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ORIGINAL ARTICLE

Spatial and seasonal variability of photosynthetically active radiation in the understory of a semi-decidual seasonal forest

Variabilidade espacial e sazonal da radiação fotossinteticamente ativa no sub-bosque de uma floresta estacional semidecidual

José Eduardo Macedo Pezzopane[1], Genilda Canuto Amaral[2], José Ricardo Macedo Pezzopane[3], Miguel Angel Herrera Machuca[4], Rogério de Souza Nóia Júnior[5]

[1]Universidade Federal do Espírito Santo – UFES, Jerônimo Monteiro, ES, Brasil
[2]University of Huelva – UHU, Huelva, Spain
[3]Embrapa Pecuária Sudeste, São Paulo, SP, Brasil
[4]University of Cordoba - UCO, Cordoba, Spain
[5]Technical University of Munich – TUM, Freising, Germany

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Abstract

The Atlantic Forest is a global *hotspot* for biodiversity conservation; however, human actions threaten and unbalance the dynamics of the natural processes of the biome. The present study investigated the incidence of solar radiation within a fragment of semi deciduous seasonal forest in the area of the Atlantic Forest Biome in southeastern Brazil. In the four seasons of the year, the leaf area index (LAI) and photosynthetically active radiation (PAR) were measured in the understory vegetation. The measurements were made at one-meter height, in ten different locations in the forest fragment, with different terrain exposure and slope. The annual average LAI was 4.5 and the PAR transmissivity was 4.1%. However, the results showed a spatial and seasonal variability of the leaf area index in the studied forest fragment. The seasonal variation of PAR in the understory vegetation was due to the LAI and to the different slopes and terrain exposures. The spatial heterogeneity in PAR availability is indicative of high plant diversity in the forest fragment.

Keywords: Leaf area index; Atlantic Forest; Forest fragment; Transmissivity.

Resumo

A Mata Atlântica é um *hotspot* global para a conservação da biodiversidade; no entanto, as ações humanas ameaçam e desequilibram a dinâmica dos processos naturais do bioma. O presente estudo investigou a incidência de radiação solar em um fragmento de floresta estacional semidecídua na área do Bioma Mata Atlântica no sudeste do Brasil. Nas quatro estações do ano foram medidos o índice de área foliar (IAF) e a radiação fotossinteticamente ativa (PAR) na vegetação de sub-bosque. As medições foram realizadas a um metro de altura, em dez locais diferentes do fragmento florestal, com diferentes exposições do terreno e declividade. O IAF médio anual foi de 4,5 e a transmissividade do PAR foi de 4,1%. No entanto, os resultados mostraram uma variabilidade espacial e sazonal do índice de área foliar no fragmento florestal estudado. A variação sazonal do PAR nas vegetações de sub-bosque deveu-se ao LAI e às diferentes declividades e exposições do terreno. A heterogeneidade espacial na disponibilidade de PAR é indicativa de alta diversidade de plantas no fragmento florestal.

Palavras-chave: Índice de área foliar; Mata Atlântica; Fragmento florestal; Transmissividade.

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INTRODUCTION

The Atlantic Forest is a tropical forest biome, housing a significant portion of the world's biodiversity (Stehmann et al., 2009). For this reason, it is considered a global *hotspot* for biodiversity conservation. However, the anthropogenic exploration of this forest, renders it to be among the most threatened biomes in the world (Araujo et al., 2015; Fundação SOS Mata Atlântica, 2017). In Brazil, the exploitation of the Atlantic Forest occurs mainly due to economic development and agricultural expansion, compromising a large part of the fragments (Almeida et al., 2011; Serrano et al., 2013). With only 12.4% of its native vegetation, the greatest threats to the biome are deforestation and forest fires (Fundação SOS Mata Atlântica, 2020a, 2020b).

In a forest, the patterns of diversity, composition and even functional characteristics of the species are usually related to different soils and microclimates along an environmental gradient (McGill et al., 2006). Studies developed in tropical forests showed that the availability of solar radiation in the understory is a determining factor in the spatial distribution of native tree species of temperate deciduous, coniferous and tropical forests (Brown 1996; Culf et al., 1996; Nicotra et al., 1999; Guariguata 2000; Balderrama & Chazdon 2005; Kenzo et al., 2011; Jans et al., 2012).

The amount of photosynthetically active solar radiation (PAR) transmitted by the vegetation canopy is basically controlled by the vegetation mass, mostly leaves, crossed by the solar radiation (Keeling & Phillips 2007; Russo et al., 2012). For this reason, studies on PAR transmissivity almost always involve the characterization of the leaf area index (LAI). However, factors such as terrain orientation and slope also affect PAR transmissivity, especially at higher latitudes due to the apparent path of the sun (Zou et al., 2007; Bennie et al., 2008; Adams et al., 2014; Barnard et al., 2017). In summary, the higher the latitude, the higher the seasonal change within a year of the angle between incident solar radiation and the direction of leaves in a forest, which will affect PAR transmissivity (Barnard et al., 2017).

Many areas of the Atlantic Forest Biome in the southeastern region of Brazil, especially the ones with latitudes from -20° to -30° is mountainous, with a huge slope and terrain exposure variation (Rezende, 1971). The semi-deciduous forests occur in this mountainous region, and many species, due to seasonal climate variation, lose their leaves (Oliveira-Filho et al., 2006), which affects the leaf area index (LAI). The interaction of the relief and LAI can cause important seasonal and spatial fluctuations in the PAR availability in the understory, generating microclimate differences within the forest fragment (Mark & Ashton, 1992; Fernandez & Myster, 1995), affecting the soil water regime and the availability of nutrients (Salim-Neto, 2011).

Thus, based on the assumption that in the Southeast region, the Atlantic Forest fragments are in an area of uneven relief, in different conditions of orientation and slope or slopes, and that they are in different successional stages, with different LAI, there is a spatial and temporal variability of the PAR transmissivity. Given all this context and knowing that the amount of solar radiation that reaches the understory is essential to define the occurrence and distribution of species, assessing how much PAR radiation reaches the interior of the forest can help in species conservation projects. Thus, the present study aimed to measure PAR and LAI in different seasons and locations (with different slope and terrain exposure) in a secondary seasonal semi deciduous forest of the Atlantic Forest Biome.

MATERIAL AND METHODS

Description of the study area

The study was carried out at the Experimental Station Mata do Paraíso, with an area of 196 ha, located in the Municipality of Viçosa, Minas Gerais state, Brazil (latitude = 20°45’ S, longitude = 42°55’ W; 690 m altitude), as presented in Figure 1a. According to the Köppen classification, the climate of the region is *Cwb*, with poorly distributed rain throughout the year, with a rainy summer (December – March) and dry winter (June - September) (Figure 1b) (Xavier et al., 2015). The average annual rainfall is 1221 mm and the average annual temperature is 19.4°C. The region's natural vegetation is classified as seasonal semi deciduous forest. The percentage of deciduous trees (*i.e.* trees that lose their leaves during winter), in the forest, varies between 20 and 50% (Veloso et al., 1991).

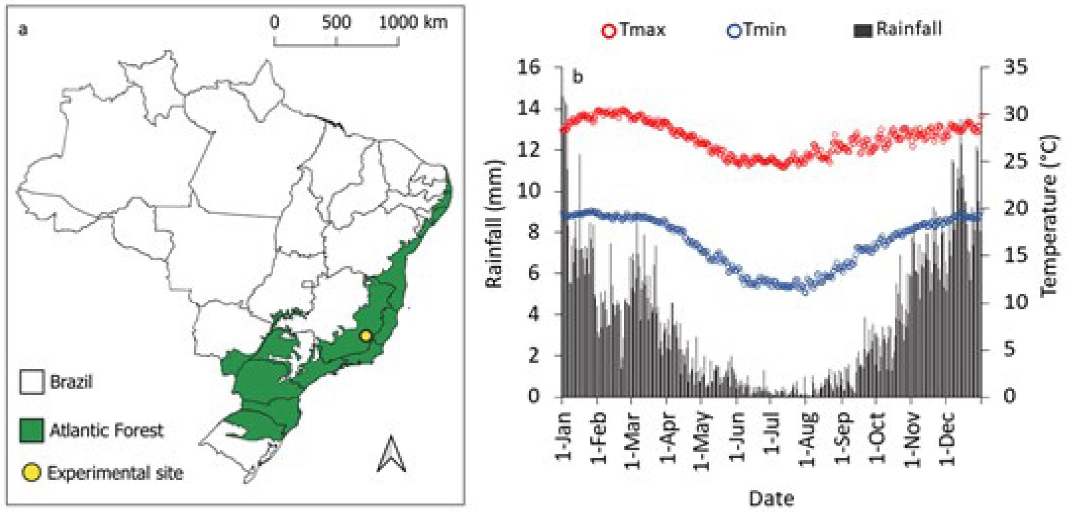

Figure 1. Experimental site for the present study and the Atlantic Forest Biome in Brazil (a). Mean daily Rainfall, maximum (Tmax) and minimum temperature (Tmin), over the 1981–2013 in the experimental site (b). The climatic data were obtained from Xavier et al. (2015).

In order to carry out a study on natural regeneration, Volpato (1994) identified ten sites at the Experimental Station Mata do Paraíso, due to slope and terrain exposure. Phytosociological surveys of natural regeneration have been carried out in these 10 sites since 1992, considering arboreal individuals with diameter at breast height less than 5 cm (DBH < 5 cm) (Volpato, 1994; Higuchi, 2003; Garcia, 2009). The slope, terrain exposure and topographic position characteristics of the ten study sites are shown in Table 1.

Table 1. Characterization of the slope, exposure and topographic position of ten sites in a forest fragment in the domain of the Atlantic Forest Biome, southeastern Brazil.

Site	Declivity (%)	Exposure *	Topographical Position
1	40	NE	Upper third
2	21	NE	Half slope
3	43	NE	Lower third
4	80	NE	Half slope
5	3	-	Lowered
6	51	SE	Lower third
7	45	SE	Half slope
8	20	SE	Half slope
9	14	SE	Lower third
10	45	SE	Upper third

* - NE = northeast; SE = southeast

Photosynthetically active solar radiation data and leaf area index

Photosynthetically active solar radiation (PAR) was measured inside ten sites, during at least two days in each site, at four times of the year (Table 2), totaling at least eight days of measurements during the year at each site, and sampling in different conditions of density of radiation flow, position of the sun and phenological stage of vegetation.

Table 2. Measurement period of photosynthetically active radiation and leaf area index in a forest fragment in the domain of the Atlantic Forest Biome, southeastern region of Brazil.

Measurement period	Central day
February 26th to March 31st	March 13th
April 23rd to May 16th	May 4th
July 31st to August 20th	August 10th
November 26th to December 21st	December 8th

PAR was measured using linear sensors (LI-COR, model LI-191, USA) connected to a datalogger CR10x (Campbell Scientific, USA). Measurements were taken at five points inside each site, at one meter of height from the ground. This height was chosen because it coincides with the limit between the plant size classes (height between 1 and 3 m) used in the studies of natural regeneration carried out in these sites. The sensors were installed in the center of subplots established by Volpato (1994).

For comparison purposes, PAR was also measured in an open area, inside the Experimental Station, with a point sensor (LI-COR, model LI-190, USA). The data were stored in a datalogger CR10x (Campbell Scientific, USA) located inside the forest and in the open area, with scanning every 5s and storing of average values every 15 minutes.

PAR measurements were done for two days at each site, within the same period, to avoid significant variation in the density of extraterrestrial solar radiation between the first and the last day of measurement. However, the presence of clouds affects the total solar radiation reaching the surface. In order to minimize the cloud effects, the results regarding the variation of the PAR inside the forest, in the 10 studied sites, were analyzed through the percentage of solar radiation transmissivity of the canopy, since measurements inside and outside the forest were simultaneously carried out.

The presence of clouds also modifies the direct and diffuse solar radiation proportion and also the forest canopy transmissivity, as observed by Huber et al. (1988). Thus, to analyze the canopy PAR transmissivity, only the day with the highest density of solar radiation flow for each measurement period was chosen.

The leaf area index (LAI) was estimated at the ten locations, at the same PAR measurement times and locations, to characterize the spatial and temporal variation of canopy density. The LAI was determined by means of two sensors (LI-COR, LI-2050, USA) connected a datalogger (LI-COR, LI-2000, USA) with one sensor installed in an open area (outside the forest) and another inside the forest. The measurements were performed under diffused light, preferably at dawn or late afternoon, or on cloudy days.

Statistical analysis

The study was conducted in a completely randomized design. The results of PAR and LAI transmissivity were statistically analyzed by means of analysis of variance in which the time factor constituted repeated measures, using the procedure GLM, option “repeated” of the SAS software. The comparative analysis between the values of PAR and LAI between periods in the same site (seasonal variability) was performed using the Tukey test at 5% probability. Due to the high number, the comparison between the average values obtained in the ten studied sites, within the same period, was carried out according to the grouping criterion proposed by Scott & Knott (1974), at 5% probability.

RESULTS AND DISCUSSION

The analysis of variance indicated significant a spatial and temporal interaction, for PAR transmissivity and LAI in the forest fragment studied, Tables 3 and 4, respectively. The average PAR transmissivity in the studied forest fragment was 4.1% and the average leaf area index was 4.5, for the four data collection times.

Table 3. Mean values of photosynthetically active radiation transmissivity by the canopy (%) in ten sites, at four times of the year, in a forest fragment of the Atlantic Forest Biome, southeastern Brazil.

Site	March	May	August	December	Average
1	4.4 *b*	5.4 *b**	12.3 *a*	13.4 *a*	8.9
2	1.5 *c*	4.1 *b*	7.0 *b*	11.2 *a*	6.0
3	1.7 *c*	1.5 *c*	3.2 *c*	4.3 *c*	2.7
4	8.1 *a*	11.5 *a*	11.3 *a*	6.4 *b*	9.3
5	0.9 *c*	0.9 *c*	2.0 *c*	2.9 *c*	1.7
6	0.9 *c*	0.8 *c*	1.3 *c*	4.3 *c*	1.8
7	1.1 *c*	0.4 *c*	1.7 *c*	3.3 *c*	1.6
8	2.0 *c*	1.4 *c*	3.7 *c*	7.8 *b*	3.7
9	1.7 *c*	1.1 *c*	1.5 *c*	6.8 *b*	2.8
10	1.8 *c*	0.6 *c*	2.6 *c*	4.9 *c*	2.5

* Averages followed by the same letter, in the vertical direction, belong to the same group, according to the Scott & Knott grouping criterion, at 5% probability.

The minimum mean PAR transmissivity was 1.6% (site 7) and the maximum 9.3% (site 4), and the minimum mean LAI was 3.6 (site 4) and the maximum was 5.2 (sites 5 and 7). It is noted that the sites with the lowest LAI showed greater PAR transmissivity. Site 2, despite the high LAI values at some periods of the year, showed high PAR transmissivity. The other studied sites, despite presenting variations in LAI between them, were classified into the groups with the highest PAR transmissivity, with the exception of sites 8 and 9 in December.

Table 4. Average values of leaf area index (LAI) in ten sites, at four times of the year, in a forest fragment in the domain of the Atlantic Forest Biome, in the southeastern region of Brazil.

Site	March	May	August	December	Average
1	4.5 *c*	4.2 *c**	3.0 *c*	3.3 *d*	3.7
2	5.4 *a*	4.9 *b*	3.6 *b*	4.2 *c*	4.5
3	5.5 *a*	5.3 *a*	4.0 *a*	4.7 *b*	4.9
4	4.2 *c*	3.7 *c*	3.1 *c*	3.4 *d*	3.6
5	5.7 *a*	5.8 *a*	4.5 *a*	4.6 *b*	5.2
6	5.1 *b*	5.9 *a*	4.1 *a*	4.8 *b*	5.0
7	5.1 *b*	5.8 *a*	4.2 *a*	5.5 *a*	5.2
8	4.9 *b*	4.4 *b*	3.6 *b*	3.9 *c*	4.2
9	5.8 *a*	5.6 *a*	4.6 *a*	4.2 *c*	5.1
10	5.0 *b*	4.5 *b*	3.4 *b*	4.2 *c*	4.3

* Averages followed by the same letter in the vertical direction, belong to the same group, according to the Scott & Knott grouping criterion, at 5% probability.

The higher transmissivity of PAR observed in sites 1 and 4, always classified in the groups with the highest transmissivity in all periods, is explained by the low LAI values, which is due to the forest clearings. A visual analysis of the field identified that, in site 1, there was a large number of small clearings while in site 4 there was a smaller number of clearings with a large size. The PAR transmissivity for site 4 corroborates the existence of large forest clearings.

Site 2, despite the high LAI values at some periods of the year, showed high PAR transmissivity. The other studied sites, despite presenting variations in LAI between them, were classified into the groups with the highest PAR transmissivity, with the exception of sites 8 and 9 in December. This can be explained by the exponential attenuation of PAR by the canopy; there is a point from which the increase in LAI does not significantly affect the transmission of solar radiation.

Analyzing the whole forest fragment, *i.e.* considering the average values observed in all the studied sites, it was possible to notice a temporal fluctuation of the LAI (Figure 2a). PAR transmissivity also varied over time throughout the year (Figure 2b). The values increased from May until December, decreasing in the measurements made in March.

The results of average PAR transmissivity in the studied forest fragment and average leaf area index corroborate the literature. Similar values of PAR transmissivity were found by Aylett (1985), Lee (1987), Rich et al. (1993), Keeling; Phillips (2007) and Venturoli et al. (2012) in tropical forests. However, Leitão et al. (2002), studying in the Amazon Forest, found the average PAR transmissivity of only 1.3%. The study of Leitão et al. (2002) was carried out in dense forest, with a very dense canopy, whereas in the presented and in the above-mentioned studies there were forest clearings present which facilitate the penetration of the solar radiation, increasing the transmissivity. Rich et al. (1993), found mean PAR transmissivity of 1.5% in closed canopies and 9.7% in forests fragments with clearings. This information is important for understanding the partition of solar radiation in these ecosystems. Thus, admitting a reflection coefficient of 2.0% for PAR, according to study by Leitão et al. (2002); from our results it is possible to conclude that the studied forest fragment absorbs about 93.9% of the total PAR available.

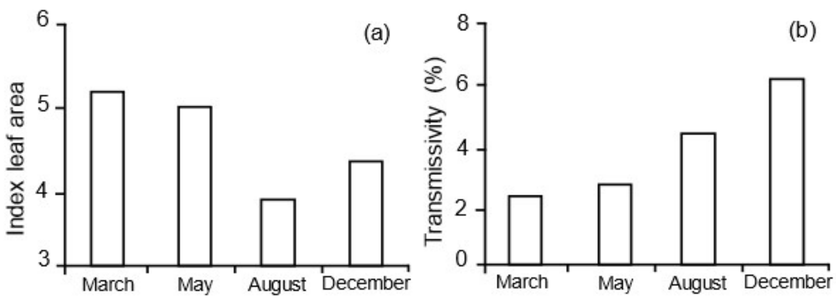

Figure 2 - Seasonal variation of the leaf area index (a) and the transmissivity of photosynthetically active solar radiation (b) in a secondary forest, in Viçosa, MG.

For a better understanding of the transmissivity of the forest canopy, Figure 3 shows the apparent trajectory of the sun.

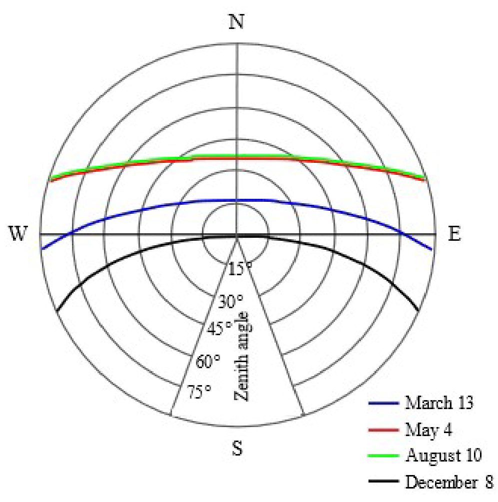

Figure 3 - Apparent trajectory of the sun on March 13, May 4, August 10 and December 8, in Viçosa, MG (latitude 20°45´ South).

The variation in LAI during the year is expected as a result of the loss of leaves in seasonal semi deciduous forest, in the cold and dry (winter) season. The highest LAI occurred in March (end of the rainy season), and the minimum value in August (end of the cold and dry season). The rainy season usually starts in October/November in this region, and due to that, the emission of new leaves occurs in November/December; therefore LAI was higher in December than in August. Also, the end of the rainy season occurs in March/April and the LAI starts to get smaller from this period onwards, as we observed in May (Figure 2a).

The previous results considered average values observed in all ten studied sites. However, due to the different LAI values and topographic conditions, such as slope, terrain exposure, a different variation of the solar radiation is expected. Analyzing each of the studied sites individually, it is noticed that there was a significant variation in the LAI values throughout the year for all the studied sites (Figure 4). The lowest LAI was observed in August, exactly coinciding with the dry and cold season of the year, for almost all sites. However, at sites 1, 4, 5, 8 and 9 there was no statistical difference between LAI in August and December. These results indicated that there was an influence of the topography of the sites on the LAI seasonal variation.

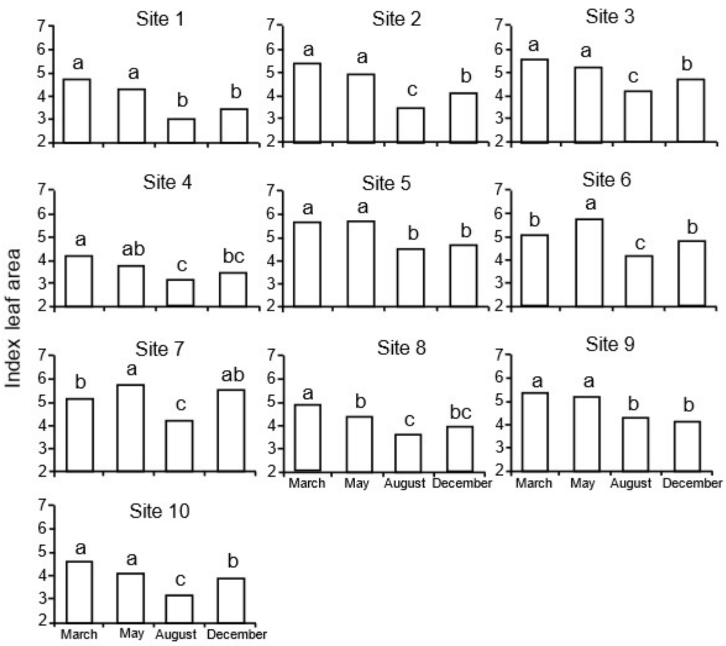

Figure 4 - Seasonal behavior of the leaf area index (IAF) in ten locations within a secondary forest, in Viçosa, MG (averages followed by the same letter in each graph do not differ by the Tukey test, at 5% of probability).

The sites with the lowest LAI had terrain exposure to the northeast (sites 1, 2 and 4), showed the greatest PAR transmissivity (Figure 5). For example, at site 1 the transmissivity increased significantly between May and August due to the decrease in LAI, which remained until December when the LAI was still low and the apparent path of the sun favored the penetration of the sun's rays. Similar results were observed at site 3, with small differences to the high LAI values. In the southwest-facing sites (sites 6, 7, 8, 9 and 10), the decrease in LAI in August did not contribute to the increase in PAR transmissivity, as the apparent path of the sun was facing the northern direction, making the solar radiation penetration in the forest canopy difficult. In these locations, transmissivity increased in December, when the sun showed a vertical movement (zenith angle close to zero) at noon. In any case, the influence of the apparent path of the sun was limited in places with the highest LAI (sites 1 and 4).

Our results suggest that it is important to consider the terrain exposure to the sun in the quantification of PAR transmissivity in mountainous forests. The variation of LAI and PAR transmissivity for sites 1, 2, 3 and 4 (Figures 6a and 6c, northeast-facing) and for sites 6, 7, 8, 9 and 10 (Figures 6b and 6d, southwest-facing), was similar throughout the year in both terrain exposure groups. However, on the northeast-facing group, the average LAI was 4.2 and, on the southwest-face group, it was 4.7. The northeast-facing group had a lower LAI and, also an apparent path of the sun more favorable to the penetration of the solar radiation in the canopy, presenting, consequently, a greater PAR transmissivity in relation to the southwest-facing group; the annual PAR transmissivity variation was also different in these groups. In the northeast-face group, the PAR transmissivity increased in August compared to May due to the decrease in the LAI in August in the northeastern areas compared to May, which remained high until December. For the southwest-facing group, the evident increase in PAR transmissivity occurred only in December, due to the apparent path of the sun.

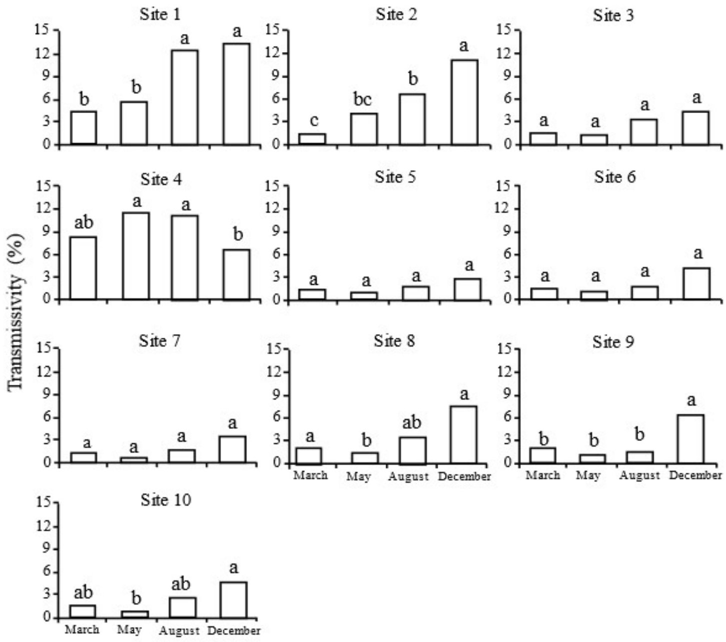

Figure 5 - Seasonal variation of the transmissivity of photosynthetically active solar radiation in ten locations within a secondary forest, in Viçosa, MG (averages followed by the same letter in each graph do not differ by the Tukey test, at 5% probability).

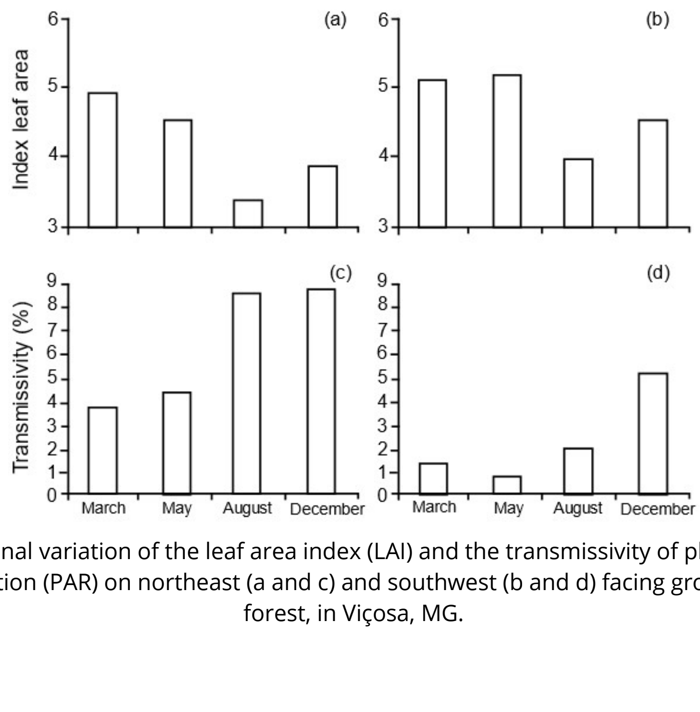

Figure 6 - Seasonal variation of the leaf area index (LAI) and the transmissivity of photosynthetically active solar radiation (PAR) on northeast (a and c) and southwest (b and d) facing groups, in secondary forest, in Viçosa, MG.

The temporal and spatial variation in PAR transmissivity is extremely important in the study of the dynamics of natural regeneration, since solar radiation affects the growth and development of plant species in the understory, as noted by Pariona et al. (2003), Carvalho et al. (2004) and Venturoli et al. (2010). The results indicated that the period of greatest carbon fixation by regenerating species probably occurs between October and December, due to the high PAR transmissivity.

The transmissivity of a forest canopy is closely linked to the LAI, since it determines the plant mass that will intercept, absorb or reflect the incident solar radiation, and locations with high LAI values usually transmit less energy, as shown in the studies by Coomes at al. (2009) and Russo et al. (2012). However, in our study the point with the maximum PAR transmissivity did not coincide with the minimum LAI value (Figure 2). We showed that the maximum value of PAR transmissivity occurred in December, when the issuance of new leaves promoted an increase in LAI. This occurred due to the apparent path of the sun, which varies throughout the year in the latitude where the studied forest fragment is located (Figure 3). On December 8, the sun has a vertical movement, with a zenith angle close to zero at noon, resulting in an increase in transmissivity. On March 13, with the increase in LAI and the sun showing a trajectory facing north again, the PAR transmissivity reached low values. On May 4 and on August 10, the sun trajectory is practically the same, remaining inclined towards the north, presenting, at noon, a zenith angle around 35°, which hinders the penetration of the sun's rays through the forest canopy.

The results showed that there was an influence of the terrain exposure, LAI and season on the PAR transmissivity of the studied forest canopy. This influence of the apparent path of the sun and the terrain exposure on the PAR transmissivity variation was also observed by Rich et al. (1993), inside a tropical forest in Costa Rica.

In the southern hemisphere where the forest fragment here studied is located, the higher the latitude, the more the sun has a northward trajectory; this variation occurs between the end of March and end of September. Results from Vianello & Alves (1991) showed that on winter solstice day (June 21), for example, the zenith angles, at noon, for latitudes 5, 15, 25, 35 and 45°, are respectively, 27, 37, 47, 58 and 70°, *i.e*. the higher the latitude in the higher the energy availability for the north-facing. Considering a latitude of 30° as the limit for the occurrence of tropical forests, the apparent path of the sun must be considered in studies of transmissivity of solar radiation, as it significantly influences the PAR regime, as shown in the present study. This heterogeneity of solar radiation in the understory was also evidenced by Lee (1987), Rich et al. (1993), Bellingham et al. (1996), Walter & Torquebiau (1997), Ohkubo et al. (2007) and Dong et al. (2012). The finding of spatial heterogeneity in energy availability is indicative of the existence of high plant species diversity among the studied sites, as detected by Volpato (1994), Fernandes (1998), Higuchi (2003), Silva (2003) and Garcia (2009).

CONCLUSIONS

The results of this study reveal that there is a spatial and seasonal variability of the LAI in the forest fragment. The seasonal variation in PAR in the understory vegetation was due to the LAI and the different slopes and terrain exposures. Spatial heterogeneity in PAR availability is indicative of high plant diversity in the forest fragment.

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