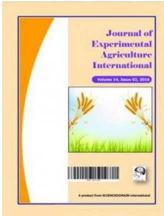

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Phenotypical Variability of Functional Groups of Plants in an Urban Rainforest

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Authors' contributions

This work was carried out in collaboration among all authors. Author MJHL managed the literature searches and wrote the first draft of the manuscript. Author VFS designed the study and performed the statistical analysis. Authors MAMS, ACBLES, AVFP, GHS, LMN, MMBA and ALAL revised the manuscript. Author MJNR performed the final approval of the manuscript.

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ABSTRACT

The functional characteristics of plants can be used to understand the changes of vegetation under different environmental pressures, since during the process of succession, the species deal with variations of luminosity, an important resource for the regeneration and growth of plants in humid tropical forests. From the perspective that along the succession there is variation of light availability and that leaf characteristics such as specific leaf area, chlorophyll content and leaf dry matter content are more plastic in groups linked to the rapid acquisition of the resource at the beginning of the succession, it was tested the hypothesis that at the beginning of the succession, where there is

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greater availability of light, leaf characteristics would be more plastic for the acquisitive group. It was initially found that the geographic distances did not influence the values of the variability indices of the groups, which allows to infer that the distance between the areas does not interfere in the variability of the leaf characteristics. To answer the hypothesis that at the beginning of the succession, in which there is greater light availability, the leaf characteristics would be more plastic for the purchasing group than for the conservative ones, a simple linear regression analysis (ARLS) was performed in the indices of variability for the groups (acquisitive and conservative) and abiotic factor (light) in each area of occurrence. However, the hypothesis that at the beginning of the succession, where there is greater light availability, the characteristics of the leaf would be more plastic for the species was rejected for the species acquisitive, since all indices were reduced for the purchasing group. It is important to take into account that the variation of leaf characteristics as a function of the light availability in an urban tropical fragment is different from what occurs in the classic succession commonly reported, pointing out that possible disturbances caused by the surroundings are the main agents of the functional structure of the community.

Keywords: Leaf characteristics; light; Atlantic rainforest; phenotypic plasticity.

1. INTRODUCTION

The evaluation of the functional characteristics of plants groups can be used to understand the changes of vegetation under different environmental pressures [1]. In forest environments, throughout the process of succession, the species deal with variations in the luminosity levels, an important resource for the regeneration and growth of plants in rainforests [2,3].

Plants respond to environmental variations through acclimatization (phenotypic plasticity) or adaptations (evolutionary response) [4]. Phenotypic plasticity is the ability to adjust the value of a given characteristic from a single genotype, according to changes in the environment within the individual lifetime, while the adaptations result from selective pressure variations along the gradient, able to produce hereditary differences among species, through evolution process [5,6,7].

The study of functional characteristics of plants has increased in recent years [8], the reason for this growth is due to the fact that these characteristics have effects on growth, reproduction and plant survival [9]. In this respect, different authors have discussed in detail the relations between physiological and ecological aspects of those characteristics [10,11]. The most abundant species in environments with greater light availability are characterized by rapid growth, low wood density, leaves with a short life cycle, high values of specific leaf area, chlorophyll content and low dry matter content. The conservative ones have greater abundance in areas with less light availability and are characterized by higher heights, stems with denser wood, leaves with longer life, high investment in dry matter, low chlorophyll content and specific leaf area [12,13].

Although the most studies focus on interspecific variation [14,15], it is understood that knowing the intraspecific variation can help to better understand the formation of communities [16,17,18,19]. The knowing role of variation within the groups of acquisitive and conservative tree species can help to understand the processes that lead to the formation and the functioning of the communities [20,21,8].

Ideally, studying intraspecific variation throughout the succession would be the ideal condition, but hardly is found species present in all successional stages, so is chosen to study the variations of the characteristic values in groups of species with quite different functional strategies, the acquisitive and conservative. These strategies are widely recognized and confirmed by the literature, especially with regard to the change of abundance of their populations throughout the succession [13,22,23,24,25].

Assuming that there is variation in light availability throughout the succession, leaf characteristics such as specific leaf area, chlorophyll content and leaf dry matter content are more plastic in groups linked to the rapid acquisition of the resource at the beginning of the succession [26,27]. In this study, was studied four areas of tropical rainforest located in a basal area gradient as a successional gradient evaluated in [28]. We hypothesized that at the beginning of the succession, where there is greater availability of light, leaf characteristics would be more plastic for the acquisitive group. If this is true, greater plasticity is expected in leaf dry matter content, specific leaf area and chlorophyll content in the species of the acquisitive group in environments with greater light availability.

2. MATERIALS AND METHODS

2.1 Study Area

The research was carried out in the Dois Irmãos State Park (PEDI), located northwest of the municipality of Recife-PE, between coordinates 7°57'21"and 8° 00'54"S; 34° 55'53"and 34° 58'38" W. In the area predominates Ombrophilous Dense Lowland vegetation [29], with geological formation Barriers and soils of the podzolic type, with subordinate latosols, usually sandy-clayey, ranging from deep to very deep, and the soil acidity varies from medium to high [30] The local climate is As' type (tropical humid or tropical coastal), with average monthly temperatures above 23ºC, average annual rainfall of 2460 mm and rainy season in the autumn-winter period [31].

2.2 Assembly of Plots, Inclusion Criterion and Floristic List

In the PEDI area, a module of the Biodiversity Research Program (PPBio), Mata Atlântica Network, is installed using the RAPELD method: consisting of a combination of Rapid Inventory (RAP) and ecological long-term research (PELD) [32]. The method consists in the opening of two straight trails of 5000 m of extension, parallel with distance of 1000 m to each other, along which sampling plots are installed according to standard protocol [32].

From the two trails installed by the PPBio researchers, was selected one, in which was analyzed four plots (250 × 40 m) each, distancing 1000 m from each other, totaling four areas. Was assume that these four areas represent different successional stages depending on the variation of the basal area [28]. Thus, was hypothesized that there is variation in light availability throughout the sequence.

For each plot, a 250 m corridor was installed, following the ground level curve, according to the protocol defined by [33]. Within each hectare 20 plots of 10 × 20 m without overlap were selected, where botanical samples were collected from all plants with stem diameter at breast height (DBH) ≥ 5 cm. Only the functional characteristics of the species present with five or more individuals in the four areas were collected.

All botanical material was identified, following the classification system [34] and deposited in the Vasconcelos Sobrinho Herbarium (HVS) at Rural Federal University of Pernambuco (UFRPE).

2.3 Light Data Collection

The total radiation (luminosity) was obtained in each of the 80 plots of 10 × 20 m drawn (20 per area). Initially hemispheric photos were taken in the center of each plot with a Nikon D50 camera with a hemispherical lens (Nikon DX 18-105 mm adapted fisheye 67-58 mm) on a tripod adjustable to one meter above the ground, horizontally leveled, positioned with the upper part aligned with magnetic north. The photographs were taken between August and December 2015, between 8:30 and 11:00 hours [35]. The image processing was done with the GLA software (Gap Light Analyzer) version 2.0 [36], in order to obtain the total radiation that crosses the canopy (luminosity).

2.4 Identification of Functional Groups

Considering that there is greater leaf plasticity in groups of species linked to the fast use of resource in environments with greater light availability, was chosen to test species with acquisitive and conservative strategies in the four areas, since these strategies are more easily identified. For this, was studied 10 functional characteristics (leaf, stem and root) of the 41 species evaluated in [28] as follows: 1) was performed a hierarchical clustering analysis based on the abundance of the 10 functional characteristics, based on the Gower dissimilarity matrix [37]. There was no phylogenetic signal for functional characteristics throughout the succession according to [28]. A nonparametric multivariate analysis of variance (PERMANOVA) was then performed to verify the optimal number of groups. The choice of the best number of groups was one in which the increase in the amount of variance was higher than 15% [38]. It is important to note that average values of all 10 characteristics (leaf, stem and root) were used in all four areas to identify the formation of both groups (acquisitive and conservative).

Plants with high chlorophyll content, higher specific leaf area, leaf area, low dry matter content [39], less dense stem and root woods, higher amount of saturated water and lower contents of dry matter [40,41,42], are related to the acquisition group resource and dominate in areas at the beginning of the succession, while plants that present low content of chlorophyll, specific leaf area, leaf area, higher dry matter content, denser stem and root woods, less saturated stem and root water and higher dry matter contents of stem and root [12] predominate in environments related to conservative use. The hierarchical cluster analysis and PERMANOVA were performed with the "ggplot2", "ggdendro", "vegan" and "cluster" packages in R [43]. As results, 13 species were identified and nine were conservative.

It is known that studying phenotypic plasticity throughout the succession would be an ideal condition, but hardly is found species in all successional stages, so was chosen to study the variations of the characteristic values in groups of species with very different functional strategies (acquisitive and conservative). For this was used the standard deviation because it is considered as a measure of dispersion around the population mean of a random variable and for indicating the degree of variation of a set of elements. Based on the characteristic values (TMSF, AFE and Cc_mass) was calculated the standard deviation of each group of species present in each area. Was considered only the species that presented standard deviation of 0.1. While species that exhibited values below or above 0.1 was not used to avoid outliers in the results. The literature reports that the standard deviation is considered an important characteristic of the normal distribution, since species with a deviation of 0.1 their characteristics tend to be closer to the mean (Table 1).

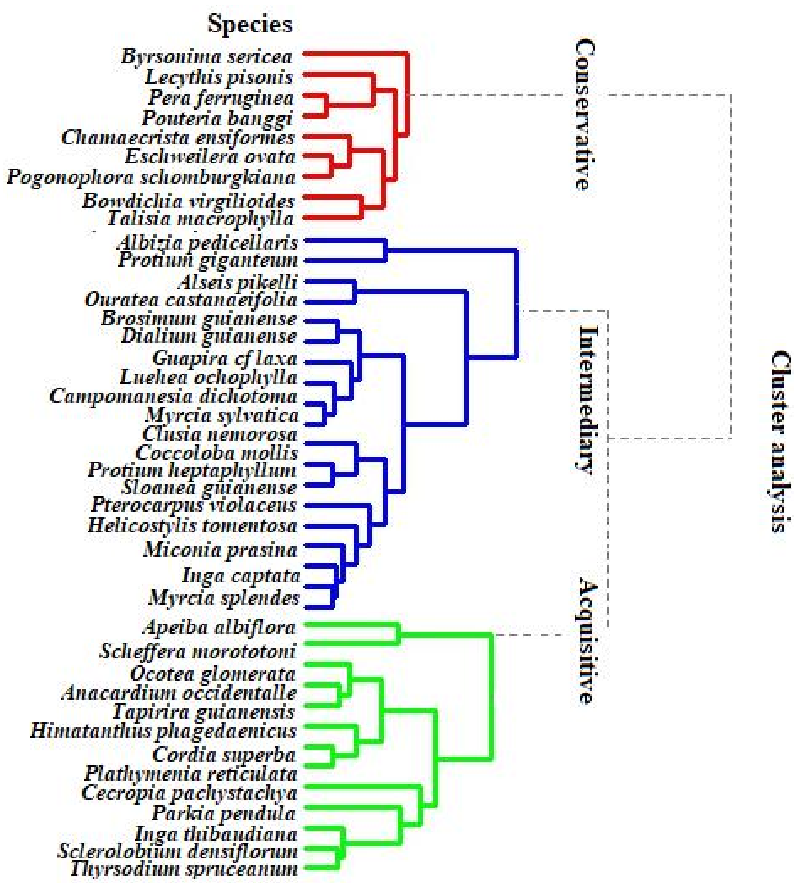

Fig. 1. Hierarchical cluster analysis performed by the ward method for the 41 species revealed that the optimal number of groups of strategies was three (k = 3), with R^2 = 0.54, studied in the four areas of an urban forest fragment
Source: Leite MJH (2017)

Table 1. Standard deviation of the functional characteristics of the acquisitive and conservative species in the four areas of a fragment of urban forest

Acquisitive species					Conservative species				
Areas	**Species**	**Standard deviation**			**Areas**	**Species**	**Standard deviation**		
		AFE	**TMSF**	**Cc_mass**			**AFE**	**TMSF**	**Cc_mass**
$A1_{>AB}$	*Inga thibaudiana* DC.	0.1359	0.0606	0.1088	$A1_{>AB}$	*Bowdichia virgilioides* Kunth	0.1282	**0.0660**	**0.0573**
	Ocotea glomerate (Nees) Mez	**0.0780**	**0.0416**	**0.0474**		*Eschweilera ovata* (Cambess.) Mart. ex Miers	0.1751	0.1024	0.1770
	Parkia pendula (Willd.) Benth	0.1867	0.1451	0.1887		*Pogonophoraschom burgkiana* Miers ex Benth.	0,1870	0.1477	0.1885
	Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	0.1224	0.0679	0.1202		*Pouteriabanggi*(Rusby) T.D. Penn.	0.1476	0.1568	0.1549
	*Sclerolobiumdensiflorum (*Benth.)	0.1706	0.1746	0.1032		*Talisia macrophylla* (Mart.) Radlk.	**0.3925**	**0.8205**	**0.2416**
	Thyrsodiumspruceanum (Benth).	**0.0475**	**0.6173**	**0.7788**					
$A2_{ABI}$	*Anacardium occidentalle* L.	0.1596	0.1970	0.1469	$A2_{ABI}$	*Bowdichia virgilioides* Kunth	**0.8704**	**0.4118**	**0.0210**
	*Cecropia pachystachya*Trécul	0.1278	0.1887	0.1293		*Byrsonima sericea* DC.	0.1470	0.1853	0.1459
	Cordia superba Cham.	0.1807	0.1819	0.1324		*Eschweilera ovata* (Cambess.) Mart. ex Miers	0.1232	0.1245	0.1357
	Himatanthusphagedaenicus(Mart.) Woodson	0.1460	0.1200	0.1294		*LecythisPisonis Cambess.*	**0.3129**	**0.0791**	**0.0998**
	Plathymenia reticulata Benth.	0.1244	0.1023	0.1802		*Peraferruginea* (Schott) Müll. Arg	0.1360	0.1054	0.1126
						Pogonophoraschom burgkiana Miers ex Benth.	0.1155	0.1047	0.1797
	Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	0.1063	0.1804	0.1304	$A3_{ABI}$	*Bowdichiavirgilioides* Kunth	0.7810	0.0705	**0.0219**
	Tapiriraguianensis Aubl.	0.1038	0.1390	0.1397		*Byrsonima sericea* DC.	0.1245	0.1031	0.1264
	Thyrsodium spruceanum Benth.	**0.1170**	**0.0181**	**0.0397**		*Chamaecrista ensiformes* (Vell.) H.S.Irwin & Barneby	0.1262	0.1026	0.1302

Acquisitive species					Conservative species				
Areas	**Species**	**Standard deviation**			**Areas**	**Species**	**Standard deviation**		
		AFE	**TMSF**	**Cc_mass**			**AFE**	**TMSF**	**Cc_mass**
$A3_{ABI}$	*Apeiba albiflora* Ducke	0.1380	0.0660	0.1214		*Eschweilera ovata* (Cambess.) Mart. ex Miers	0.1349	0.1208	0.1582
	Cecropia pachystachya Trécul	0.1409	0.1377	0.1296		*Lecythis Pisonis* Cambess.	**0.8827**	**0.5922**	**0.3496**
	Ocotea glomerate (Nees) Mez	**0.0519**	**0.0344**	**0.0422**		*Pera ferruginea* (Schott) Müll. Arg	0.1406	0.1306	0.1876
	Plathymenia reticulata Benth.	0.3646	0.1417	0.1494	$A4_{<AB}$	*Pogonophoraschom burgkiana* Miers ex Benth.	0.1761	0.1348	0.1312
						Chamaecrista ensiformes (Vell.) H.S. Irwin & Barneby	0.1551	0,1977	0.1713
						Peraferruginea (Schott) Müll. Arg	0.1368	0.0503	0.1296
						Pogonophoraschom burgkiana Miers ex Benth.	0.1285	0.1345	0.1502

DP_AFE – Standard deviation of the leaf area, DP_TMSF - Standard deviation of leaf dry matter, DP_Cc_mass - Standard deviation of chlorophyll content, $A1_{>AB}$ (area with greater basal area), $A2_{ABI}$ (basal intermediate area), $A3_{<AB}$ basal area) and $A4_{<AB}$ (area with the lowest basal area)

Table 2. List of functional characteristics analyzed in an urban Rainforest fragment, adapted from [47]

Functional feature	Description	Functional relationship
AFE	Specific leaf area (AF / PS) Dry matter content of leaf (PUF-PSF)	Photosynthetic rate, leaf longevity, relative growth rate
TMSF	Chlorophyll Concentration	Resistance to physical hazards (herbivory)
Cc_mass	(Cmassa, chlorophyll content * (AFE / 10000)	Photosynthetic process, acting in the conversion of light energy into chemical energy

AFE - specific leaf area ($cm^2.mg^{-1}$); CC_mass - concentration of chlorophyll ($micromol.g^{-1}$); TMSF - leaf dry matter content ($mg.g^{-1}$)

2.5 Functional Characteristics

From the 10 characteristics studied in [28], only three foliar characteristics were studied because they are considered very plastic: specific leaf area, chlorophyll content and leaf dry matter content [26,27,44] in the 22 species selected in the two groups, nine conservative and thirteen acquisitive. The data collection occurred in five individuals per species. From each individual, 10 mature leaves were collected at the intermediate height of the crown (exposed to the sun), without evident symptoms of pathogen or herbivore attack [39]. For the determination of the leaf area (FA), the "Image-Tool" program was used [45]. The specific leaf area (AFE) was the ratio between leaf area and dry weight (Table 2).

The chlorophyll content in the leaves was measured with the aid of a SPAD chlorophyll meter (Minolta SPAD 502 D Sprectrum Technologies Inc., Plainfield, Il, USA). The content of chlorophyll by mass was determined by the following formula: (Cmassa; Chlorophyll content* (AFE / 10000 [46])). After rehydration, the leaves were weighed in an analytical scale to obtain the saturated weight of water. They were then scanned for leaf area measurement using the computer program "Image-Tool" [45].

2.6 Phenotypic Plasticity

Was calculated the phenotypic plasticity index proposed by [26] for three leaf characteristics (AFE, Cc_mass and TMSF) of the 13 species of the group of the acquisitive and nine conservative species, in each of the four areas. This index can vary from zero to one, with IP 1 inferring high plasticity. In order to calculate the IP, the following formula was used: IP = maximum average value - minimum average value / maximum average value of each characteristic for each group of acquisitive and conservative species in each area.

2.7 Data Analysis

In order to verify if the phenotypic plasticity indices of the two groups of species were influenced by the geographic distances, was used the Mantel Partial test in each of the 80 plots drawn (20 per area).

The Mantel Partial test and simple regression analysis were performed using the nortest, vegan and APE packages in the R environment version 3.0.2 [43].

To test the hypothesis that at the beginning of the succession, where there is greater light availability, leaf characteristics would be more plastic for the acquisitive group, a simple linear regression analysis (ARLS) was performed, on the plasticity indices of the groups (acquisitive and conservative, response variables) and abiotic factor (light) in each area.

3. RESULTS

According to the Partial Mantel test, the geographic distances did not influence the values of the plasticity indices of the groups ($r = -0.2977$; $p = .001$). This result allows to infer that the distance between the areas does not interfere in the plasticity of the foliar characteristics.

To test the hypothesis that at the beginning of the succession, where there is greater light availability, leaf characteristics would be more plastic for the acquisitive group, was performed a simple linear regression analysis between the light percentages and the plasticity indices of the two groups of species with and conservative strategies (Fig. 2).

The results of this analysis revealed that within the acquisitive species, as the light percentages

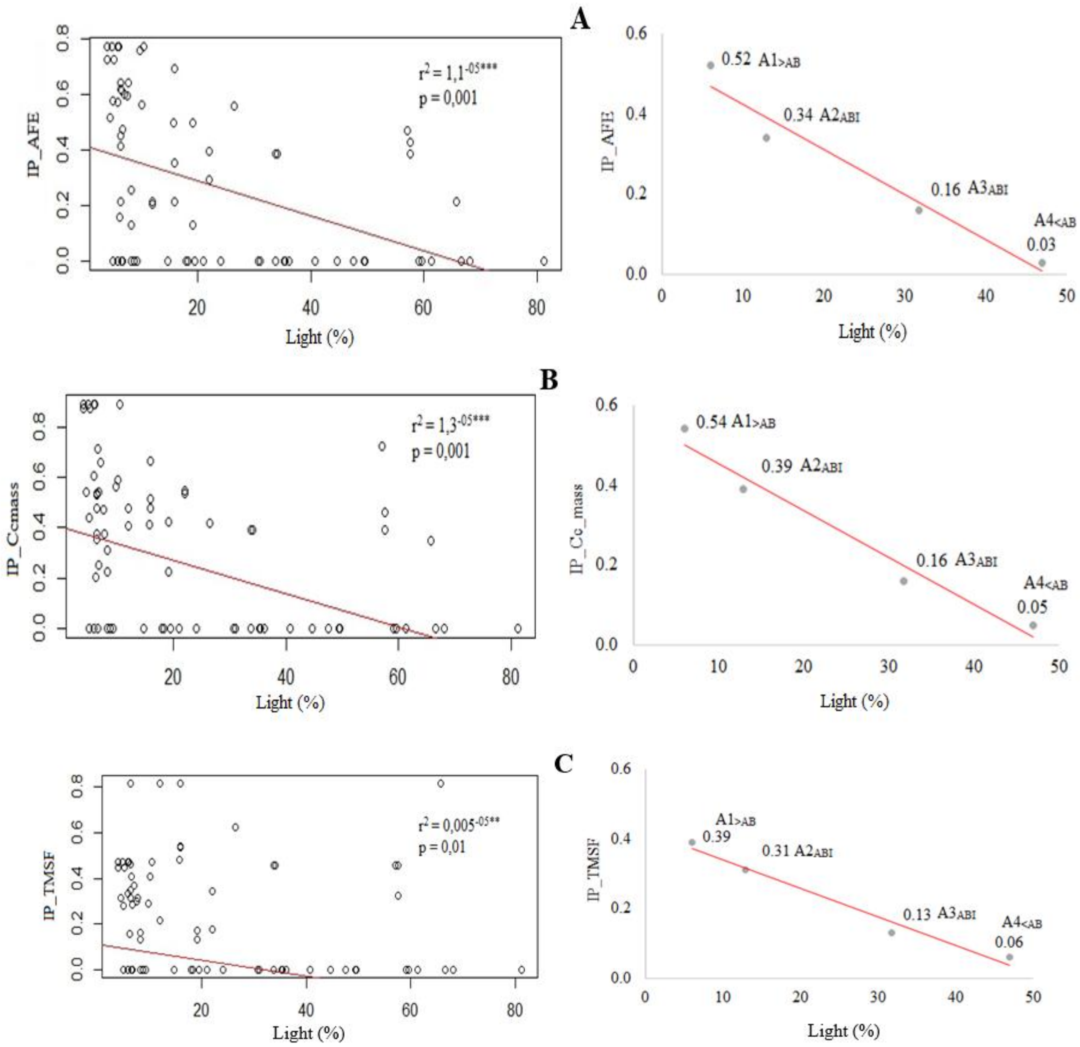

Fig. 2. Simple regression analysis between light percentages and phenotypic plasticity indices of the group with acquisition strategy in the four areas of a fragment of urban Rainforest. A, B and C (purchasing group). IP_AFE (specific leaf area index), IP_Cc_mass (plasticity index of chlorophyll content), IP_TMSF (leaf dry matter content plasticity index)

IP_AFE - IP of specific leaf area (acquisition group, A), IP_ Cc_mass - IP of chlorophyll content by mass (acquisitive group, B), IP_TMSF - IP of leaf dry matter content (acquisitive group, C), IP_ Cc_mass - IP of chlorophyll content (conservative group, D). (Area with the lowest basal area), A2ABI (intermediate basal area), A3 <AB (intermediate basal area) and A4 <AB (area with the lowest basal area). F values were obtained with ANOVA (= P <.05; ** = P <.01; *** = P <.001)*

increased throughout the succession, all leaf characteristics (IP_AFE, IP_Cc_mass and IP_TMSF) presented lower plasticity (Fig. 2). In relation to the conservative group, was observed no relation with the abiotic light factor in the succession.

Was observed that the acquisitive group presented lower values of IP_AFE (0.03), IP_Cc_mass (0.05) and IP_TMSF (0.06) in the initial phase of the succession (A4 <AB), environment with higher incidence of light (46.97%). In the environment with less light (6.09%, A1 <AB) this group was more plastic, with higher value of IP_AFE (0.52), IP_Cc_mass (0.58) and IP_TMSF (0.31). Thus, was rejected the hypothesis that at the beginning of the succession, where there is greater availability of light, leaf characteristics would be more plastic for the acquisitive group (Fig. 2).

4. DISCUSSION

The hypothesis that at the beginning of the succession, where there is greater light availability, leaf characteristics would be more plastic for the acquisitive species was rejected. Since, as the light availability within the acquisitive group increased, the plasticity indices of the characteristics such as TMSF, AFE and Cc_mass decreased. It is important to emphasize that although these characteristics are highly plastic in more open environments, their plasticity may have been reduced due to the constant perturbations in the area, especially in the environment with a higher incidence of light (46.97%, A4 <AB). Lower AFE and Cc_mass values were found in the more open area (A4 <AB), which expected higher values. These results point to the hypothesis that because these characteristics are highly plastic, especially in more open environments, the anthropic actions occurred in this area, caused that these characteristics did not suffer increase of their values. Is worth to mention that the species occurring in these environments present a short life cycle, colonize faster, invest more in height and present high mortality, leading species of these environments to be more susceptible to changes.

While the areas with lower incidences of light (A1> AB, 6.09% and A2ABI, A3ABI 12.94%), the values of those characteristics increased as they decreased light availability, contrary to expectations. It is possible to hypothesize that this increase in plasticity in these areas has occurred because species that grow in shaded environments experience several ontogenetic changes in relation to low irradiance during the life cycle and therefore may demonstrate greater plasticity in such characteristics.

According to [48,26], the plasticity of physiological characteristics are more plastic in open environments, because they present rapid responses in the short term in relation to the availability of the resource. However, there is evidence to suggest that the adjustments are not necessarily related to the successional status of species [49,50].

For [51,52] phenotypic plasticity is more observed in seedlings, especially in the pioneer ones, because they are more prone to acclimatization. On the other hand, [53] observed that the leaf plasticity of pioneer species may be lower in shaded environments, because they cannot survive long in this environment.

It is important to mention that, although the foliar characteristics are highly plastic in more open environments, the plasticity can be reduced by the perturbations occurring in the area where is found [54,55]. What could be proven with the results found in the present research (lower IP_AFE, IP_Ccmass and IP_TMSF) in the environment with greater incidence of light. The perturbations occurred in the area may have contributed to this reduction of plasticity (Leite et al., 2019), is important to note that species occurring in these environments present a short life cycle, being more susceptible to changes in their values. For [56,57] both conservative and acquisitive species can be plastic in characteristics important for its functions. These authors also observe that groups of species adapted to high irradiation may have greater plasticity in leaf characteristics related to photosynthesis, such as nitrogen content and that shade tolerant species may present greater plasticity in specific leaf area and chlorophyll content.

5. CONCLUSIONS

Different from what is expected, at the beginning of the succession, where there is greater availability of light, the leaf characteristics would be less plastic for the acquisitive group, this disturbances could change the classical path of succession in function of population dynamics, especially in the area with greater light availability, which probably led to higher plant mortality of the acquisition group, as a result, the variability of $A4_{<AB}$ leaf characteristics decreased.

This research showed that the variation of leaf characteristics, as a function of the light availability, in an urban Rainforest fragment is different from what occurs in the classic succession commonly reported, pointing out that possible disturbances caused by the surroundings are the main agents of the functional structure of the community.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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