. 2014, McGill et al. 2006). In addition, the plants morphological traits are genetically determined but can also be strongly influenced by the environment in which they are inserted as a form of adaptation, with the interaction of genetic and environmental effects acting together to model the phenotype (Schlichting 2002, Mizutani & Kanaoka 2017).

Plants ability in changing phenotypic characters as a result of interaction with the environment can contribute to functional stability, especially when phenotypic plasticity acts on characters linked to survival, becoming a very important tool for adaptation (Turcotte & Levine 2016, Matesanz &

1. Universidade Federal de Lavras, Departamento de Ciências Florestais, Avenida Doutor Sylvio Menicucci, 1001, Kennedy, 37200-900 Lavras, MG, Brasil
2. Universidade Federal de Lavras, Departamento de Ecologia e Conservação, Avenida Doutor Sylvio Menicucci, 1001, Kennedy, 37200-900 Lavras, MG, Brasil
3. Universidade Federal de Juiz de Fora, Departamento de Botânica, Rua José Lourenço Kelmer, s/n, Martelos, 36036-330 Juiz de Fora, MG, Brasil
4. Autor para correspondência: lucasdezideriο01@gmail.com

Ramírez-Valiente 2019). Thus, these species with plasticity potential to traits associated with surviving show adaptive strategies in different types of environments since the changes produced may result in increased environmental tolerance by the species (Fréjaville et al. 2019, Pérez-Ramos et al. 2019).

The leaf is the organ that has a greater exposure to environmental variables compared to other plant components (Fahn 1986), thus presenting more structural variations (Lewis 1972, Marques et al. 1999). In addition, the leaf is responsible for vital functions such as photosynthesis, breathing, perspiration, conduction and tree sap flow. These traits result from the direct exposure of the limbus to sunlight rays and absorption of carbon dioxide, that are both essential for photosynthesis processes (Lewis 1972, Taiz & Zeiger 2004). Therefore, the specialization of leaves due to the tree shade tolerance may result in leaves adapted to different environmental conditions (sunlight leaves and shade leaves) (Menezes et al. 2009).

Leaf functional traits are related to light conditions in the environment since these aspects may influence the development and caption ability of resources such as water and nutrients to the leaf and consequently to the plant (Keenan & Niinemets, 2016, Zhang et al. 2020). In addition, leaf traits guide understanding of the ecosystem function and structure in response to environmental changes (Keenan; Niinemets, 2016).

A representative species considering the tree community adaptability in relation to environmental factors, as well as intrinsic species characteristics and their components is *Myrcia splendens* (Sw.) DC. This species is considered an endemic plant in Brazil, as well as a generalist with wide environmental condition adaptation and is consequently present throughout the national territory (Amorim & Melo Júnior 2016). *M. splendens* presents great divergence regarding its taxonomy, having numerous synonyms (Amorim & Melo Júnior 2016, Flora do Brasil 2018). In addition, the species is characterized by zoochoric dispersion, in which its fruits are widely appreciated and dispersed by the avifauna. The species is classified as a pioneer regarding the successional stage, with flowering occurring between September and October and the fruiting beginning in December. In addition, *M. splendens* is widely used in recovery projects for degraded areas due to its rapid growth (Oliva et al. 2018, Schmitt et al. 2018).

Morphological variations between sunlight and shade areas are expected considering *Myrcia splendens* (Sw.) DC. species occurrence in different environmental conditions since light incidence determines the plant growth and establishment. Considering the different environmental conditions (sunlight and shade), we expect that in the under direct sunlight area the foliar traits are related to the protection of leaf tissues and reduction of photoinhibition (e.g. higher dry biomass and leaf dry matter content and lower specific leaf area). In contrast, in shaded area where there is greater canopy formation and plants do not receive direct light, leaf traits with an opposite pattern are expected, conditioned by the need to intercept and use the little available light. In this sense, this study aimed to evaluate leaf morphological variations between individuals of the *Myrcia splendens* (Sw.) DC. species under different environmental conditions (light and shade) in an urban forest community in the municipality of Juiz de Fora, Minas Gerais State (Brazil).

Material and methods

Study area - The data used in this study is from an urban fragment located on the Federal University of Juiz de Fora campus, in the municipality of Juiz de Fora, Minas Gerais State, Brazil. The fragment is called "Mata do ICB" and is characterized by having an open canopy area and another with an advanced regeneration stage as well as canopy formation, in which the light incidence into the understory trees is more difficult (Figure 1). In addition, the area is the result of abandonment of exotic pasture, followed by natural regeneration for at least 50 years (Menon & Carvalho 2012, Moreira & Carvalho 2013).

The Juiz de Fora municipality is located in the Zona da Mata mountainous areas and the predominant vegetation of the fragment is Seasonal Semi-deciduous Forest (IBGE 2012). The main soil in the region is Dystrophic Red Yellow Latosol (FEAM 2011), and the climate is Cwa according to the Koppen classification, which is characterized as mesothermal, meaning there is a hot and rainy summer and a cold and dry winter (Alvares et al. 2013). The region has an altitude of approximately 850 meters, mean annual precipitation of 1536 mm and the mean annual temperature of 18.9 °C.

Sampling and data collection - The data sampling occurred during July, 2014 and consisted of collecting *Myrcia splendens* leaves in the "Mata do ICB", considering the open canopy area, and the one with an advanced regeneration stage as well as canopy formation. The sun leaves were collected in the area where there is no canopy formation and in places where the individuals were under direct sunlight. In contrast, the leaves of the shade plants were collected from inside the fragment with the highest canopy formation, which makes it difficult for the understory plants to receive direct light (Figure 2).

Branches from five individuals were collected in each area using the criteria selection of height greater than six meters and diameter at 1.30 meters above the ground (DBH) greater than 5 cm. All individuals were at a minimum distance of 10 meters from each other and 20 leaves were selected from each tree, totaling 100 leaves per area (adapted from Pérez-Harguindeguy et al 2013). The leaf collection took place between the second and sixth knots in the apex-base direction.

The *M. splendens* leaves were moistened and packed in plastic bags for later measurement of their fresh biomass (g) in an analytical scale with an accuracy of 0.001 g. The leaf area was measured using the Image J program (Rasband 1997), which is specialized in image analysis. Next, photographs were taken from a Nikon Coolpix P510 camera and were darkened (black and white scale) using the Adobe Photoshop CS6 program to determine leaf area. The leaves were subsequently dried in an oven at 80 °C for 48 hours, thus enabling to measure their respective dry biomass (g) (Pérez-Harguindeguy et al. 2013). The above information was then used to estimate the leaf water content as a function of the difference between fresh and dry biomass. The leaf dry matter content (LDMC) was estimated by dividing the dry biomass by the fresh biomass (mg g^{-1}). In addition, the specific leaf area (SLA) was calculated by the ratio between leaf area (cm^2) and dry biomass (g). These traits were selected based on their influence to photosynthetic rate, energy and water balance, and light interception by the leaves (Evans & Poorter 2001, Valladares & Niinemets 2008).

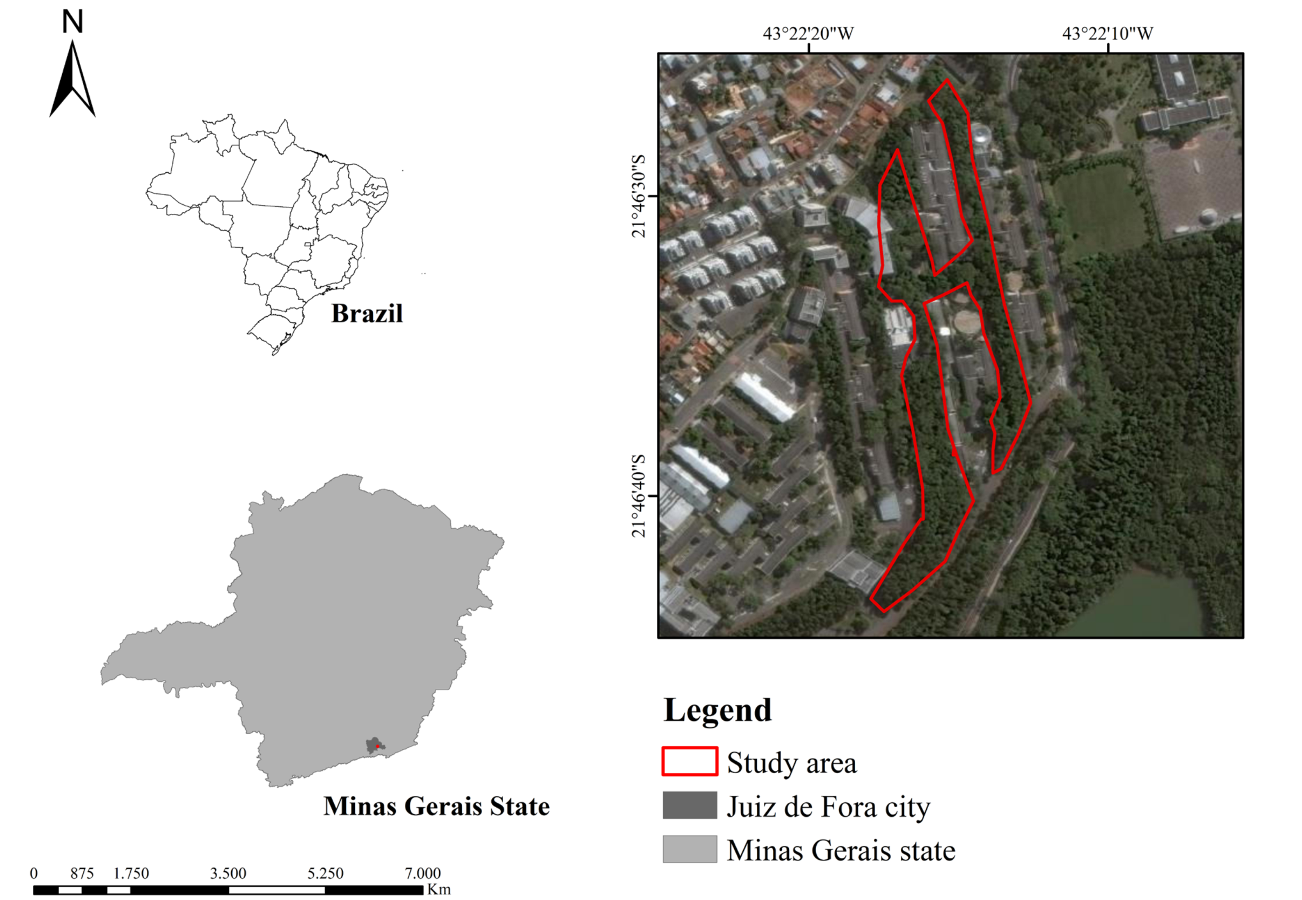

Figure 1. Study area location of an urban fragment denominated Mata do ICB, in the municipality of Juiz de Fora, Minas Gerais State, Brazil.

Data analyses - Pearson's correlation coefficient was calculated using the R software program (R Core Team 2017) in order to verify the correlation between the variables analyzed. Thus, the classification proposed by Dancey and Reidy (2005) was considered to establish the correlation degree, in which: r = 0.10 to 0.39 (weak); 0.40 to 0.69 (moderate); and 0.70 to 1 (strong). The variables which showed a high correlation with each other were removed in the following analyzes, since both had a high statistical dependence on each other.

The means and the respective standard deviations were calculated considering the variables selected between morphological traits (dry biomass, water content, specific leaf area, leaf dry matter content). In addition, an Analysis of variance was performed to assess the possible differences between the environments, and the means were compared by the Mann-Whitney test at 5% probability ($p < 0.05$). All analyzes were performed using the Past 1.34 (Hammer et al. 2001). Lastly, a *Boxplot* for each variable according to the areas was elaborated using the R software program (R Core Team 2017).

Results

Considering the light and shade environmental conditions and analyzing the Pearson's correlation coefficient, we found that the functional traits dry biomass (0.91), water content (0.92) and leaf area (0.78) with fresh biomass showed greater correlation in the sunlight environment. In addition, the leaf area (0.71) showed a high correlation with dry biomass (Table 1).

The shade environment showed the same variables with high correlation as the light environment. In addition, the LDMC showed negative correlation with leaf area (Table 1). A positive correlation allows to predict that the traits move in the same direction, while a negative correlation predisposes that the variables of interest move in opposite directions. Thus, the dry biomass, water content, LDMC and SLA variables were those which did not show correlation between them.

We proceeded an analysis of variance with the variables that did not show any correlation with each other (dry biomass, water content, LDMC and SLA). These variables provide information such as water balance, resistance and lifetime of the arboreal individual. We found that most of the quantitative morphological traits (dry biomass ($p = < 0.0001$), SLA ($p = < 0.0001$) and LDMC ($p = < 0.0001$)) differed significantly between the two areas. This finding indicates some variability within the species occurring in the shade and light environments. The water content did not present statistical difference between the studied areas ($p = 0.1589$) (Figure 3).

Discussion

Regarding both study areas, the traits which showed high correlation between each other were dry biomass, fresh

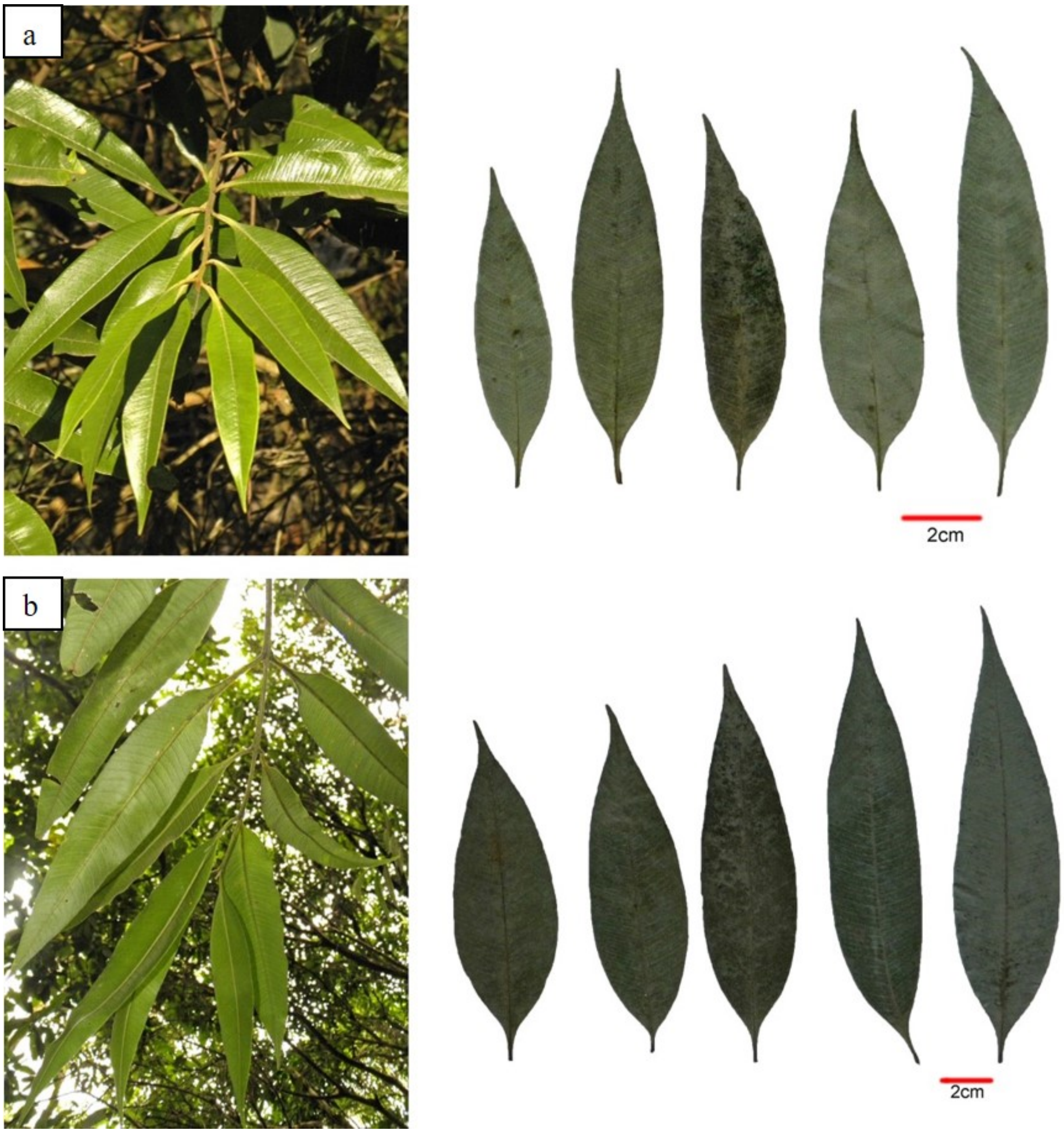

Figure 2. Aspect of the *Myrcia splendens* (Sw.) DC. leaf in the two sampled areas, Mata do ICB, municipality of Juiz de Fora, Minas Gerais State, Brazil. a: Sunlight area; b: Shade area.

Table 1: Pearson's correlation coefficient between the morphological variables quantified in the light and shade environments for the *Myrcia splendens* (Sw.) DC. species. FB: fresh biomass; DB: dry biomass; WC: water content; LA: leaf area; SLA: specific leaf area; LDMC: leaf dry matter content.

			Light			
	FB	DB	WC	LA	SLA	LDMC
FB	1.00					
DB	0.91	1.00				
WC	0.92	0.68	1.00			
LA	0.78	0.71	0.72	1.00		
SLA	-0.14	-0.33	0.07	0.40	1.00	
LDMC	0.07	0.45	-0.32	-0.02	-0.61	1.00
			Shade			
	FB	DB	WC	LA	SLA	LDMC
FB	1.00					
DB	0.94	1.00				
WC	0.95	0.78	1.00			
LA	0.87	0.76	0.87	1.00		
SLA	-0.39	-0.59	-0.16	0.24	1.00	
LDMC	-0.01	0.30	-0.29	-0.95	-0.61	1.00

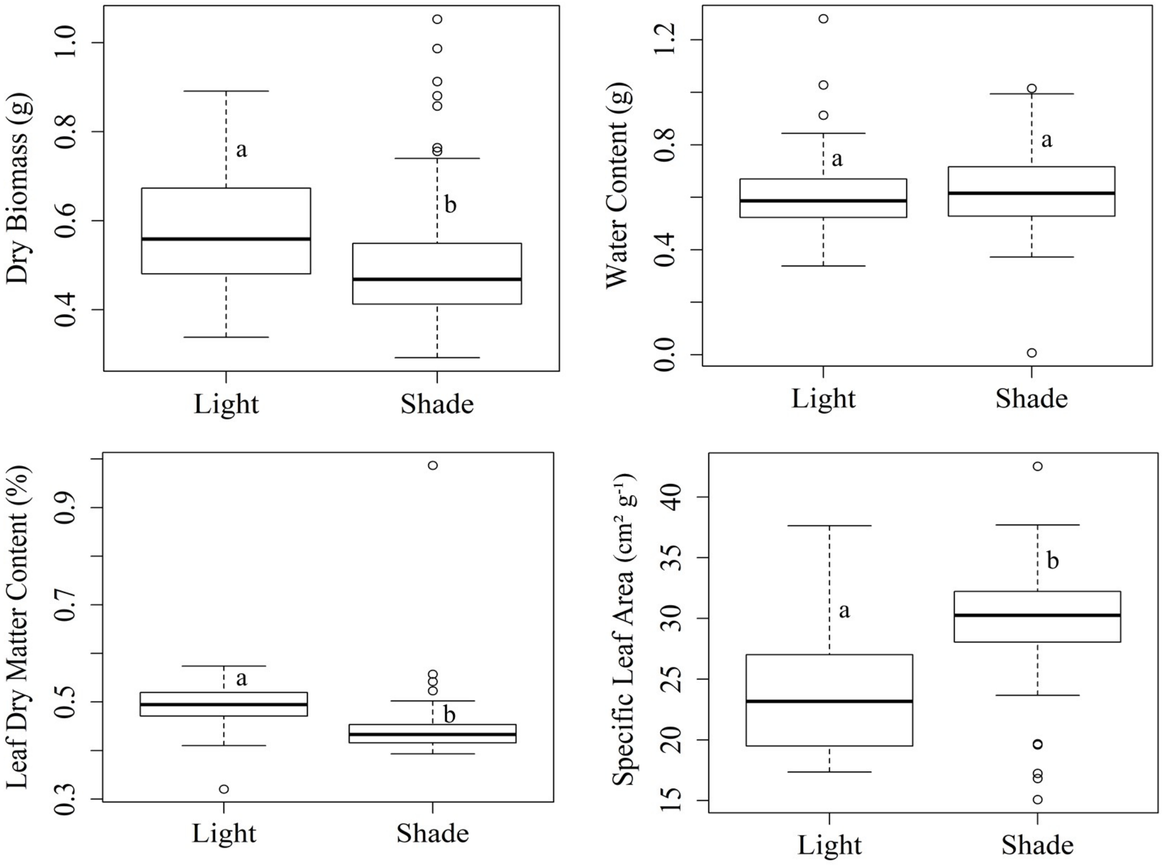

Figure 3. Morphological traits effect in light and shade environments in Mata do ICB, in the municipality of Juiz de Fora, Minas Gerais State, Brazil, for the *Myrcia splendens* (Sw.) DC. species. * Different letters for the same variable represent statistically different values (Mann-Whitney test, $p < 0.05$).

biomass, leaf area, SLA and water content. These variables are related to water storage capacity, biomass, leaf carbon and plant physiology (Ali et al. 2017, Klamerus-Iwan et al. 2018). Thus, these aspects may be linked to defense and protection mechanisms, implying in a greater leaf longevity (Boeger & Wisniewski 2003, Edwards et al. 2000).

The leaf water content for the areas showed no statistical difference. This fact may be linked to the mesophilic cells turgor maintenance, which causes less water loss from the leaves (Willadino & Camara 2010). Water preservation is important to these leaves since the species is semi-deciduous, thus allowing to carry out the vital processes throughout the individual's life (Lorenzi 1998).

The dry biomass exhibited a higher value in the light area when compared to shaded area. This result indicates a tendency for plants to be investing in a greater amount of mechanical tissue than photosynthetic tissues (Vendramini et al. 2002). In addition, *Myrcia splendens* is characterized as a species with great phenotypic plasticity capacity. Thus, the dry biomass is considered as response to the plant good adaptation to different environmental conditions (Amorim & Melo Júnior 2016).

We observed a variation in the SLA value between the areas, and which was greater in the shaded area. This aspect can be explained by the light availability from the environment which significantly influences the SLA values, considering that there is a positive correlation between the SLA and the photosynthetic efficiency by the species leaf mass (Evans & Poorter 2001). Also, the SLA value difference in an environmental gradient may be related to the within-species variability (Carlucci et al. 2014). Therefore, the increase in SLA for the shaded environment may favor the growth and reproduction of *M. splendens* in the forest understory, where low available irradiation mostly occurs in the form of inconstant diffused light beams (Chazdon & Pearcy 1991).

The shade leaves tend to be thinner and present less concentrated leaf biomass per unit area, which increases their SLA and consequently the light interception per unit of leaf biomass invested (Valladares & Niinemets 2008). The higher SLA value in the shaded environment can also be related to the reduction in the investment of structures such as the epidermis, which help plants in their protection mechanisms against photoinhibition (Pearcy 2007).

The LDMC is a functional parameter which considers the aspects of plant growth, acquisition and use of resources, as well as carbon assimilation (Wilson et al. 1999, Vile et al. 2006, Hodgson et al. 2011). Light incidence is a major factor in the forest and its high intensity promotes less investment in leaf formation and consequently causes a change in the resource usage strategy (acquisitive) (Klipel et al. 2021), causing a lower LDMC in the light environment (Carreño -Rocabado et al. 2012). SLA and LDMC differences in shade environment reflect an important trait variation axis from conservative and stress-tolerant strategies to acquisitive and opportunistic strategies along gradients of light availability (Klipel et al. 2021, Wright et al. 2004).

The results showed that the morphological variables of dry biomass, SLA and LDMC had statistical difference between the sunlight and shade environments. This fact may be explained by the fact that *Myrcia splendens* species is characterized as heliophyte and hygrophyte, meaning that it is a plant with great adaptation to intensive insolation and moisture (BFG 2018). In addition, the morphological plasticity from *Myrcia splen*dens is proven by the species anatomic and structural characteristics in which the tree individuals will create establishment and survival mechanisms according to the ecosystem (Amorim & Melo Júnior 2016, Larocca et al. 2015).

Studies of morphological variation into areas with different luminosity conditions showed such similarity to the traits found in our study when considering species with great adaptability (Borges et al. 2019, Krupek & Lima 2012, Silva et al. 2019). In this sense, the adaptative variations of *Myrcia splendens* allow its occurrence in different vegetation types, since the individual is able to explore new niches with efficiency (Amorim & Melo Júnior 2016). Thus, the species is considered as generalist and the pattern found is common to other species of this group (Naves & van den Berg 2012).

Conclusions

We have noticed that there is leaf morphological variability in the *M. splendens* species in light and shade environments, since this showed statistical difference for the dry biomass, SLA and LDMC traits. This finding contributes to understanding the development of this species in different environmental conditions and contributes to creating growth strategies.

Considering the geographic distribution, as well as the relevant abundance in the study region, more studies should be developed with this species, such as anatomical and physiological studies, so that the plant establishment strategy can be better explained.

Acknowledgements

The authors give thanks to the Programa de Pós-graduação em Ecologia, Universidade Federal de Juiz de Fora and Universidde Federal de Lavras, for the structure required for the development of the study. This study was supported in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil - Finance Code 001. In addition, the authors thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the Fundação de Amparo à Pesquisa do Estado de Minas Gerais. F.A.C. hold a CNPq productivity fellowship.

Conflicts of interest

There is no conflict of interest.

Author Contributions

Lucas Deziderio Santana: Contribution in the concept and methodology of study, investigation, data Curation, writing - original draft and writing - review & editing.

Kelly Marianne Guimarães Pereira: Contribution to data analysis, interpretation and writing - Review & Editing.

Natielle Gomes Cordeiro: Contribution to data analysis, interpretation and writing - Review & Editing.

Ana Cristina Atala Alves: Contribution in the concept, methodology of study, data collection and critical revision.

Fabrício Alvim Carvalho: Contribution in the concept and methodology of study, funding acquisition, data curation and critical revision.

Literature cited

Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. & Franco, M. 2014 Functional traits explain variation in plant life history strategies. Proceedings of the National Academy of Sciences of the United States of America 111: 740-745.

Ali, A.M., Darvishzadeh, R., Skidmore, A.K. & van Duren, I. 2017. Specific leaf area estimation from leaf and canopy reflectance through optimization and validation of vegetation indices. Agricultural and Forest Meteorology 236: 162-174.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Gonçalves, J.L. de M. & Sparovek, G. 2013. Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22: 711-728.

Amorim, M.W. & Melo Júnior, J.C.F. de. 2016. Plasticidade morfológica de Myrcia splendens (S.w.) CD. (Myrtaceae) ocorrente em Mata Atlântica e Cerrado. Iheringia 71: 261-268.

BFG. 2018. Brazilian Flora 2020: Innovation and collaboration to meet Target 1 of the Global Strategy for Plant Conservation (GSPC). Rodriguesia 69: 1513-1527.

Boeger, M.R.T. & Wisniewski, C. 2003. Comparação da morfologia foliar de espécies arbóreas de três estádios sucessionais distintos de floresta ombrófila densa (Floresta Atlântica) no Sul do Brasil. Revista Brasileira de Botânica 26: 61-72.

Borges, E.R., Prado-Junior, J., Santana, L.D., Delgado, C.N., Raymundo, D., Ribeiro, J.H.C., Rossatto, D.R., Carvalho, F.A. 2019. Trait variation of a generalist tree species (*Eremanthus erythropappus*, Asteraceae) in two adjacent mountain habitats: savanna and cloud forest. Australian Journal of Botanic 66: 640-646.

Carlucci, M.B., Debastiani, V.J., Pillar, V.D. & Duarte, L.D.S. 2014. Between- and within-species trait variability and the assembly of sapling communities in forest patches. Journal of Vegetation Science 26: 21-31.

Carreño-Rocabado, G., Peña-Claros, M., Bongers, F., Alarcón, A., Licona, J-C. & Poorter, L. 2012. Effects of disturbance intensity on species and functional diversity in a tropical forest. Journal of Ecology 100: 1453-1463.

Chazdon, R.L. & Pearcy, R.W. 1991. The Importance of Sunflecks for Forest Plants Understory periods of radiation. BioScience 41: 760-766.

Chou, C.B., Hedin, L.O. & Pacala, S.W. 2018. Functional groups, species and light interact with nutrient limitation during tropical rainforest sapling bottleneck. Journal of Ecology 106: 157-167.

Dancey, C. & Reidy, J. 2006. Estatística Sem Matemática para Psicologia: Usando SPSS para Windows. 3rd ed. Artmed, Porto Alegre.

Edwards, C., Read, J., Sanson, G. 2000. Characterising sclerophylly: Some mechanical properties of leaves from heath and forest. Oecologia 123: 158-167.

Evans, J.R. & 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 and Environment 24: 755-767.

Fahn, A. 1986. Structural and functional properties of trichomes of xeromorphic leaves. Annals of Botany 57: 631-637.

FEAM - Fundação Estadual do Meio Ambiente. 2010. Mapa de solos do Estado de Minas Gerais. Available at <http://www.feam.br/noticias/1/949-mapas-de-solo-doestado-de-minas-gerais> (access in 02-IX-2013).

Flora do Brasil 2020 em construção. Jardim Botânico do Rio de Janeiro. Available at <http://floradobrasil.jbrj.gov.br/ > (access in 20-X-2018).

Fréjaville, T., Fady, B., Kremer, A., Ducousso, A. & Garzón, M.B. 2019. Inferring phenotypic plasticity and population responses to climate across tree species ranges using forest inventory data. Global Ecology and Biogeography 28: 1259-1271.

García-Palacios, P., Gross, N., Gaitán, J. & Maestre, F.T. 2018. Climate mediates the biodiversity - ecosystem stability relationship globally. Proceedings of the National Academy of Sciences of the United States of America 115: 8400-8405.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2001. PAST: Paleontological Statistics Software package for education and data analysis. Palaeontologia Electronica 4: 1-9.

Hodgson, J.G., Montserrat-Martí, G., Charles, M., Jones, G., Wilson, P., Shipley, B., Sharafi, M., Cerabolini, B.E.L., Cornelissen, J.H.C., Band, S.R., Bogard, A., Castro-Díez, P., Guerrero-Campo, J., Palmer, C., Pérez-Rontomé, M.C., Carter, G., Hynd, A., Romo-Díez, A., Torres Espuny, L. de & Royo Pla, F. 2011. Is leaf dry matter content a better predictor of soil fertility than specific leaf area? Annals of Botany 108: 1337-1345.

IBGE - Instituto Brasileiro de Geografia e Estatística. 2012. Manual Técnico da Vegetação Brasileira. 2nd ed. Rio de Janeiro.

Jagodzinski, A.M., Dyderski, M.K., Rawlik, K. & Katna, B. 2016. Seasonal variability of biomass, total leaf area and specific leaf area of forest understory herbs reflects their life strategies. Forest Ecology and Management 374: 71-81.

Keenan, T.F. & Niinemets, Ü. 2016. Global leaf trait estimates biased due to plasticity in the shade. Nature Plants 3: 1-6.

Klamerus-Iwan, A., Blonska, E., Lasota, J., Waligórski, P. & Kalandyk, A. 2018. Seasonal variability of leaf water capacity and wettability under the influence of pollution in different city zones. Atmospheric Pollution Research 9: 455-463.

Klipel, J., Bergamin, R.S., Seger, G.D. dos S., Carlucci, M.B. & Müller, S.C. 2021. Plant functional traits explain species abundance patterns and strategies shifts among saplings and adult trees in Araucaria forests. Austral Ecology 46: 1084-1096.

Krupek, R.A. & Lima, A.G. 2012. Variação na estrutura foliar de guabiroba (*Campomanesia xanthocarpa* Berg.) sob diferentes condições de luminosidade em um remanescente de Floresta Ombrófila Mista. Ambiência 8: 293-305.

Larocca, D.G., Tiago, A.V., Veiga, J.B. da, Tiago, P.V. & Silva, I.V. 2015. Morfoanatomia de *Myrcia splendens* (SW.) DC. (Myrtaceae) ocorrente em um encrave de Savana Amazônica. Enciclopédia Biosfera 11: 2308-2318.

Lewis, M.C. 1972. The physiological significance of variation in leaf structure leaf structure. Science Reviews 60: 25-51.

Lorenzi, H. 1998. Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. 2nd ed. Instituto Plantarum de Estudos da Flora Ltda, Nova Odessa.

Marques, A.R., Garcia, Q.S. & Fernandes, G.W. 1999. Effects of sun and shade on leaf structure and sclerophylly of *Sebastiania myrtilloides* (Euphorbiaceae) from Serra do Cipó, Minas Gerais, Brazil. Boletim Botânico 18: 21-27.

Matesanz, S. & Ramírez-Valiente, J.A. 2019. A review and meta-analysis of intraspecific differences in phenotypic plasticity: Implications to forecast plant responses to climate change. Global Ecology and Biogeography 28: 1682-1694.

McGill, B. J., Enquist, B.J., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21: 178-185.

Menon, T.A. & Carvalho, F.A. 2012. Estrutura populacional de *Pinus elliottii* em áreas de regeneração florestal em Juiz de Fora, MG. Pesquisa Florestal Brasileira 32: 367-372.

Menezes, N.L., Silva, D.C. & Pinna, G.F.A.M. 2009. Folha. In: Apezzato-da-Glória, B. & Carmello-Guerreiro, S. M (eds.). Anatomia Vegetal. 2nd ed. Editora UFV, Viçosa, pp. 303-311.

Mizutani, M. & Kanaoka, M.M. 2017. Environmental sensing and morphological plasticity in plants. Seminars in Cell and Developmental Biology 83: 69-77.

Moreira, B. & Carvalho, F.A. 2013. A comunidade arbórea de um fragmento urbano de Floresta Atlântica após 40 anos de sucessão secundária (Juiz de Fora, Minas Gerais). Biotemas 26: 59-70.

Naves, R.P. & van den Berg, E. 2012. Caracterização de uma Floresta Estacional Semidecidual em Varginha, MG. E comparação com remanescentes da região. Cerne 18: 361-370.

Oliva, E.V., Reissmann, C.B., Marques, R., Bianchin, J.E., Dalmaso, A. & Winagraski, E. 2018. Florística e estrutura de duas comunidades arbóreas secundárias com diferentes graus de distúrbio em processo de recuperação. Ciência Florestal 28: 1088-1103.

Pearcy, R.W. 2007. Responses of Plants to Heterogeneous Light Environments. In: Pugnaire F. I. & Valladares F (eds). Functional plant ecology. CRC Press, Florida - USA, pp. 213-258.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., Vos, A.C. de, Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S. & Cornelissen, J.H.C. 2013. New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61: 167-234.

Pérez-Ramos, I.M., Matías, L., Gómez-Aparício, L. & Godoy, O. 2019. Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. Nature Communications 10: 1-11.

Perot, T., Mårell, A., Korboulewsky, N., Seigner, V. & Balandier, P. 2017. Modeling and predicting solar radiation transmittance in mixed forests at a within-stand scale from tree species basal area. Forest Ecology and Management 390: 127-136.

Rasband, W. S. 1997. ImageJ 1.34n. National Institutes of Health. Available at <http://imagej.nih.gov/ij/> (access in 25-VII-2014).

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2017. Available at <https://www.r-project.org/> (access in 25-VI-2018).

Schlichting, C.D. 2002. Phenotypic plasticity in plants. Plant Species Biology 17: 85-88.

Schmitt, T., Andrade, V.C.L. de, Candido, J.B. & Souza, P.B. de. 2018. Análise fitossociológica para a recuperação de áreas degradadas utilizando espécies de Cerrado. Global Science and Technology 11: 65-77.

Silva, M.C., Teodoro, G.S., Bragion, E.F.A., van den Berg, E. 2019. The role of intraspecific trait variation in the occupation of sharp forest-savanna ecotones. Flora, 253: 35-42.

Sultan, S.E. 2003. Phenotypic plasticity in plants: a case study in ecological development. Evolution and Development 5: 25-33.

Taiz, L. & Zeiger, E. 2004. Fisiologia vegetal. 3rd ed. Artmed, Porto Alegre.

Tang, H. & Dubayah, R. 2017. Light-driven growth in Amazon evergreen forests explained by seasonal variations of vertical canopy structure. Proceedings of the National Academy of Sciences of the United States of America 114: 2640-2645.

Turcotte, M.M. & Levine, J.M. 2016. Phenotypic Plasticity and Species Coexistence. Trends in Ecology & Evolution 31: 803-813.

Valadares, F. & Niinemets, Ü. 2007. The Architecture of plant crowns: from design rules to light capture and performance. In: Pugnaire, F. I. &Valadares, F (eds.). Functional Plant Ecology. Boca Raton, CRC Press. pp. 101-149.

Vendramini, F., Díaz, S., Gurvich, D.E., Wilson, P.J., Thompson, K. & Hodgson, J.G. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. New Phytologist 154: 147-157.

Vile, D., Shipley, B. & Garnier, E. 2006. Ecosystem productivity can be predicted from potential relative growth rate and species abundance. Ecology Letters 9: 1061-1067.

Violle, C., Navas, M-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. 2007. Let the concept of trait be functional! Oikos 116: 882-892.

Willadino, L. & Camara, T.R. 2010. Tolerância das plantas à salinidade: aspectos fisiológicos e bioquímicos. Enciclopédia Biosfera 6: 1-23.

Wilson, P.J., Thompson, K. & Hodgson, J.G. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytologist 143: 155-162.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M-L., Niinemets, Ü., Oleksyn, J., Osada, N., Pooter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. 2004. The worldwide leaf economics spectrum. Nature 428: 821-827.

Zhang, Y-L., Moser, B., Li, M-H., Wohlgemuth, T., Lei, J-P. & Bachofen, C. 2020. Contrasting leaf trait responses of conifer and broadleaved seedlings to altered resource availability are linked to resource strategies. Plants 9: 1-15.

Received: 17/06/2020
Accepted: 03/11/2021
Associate Editor: Cláudia Baider

ISSN da publicação *online* 2236-8906