

Contribution of *Pseudobombax aff. petropolitanum* to Nutrient Cycling in Woody Vegetation from a Neotropical Inselberg

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Abstract

The aim of the study was to investigate *Pseudobombax aff. petropolitanum* (PP) contribution on annual fine litterfall, carbon content, and nutrient concentration, compared to other woody species (OS) on a neotropical inselberg in Espírito Santo state, Brazil. Annual fine litterfall was systematic monthly collected (November 2011–October 2012) by means of 15 littertraps (0.25 m²) placed in five transects, oven-dried (65 °C, 72 h), weighed, and C content and nutrients concentration (N, P, K, Ca, Mg, S, B, Cu, Fe, Mn, Zn) were estimated. PP performed lower litterfall, C content, and nutrient concentration excepting higher K concentration, compared to OS. The results suggested that PP performed higher nutrient conservation, which indicated its potential in restoring degraded areas observed in the inselberg.

Keywords: Atlantic Forest, ecosystem functioning, litterfall, rocky outcrop, rupestrian ecosystem.

1. INTRODUCTION AND OBJECTIVES

Inselbergs are Precambrian granitic and gneissic rocky outcrops, usually monolithic and are critical spots for conservation of plant diversity (Porembski, 2007; Hopper *et al.*, 2016). In southeastern Brazil, inselbergs within the Atlantic Rainforest biome represent a global hotspot of rupicolous plants, whose beta diversity, i.e., species turnover between individual inselbergs, is unusually high due to high degree of habitat specialization even when comparing inselbergs in the same region that increase as the geographical distance increases (Porembski, 2007; Couto *et al.*, 2016; Pinto-Junior *et al.*, 2020).

In general, soils on inselbergs are poorly developed, shallow, highly susceptible to leaching, and characterized by coarse sandy texture, high levels of exchangeable aluminum, low nutritional quality, and variable levels of organic matter (Benites *et al.*, 2007).

The development of different types of plant communities on inselbergs (see Porembski 2007), which includes woody vegetation characterized by high light demands, presence of low trees and shrubs, adapted to shallow soils and with poor water and nutrients retention (Francisco *et al.*, 2018; Couto *et al.*, 2022) naturally depends, among other factors, on nutrient cycling.

Nutrient cycling is an important soil entry route for nutrients derived from senescent plant material, and studies have focused on litterfall and its nutrient concentration in forest ecosystems, such as Ombrophilous Forest (Bianchin *et al.*, 2017; Camara *et al.*, 2018a; 2018b), Semideciduous Forest (Scheer *et al.*, 2011; Machado *et al.*, 2018; Carvalho *et al.*, 2019; Dick & Schumacher, 2020; Menezes *et al.*, 2020; Câmara *et al.*, 2021; Lagemann *et al.*, 2022), and Deciduous Forest (Schumacher *et al.*, 2018; Araújo *et al.*, 2020). Regardless of the forest typology being subject to greater or lesser seasonality, climate conditions influence nutrient cycling (Scheer *et al.*, 2011; Bianchin *et al.*, 2017; Dick & Schumacher, 2020).

However, these relevant key issues for the general understanding of inselberg functioning besides studies on C stock estimates, have been neglected, with only one published study focusing on accumulation of litter on topsoil and its nutrient concentration (Freitas *et al.*, 2015). Furthermore, such research can support the development of strategies aimed at the management, conservation, and restoration of degraded areas, especially by mined land, commonly found in Espírito Santo (Couto *et al.*, 2017), besides deforestation, induced fires, and uncontrolled tourism (Benites *et al.*, 2007).

Generally, a high abundance of a particular species is an indication of its nutrient cycling efficiency, a necessary characteristic for the sustainable development of ecosystems. Studies reported a high abundance of the lithophytic endemic *Pseudobombax* aff. *petropolitanum* A. Robyns (Malvaceae: Bombacoideae) in woody inselberg vegetation at Atlantic Forest of Espírito Santo state (Couto *et al.*, 2017, 2019, 2022; Francisco *et al.*, 2018), from now on, PP. The PP is endemic to inselbergs of Rio de Janeiro and Espírito Santo States (Carvalho-Sobrinho & Yoshikawa 2022), and functions as a nucleus of biodiversity expansion in this ecosystem (Couto *et al.*, 2016, 2017, 2019, 2022; Francisco *et al.*, 2018). In the municipality of Mimoso do Sul, Espírito Santo, 105 species of vascular epiphytes were observed colonizing thick and exposed roots on the rocky surface and horizontal branches of PP, which can reach a height of 15 m (Couto *et al.*, 2016, 2019), with one single PP individual contributed 46 % of the total wealth of the epiphytic community (Francisco *et al.*, 2018).

This study provides important contributions to the understanding of the dynamics of fine litterfall and nutrients concentration by woody vegetation on a neotropical inselberg. This study aimed to investigate PP contribution on annual fine litterfall, carbon content, and nutrient concentration, compared to other woody species (OS) on a neotropical inselberg in Espírito Santo state, Brazil. We tested the hypothesis that the local abundance of PP is a function of adaptive mechanisms such as low litterfall and low nutrient concentration due to high nutrient conservation.

2. MATERIALS AND METHODS

This study was conducted in an area of inselberg woody vegetation on an ancient relief, naturally isolated landform, with very shallow soil, classified as humic Litholic Neosol, currently surrounded by forest fragments (Montane Seasonal Semideciduous and Dense Ombrophilous Forests), agricultural crops, mainly *Coffea arabica* L., and threatened by the ornamental stone mining industry (Couto *et al.*, 2016, 2017, 2019). The montane inselberg is locally known as “Afloramento do Toti” (20°56'18"S 41°32'38"W), which covers an area of about 2.5 ha at elevations ranging from 700 to 780 m a.s.l. on Pedra dos Pontões, municipality of Mimoso do Sul, Espírito Santo State, Brazil (Figure 1A, 1B, and 1C).

Pedra dos Pontões has a high richness and diversity of endemic endangered species, besides low similarity in terms of floristic composition when compared to other inselbergs in state (Couto *et al.*, 2017; Pinto-Junior *et al.*, 2020), for which it has been recognized as a priority conservation area (Couto *et al.*, 2016, 2017). The inselberg woody vegetation has a prominent presence of sparse stands of PP (Figure 1D), with some tall individuals for the area (average height of 7.7 m ± 3.3 and average diameter at breast height of 46.4 cm ± 31.9), forming small groups in some cases (Couto *et al.*, 2016).

For the physical-chemical characterization of the soil, a total of 20 samples were collected, at a depth of 10 cm, four per transect. The samples were homogenized, and the air-dried fine earth prepared in the laboratory. We proceeded to the followed soil analyzes (Silva, 2009): pH (in water - 1:2.5 ratio) was 4.5, the concentrations of P, K, and Na were 32, 76, and 7 mg dm⁻³, respectively, the concentrations of exchangeable Ca, Mg, Al, and H+Al were 0.5, 0.3, 1.4, and 12.8 cmol_c dm⁻³, respectively, the concentrations of exchangeable Fe, Cu, Zn, and Mn were 44, 0.2, 1.6, and 5 mg dm⁻³, respectively. The effective Cation Exchange Capacity (CEC) was 2.4, the CEC pH 7 was 13.8, the sum of bases was 1 cmol_c dm⁻³, the base saturation index was 7.4, and aluminum saturation index was 57.1 %.

According to the Köppen classification, the climate of the study area is Cwb, characterized by cold and dry winters and wet summers (Alvares *et al.*, 2013). Climatic data during the study period (from November 2011 to October 2012), were collected by the Alegre Meteorological Station which is situated at a straight-line distance of 18 km from the study site and obtained from the National Institute of Meteorology website. In this period, the monthly average temperature varied from 20.3 °C (August, winter) to 26.8 °C (February, summer), and the accumulated precipitation varied from 10.2 mm (July, winter) to 258.2 mm (December, summer) (Figure 2).

Figure 1. Location of the study area in relation to South America, Brazil, Espírito Santo State (A), and municipality of Mimoso do Sul (B). Field photograph of inselberg woody vegetation (C) and *Pseudobombax* aff. *petropolitanum* flowering (D). Photos by Dayvid R. Couto.

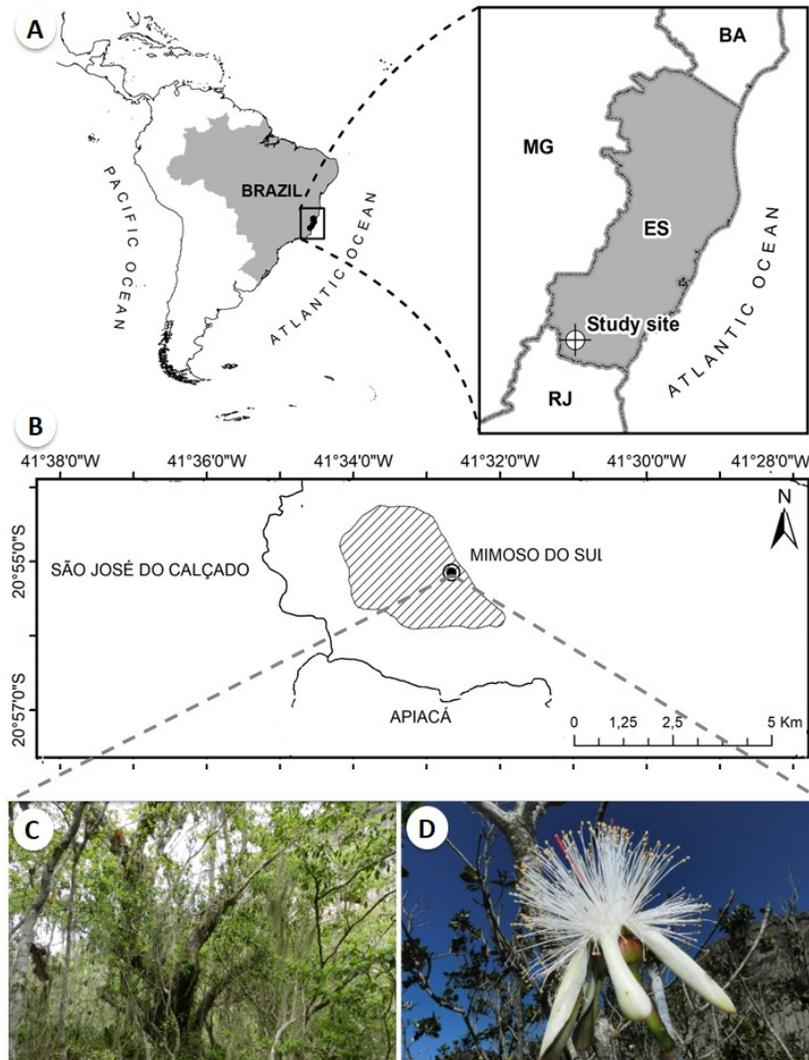
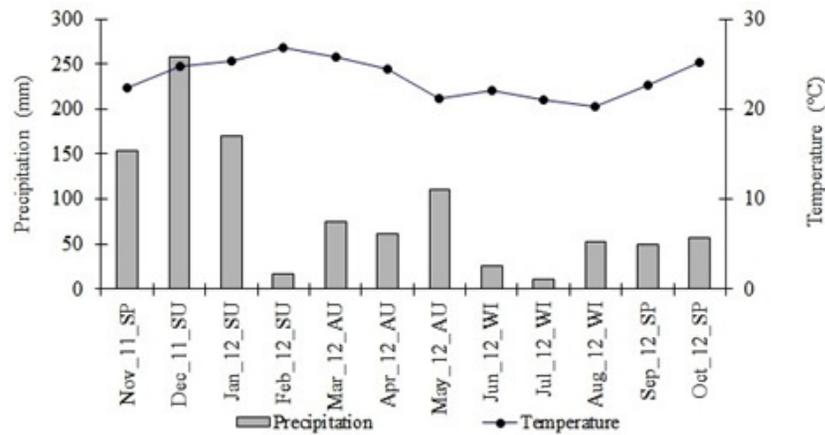


Figure 2. Monthly accumulated precipitation and mean temperature from November/2011 to October/2012, in Mimoso do Sul, Espírito Santo State, Brazil. Source: National Institute of Meteorology website. Spring (SP), Summer (SU), Autumn (AU), Winter (WI).



The annual accumulated precipitation and mean annual temperature were 1,038.80 mm and 23.5 °C, respectively (Figure 2). The maximum accumulated precipitation (approximately 445.0 mm) was registered in summer, intermediate values (260.6 mm and 245.2 mm) were observed in spring and autumn, respectively, and the minimum value (88.0 mm) in winter. The highest average temperature (approximately 25.7 °C) was verified in summer, followed by intermediate values registered in autumn and spring (23.8 °C and 23.4 °C, respectively), and the lowest value (21.1 °C) in winter.

Fine litterfall was systematic monthly collected from November 2011 to October 2012 along five transects (2 m × 50 m) spaced 10 m apart from each other on the northeastern slope of the inselberg. In each transect (pseudo-replicate) were placed five 0.70 m high wooden frames measuring 0.50 m × 0.50 m (0.25 m²), with a 2 mm mesh nylon screen at the bottom, approximately 25 m apart from each other, totaling 15 collectors.

All collected material was stored in plastic bags. At the laboratory, the material was transferred to paper bags, dried in an air-circulating oven (65 °C, 72 h), individualized into the fractions: (i) litterfall from PP and (ii) litterfall from OS (*sensu* Francisco *et al.*, 2018), and weighed to the nearest 0.01 g on a precision balance to obtain the litterfall dry biomass (kg ha⁻¹). OS included the terrestrial/hemiepiphyte species *Oreopanax capitatus* (Jacq.) Decne. & Planch. (Araliaceae), terrestrial/rupicolous species *Clusia mexiae* P.F.Stevens (Clusiaceae), *Eremanthus crotonoides* (DC.) Sch. Bip. (Asteraceae), *Eugenia brasiliensis* Lam. (Myrtaceae), *Guapira opposita* (Vell.) Reitz (Nyctaginaceae), *Handroanthus* sp. (Bignoniaceae), the terrestrial species *Croton floribundus* Spreng. (Euphorbiaceae) and *Vernonanthura polyanthes* (Sprengel) Vega & Dematteis (Asteraceae). Both fractions include the respective leaves, branches, reproductive structures (flowers, fruits, seeds), bark, and other plant residues.

Subsequently, samples were ground in a Wiley-type mill and stored in plastic bottles. Samples from three transects were randomly chosen monthly and subjected to analyses of macronutrient (N, P, K, Ca, Mg, and S) and micronutrient (B, Cu, Fe, Mn, and Zn) concentration (g kg⁻¹ and mg kg⁻¹, respectively) (Tedesco *et al.*, 1995; Miyazawa *et al.*, 1999). B was extracted by dry digestion and the other nutrients by wet digestion. N concentration was determined by the Kjeldahl method; P, S, and B concentrations by UV-Vis spectrophotometry; and K, Ca, Mg, Cu, Fe, Mn, and Zn concentrations by atomic absorption spectrophotometry. We considered C content is 47.0 % of the dry necromass (Martinelli *et al.*, 2017).

The data were individualized in seasons (spring: September, October, and November; summer: December, January, and February; autumn: March, April, and May; winter: June, July, and August), following the methodology of other studies (Bianchin *et al.*, 2017). The interaction effects between season

(spring, summer, autumn, winter) and litterfall fraction (PP, OS) were investigated within five pseudo-replicates for both litterfall and C content, and three pseudo-replicates for nutrient concentration.

Data were subjected to Repeated Measures Analysis of Variance (ANOVA), in which sampling periods (four seasons; within-subjects factor or within effects) and litterfall fractions (between-subjects factor or between effects) were considered as sources of variation. To evaluate the isolated effects of litterfall fraction on the variables, the homogeneity of variance was tested by Levene's test. When homoscedasticity assumptions were met, means were compared by the parametric Fisher's least significant difference test; otherwise, means were compared by the nonparametric Mann-Whitney *U*-test. Those univariate analyses were performed using Statistica version 8.0 (StatSoft, Inc., Dell, Tulsa, USA) considering *P* < 0.05 as significant.

Multivariate analyzes were also performed, using the PAST software version 2.17c, to carry out a global analysis in which all variables were considered. In this sense, the principal component analysis allows the recognition of association between the litterfall fractions within seasons and a large set of variables, while the hierarchical clustering by using the Gower coefficient allows to identify dissimilarities between de litterfall fractions within the seasons.

3. RESULTS

Litterfall occurred throughout the annual period, with maximum monthly values in March 2012 (autumn) for both fractions (PP: 575.20 ± 270.96 kg ha⁻¹, OS: 721.49 ± 209.52 kg ha⁻¹) and total litterfall (1,296.69 ± 182.73 kg ha⁻¹) (Figure 3).

The interaction between litterfall fraction and season significantly affected litterfall and contents of C (*P* = 0.0360, for both variables), concentrations of N, P, K, Ca, Mg, B, Cu, Fe, Mn, Zn (*P* = 0.0000, for these ten variables), and S (*P* = 0.0002). There were no significant differences between the litterfall fractions, regarding litterfall and C content in autumn and winter, concentration of K in spring, Mg in summer, both P and S in winter (Tables 1 and 2).

Despite this, there were two patterns of results for the effect of the litterfall fraction. The first one, which was the most frequent, refers to significantly higher litterfall and C content in spring, summer, and annual period, besides concentration of N, Ca, B, Fe, Mn, and Zn in the four seasons and annual period, P, S and Cu, in spring, summer, autumn, and annual period, Mg in spring, autumn, and annual period nutrient in litterfall from OS (Tables 1, 2, and 3).

The second pattern indicated the opposite response, that is, significantly higher values in litterfall from PP, that was recorded for K concentration in summer, autumn, winter, and annual period, Mg and Cu in winter (Tables 2 and 3).

Figure 3. Monthly seasonality of litterfall from *Pseudobombax* aff. *petropolitanum* (PP), other woody species (OS), and total litterfall (TL) on a neotropical inselberg in Espírito Santo State, Brazil, from November 2011 to October 2012. The vertical bars in the graph indicate the standard deviation. Spring (SP), Summer (SU), Autumn (AU), Winter (WI).

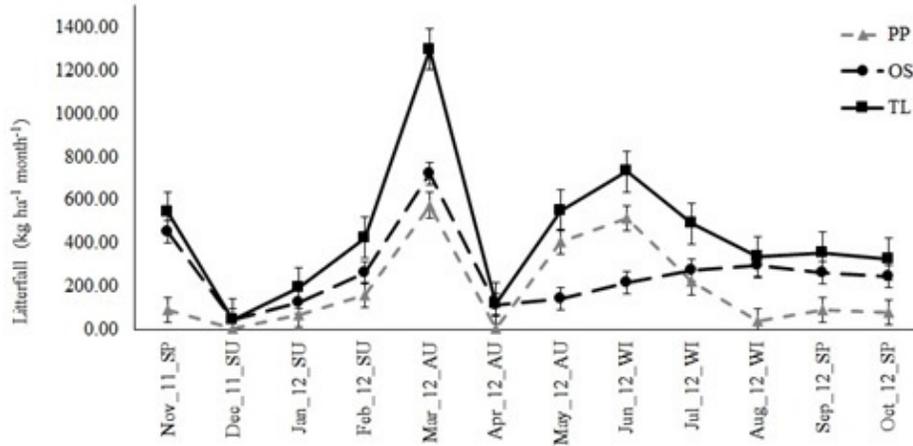


Table 1. Seasonal and annual values of litterfall and carbon content from *Pseudobombax* aff. *petropolitanum* (PP), other woody species (OS), and total litterfall (TL) on a neotropical inselberg in Espírito Santo State, Brazil, from November 2011 to October 2012¹.

Season	Litterfall			Carbon content		
	PP	OS	TL	PP	OS	TL
kg ha ⁻¹						
Spring	261.09 B (87.92)	962.59 A (206.12)	1,223.68 (272.08)	122.71 B (41.32)	452.42 A (96.88)	575.13 (127.88)
Summer	231.92 B (112.50)	427.25 A (96.49)	659.17 (119.55)	109.00 B (52.87)	200.81 A (45.35)	309.81 (56.19)
Autumn	990.96 A (231.85)	978.35 A (297.43)	1,969.31 (359.18)	465.75 A (108.97)	459.82 A (139.79)	925.57 (168.81)
Winter	773.17 A (244.68)	785.07 A (601.31)	1,558.24 (677.90)	363.39 A (115.00)	368.98 A (282.62)	732.37 (318.62)
Annual	2,257.15 B (322.13)	3,153.25 A (683.31)	5,410.40 (729.16)	1,060.86 B (151.40)	1,482.03 A (321.16)	2,542.89 (342.71)

¹ Data are the mean and standard deviation (in parentheses) of five replications. Values followed by different letters, comparing litterfall fractions in each season, indicates significant differences ($p < 0.05$) by the parametric Fisher's least significant difference test or by the nonparametric Mann-Whitney test.

Table 2. Seasonal and annual macronutrient concentration from *Pseudobombax* aff. *petropolitanum* (PP), other woody species (OS), and total litterfall (TL) on a neotropical inselberg in Espírito Santo State, Brazil, from November 2011 to October 2012¹.

Litterfall	Macronutrient concentration					
	N	P	K	Ca	Mg	S
(g kg ⁻¹)						
Spring						
PP	9.64 B (0.44)	0.73 B (0.05)	4.99 A (0.44)	6.51 B (0.19)	2.27 B (0.15)	0.89 B (0.13)
OS	18.28 A (0.07)	2.30 A (0.04)	4.48 A (0.29)	14.55 A (0.03)	3.52 A (0.02)	1.59 A (0.18)
TL	13.96 (0.24)	1.52 (0.04)	4.74 (0.17)	10.53 (0.09)	2.89 (0.08)	1.24 (0.14)
Summer						
PP	9.22 B (0.27)	0.68 B (0.02)	4.45 A (0.04)	12.49 B (0.21)	3.56 B (0.03)	0.86 B (0.05)
OS	17.23 A (0.47)	2.62 A (0.08)	3.75 A (0.18)	15.08 A (0.70)	3.74 A (0.15)	1.50 A (0.11)
TL	13.22 (0.16)	1.65 (0.03)	4.10 (0.07)	13.78 (0.35)	3.65 (0.07)	1.18 (0.04)
Autumn						
PP	7.99 B (0.27)	0.55 B (0.02)	2.41 A (0.03)	12.73 B (0.07)	3.33 B (0.05)	0.77 B (0.02)
OS	18.90 A (0.12)	1.83 A (0.13)	1.57 B (0.18)	18.29 A (0.95)	3.82 A (0.24)	1.44 A (0.13)
TL	13.45 (0.18)	1.19 (0.06)	1.99 (0.10)	15.51 (0.46)	3.57 (0.10)	1.11 (0.06)

Table 2. Continued...

Litterfall	N	P	K	Ca	Mg	S
	(g kg ⁻¹)					
Winter						
PP	12.76 B (0.29)	1.17 A (0.24)	6.09 A (0.42)	8.97 B (0.27)	3.59 A (0.17)	1.13 A (0.05)
OS	15.67 A (0.07)	1.39 A (0.03)	2.71 B (0.05)	13.76 A (0.40)	3.05 A (0.14)	1.22 A (0.04)
TL	14.21 (0.12)	1.28 (0.11)	4.40 (0.18)	11.36 (0.33)	3.32 (0.15)	1.17 (0.04)
Annual						
PP	9.90 B (0.06)	0.78 B (0.06)	4.49 A (0.22)	10.17 B (0.10)	3.19 B (0.07)	0.91 B (0.03)
OS	17.52 A (0.09)	2.03 A (0.06)	3.13 B (0.12)	15.42 A (0.50)	3.53 A (0.13)	1.44 A (0.08)
TL	13.71 (0.07)	1.41 (0.04)	3.81 (0.12)	12.80 (0.30)	3.36 (0.10)	1.18 (0.06)

¹Data are the mean and standard deviation (in parentheses) of three replications. Values followed by different letters, comparing litterfall fractions in each season, indicates significant differences ($p < 0.05$) by the parametric Fisher's least significant difference test or by the nonparametric Mann-Whitney test.

Table 3. Seasonal and annual micronutrient concentration from *Pseudobombax aff. petropolitanum* (PP), other woody species (OS), and total litterfall (TL) on a neotropical inselberg in Espírito Santo State, Brazil, from November 2011 to October 2012¹.

Litterfall	B	Cu	Fe	Mn	Zn
	(mg kg ⁻¹)				
Spring					
PP	28.02 B (0.78)	7.93 B (0.30)	139.61 B (17.14)	246.78 B (26.37)	37.53 A (1.62)
OS	70.00 A (0.65)	11.75 A (1.35)	183.94 A (7.20)	487.78 A (12.51)	50.88 A (0.99)
TL	49.01 (0.51)	9.85 (0.83)	161.78 (11.67)	367.28 (14.37)	44.21 (1.30)
Summer					
PP	46.00 B (0.33)	5.34 B (0.16)	119.17 B (7.67)	132.33 B (1.46)	20.81 B (0.32)
OS	74.60 A (0.91)	9.28 A (0.34)	221.83 A (8.74)	593.06 A (15.03)	40.64 A (0.84)
TL	60.79 (0.41)	7.31 (0.11)	170.50 (7.94)	362.69 (7.47)	30.72 (0.33)
Autumn					
PP	44.24 B (0.53)	5.74 B (0.54)	124.67 B (10.36)	151.83 B (9.40)	17.25 B (0.56)
OS	91.42 A (3.56)	11.13 A (0.58)	207.00 A (3.17)	551.11 A (37.38)	34.68 A (1.14)
TL	67.83 (1.52)	8.44 (0.54)	165.83 (3.81)	351.47 (14.52)	25.96 (0.47)
Winter					
PP	35.86 B (1.30)	9.83 A (0.69)	121.83 B (7.26)	127.11 B (2.00)	29.83 B (1.88)
OS	45.79 A (1.12)	8.22 B (0.23)	319.83 A (37.26)	452.78 A (15.77)	37.40 A (1.16)
TL	40.82 (1.00)	9.03 (0.45)	220.83 (17.40)	289.94 (8.73)	33.62 (1.45)
Annual					
PP	38.78 B (0.52)	7.21 B (0.27)	126.32 B (6.49)	164.51 B (7.56)	26.35 B (0.55)
OS	70.45 A (0.51)	10.10 A (0.47)	233.15 A (9.88)	521.18 A (11.53)	40.90 A (0.79)
TL	54.61 (0.08)	8.65 (0.32)	179.74 (3.46)	342.85 (4.01)	33.63 (0.65)

¹Data are the mean and standard deviation (in parentheses) of three replications. Values followed by different letters, comparing litterfall fractions in each season, indicates significant differences ($p < 0.05$) by the parametric Fisher's least significant difference test or by the nonparametric Mann-Whitney test.

Litterfall from PP presented negative eigenvectors, whereas litterfall from OS presented positive eigenvectors, due to the position in the left portion and right portion of the Principal Component 1, respectively (Figure 4A). Principal Component Analysis explained approximately 76.0 % of the variability in the original variables, most of which was explained by Principal Component 1, when compared to Principal Component 2 (Table 4).

Litterfall from OS was associated with maximum mean values of all variables analyzed, except for K concentration,

whose maximum mean value was associated with litterfall from PP (Figure 4A). The eigenvector of N, S, and Mn concentration presented the higher influence on the Principal Component 1, due to the higher values of correlation coefficient (> 0.90) (Table 4). Nonetheless, the eigenvector of P, Ca, B, and Cu concentration also presented significant correlation coefficient values (> 0.70) with the Principal Component 1 (Table 4). The eigenvector of none of the analyzed variables showed significant correlation coefficient values (> 0.70) with the Principal Component 2.

Figure 4. Ordering and classification diagrams resulting from multivariate analysis of principal components (A) and hierarchical clustering (B) considering litterfall (LTF), nutrient concentration (CC) from *Pseudobombax* aff. *petropolitanum* (PP) and other woody species (OS), on a neotropical inselberg in Espírito Santo State, Brazil, from November 2011 to October 2012. Spring (SP), Summer (SU), Autumn (AU), Winter (WI).

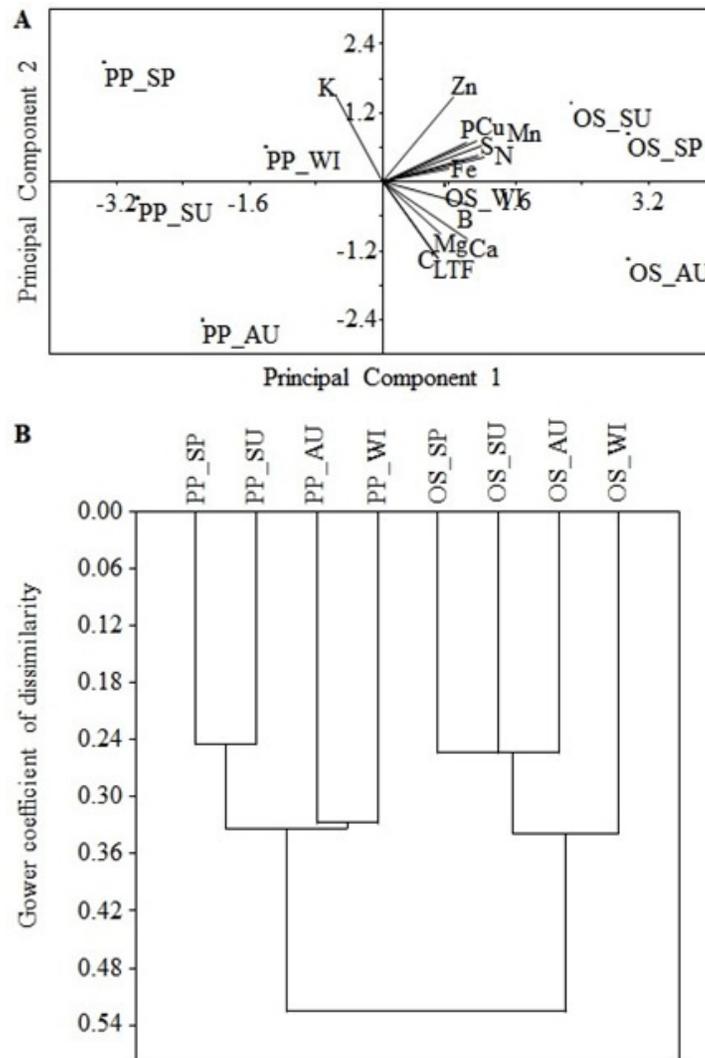


Table 4. Eigenvector of litterfall (LTF), carbon content (CT), and nutrient concentration (CC) from *Pseudobombax aff. petropolitanum* (PP) and other woody species (OS), on a neotropical inselberg in Espírito Santo State, Brazil, from November 2011 to October 2012, in Principal Components (PC) 1 and 2 from the multivariate Principal Components Analysis.

Variable	Eigenvector (PC 1)	Variable	Eigenvector (PC 2)
LTF	0.53	LTF	-0.60
CT_C	0.53	CT_C	-0.60
CC_N	0.97	CC_N	0.19
CC_P	0.90	CC_P	0.33
CC_K	-0.44	CC_K	0.67
CC_Ca	0.81	CC_Ca	-0.45
CC_Mg	0.55	CC_Mg	-0.41
CC_S	0.95	CC_S	0.29
CC_B	0.88	CC_B	-0.20
CC_Cu	0.80	CC_Cu	0.31
CC_Fe	0.63	CC_Fe	0.10
CC_Mn	0.91	CC_Mn	0.21
CC_Zn	0.68	CC_Zn	0.66
Proportion of variance (%)	57.37	Proportion of variance (%)	18.40
Total variance (%)			75.77

The vectors of N, P, S, Cu, Fe, and Mn concentration were positioned in the same direction and formed acute angles between them (high correlation between them) (Figure 4A). The same pattern was verified for the vectors of Ca and Mg concentration, while the vectors of litterfall and C content variables overlapped.

The hierarchical cluster analysis pointed to the dissimilarity between the litterfall fractions. In fact, litterfall from PP within the seasons grouped by a dissimilarity distance of approximately 0.52 (or 52.0 %), in relation to the litterfall from OS (Figure 4B).

4. DISCUSSION

The continuous fine litterfall throughout the year in the inselberg woody vegetation, although seasonality is observed in this process, is a phenomenon commonly observed in the Atlantic Forest biome, regardless of phytophysiology, successional stage, altitude, and distance from the edge towards the interior of plant community (Martinelli *et al.*, 2017; Sousa-Neto *et al.*, 2017; Camara *et al.*, 2018a, 2018b; Machado *et al.*, 2018; Schumacher *et al.*, 2018; Carvalho *et al.*, 2019; Araújo *et al.*, 2020; Dick & Schumacher, 2020; Menezes *et al.*, 2020; Câmara *et al.*, 2021; Lagemann *et al.*, 2022). The maximum monthly litterfall in inselberg (PP, OS, total litterfall) verified in March 2012 (end of the rainy season and beginning of the dry season) was probable a function of low accumulated precipitation, which was only 74.40 mm (approximately 7.2 % of annual precipitation). The accumulated precipitation in the previous month (February) was even lower (17.40 mm) for the summer. Therefore, the

extremely low rainfall in the previous month also impacted the maximum litterfall in the following month.

The inselberg is surrounded by fragments of Dense Ombrophilous Forest and Seasonal Semideciduous Forest. However, the maximum litterfall in response to low precipitation approached what is commonly found in Seasonal Semideciduous Forest areas, as a mechanism for decreasing evapotranspiration with leaf fall, the main component of litterfall, in periods of lower precipitation and soil water availability (Carvalho *et al.*, 2019; Dick & Schumacher, 2020; Câmara *et al.*, 2021; Lagemann *et al.*, 2022). This pattern is also verified in Deciduous Forest (Schumacher *et al.*, 2018; Araújo *et al.*, 2020), in contrast to evergreen forests where maximum litterfall is usually observed in the wet season (Sousa-Neto *et al.*, 2017; Camara *et al.*, 2018a, 2018b).

Total annual fine litterfall and its carbon content in inselberg (approximately 5.41 Mg ha⁻¹ year⁻¹ and 2.54 Mg ha⁻¹ year⁻¹, respectively) were both the same for the average in South American tropical forests that grow in white sand and poor soils (Chave *et al.*, 2010), but lower than the average obtained from 105 estimates from 45 sites in the Atlantic Forest biome in Brazil (8.0 Mg ha⁻¹ year⁻¹ and carbon content 3.76 Mg ha⁻¹ year⁻¹), which included secondary and old growth fragments from both seasonal and evergreen forests (Martinelli *et al.*, 2017). This pattern is due to the low primary productivity caused by soil nutritional deficiency on inselbergs (Benites *et al.*, 2007), compared with forest vegetation developing under more structured, deep, and fertile soils (Hopper *et al.*, 2016).

However, considering the same comparison, total annual fine litterfall and carbon content in inselberg were higher than the respective lowest values (3.5 Mg ha⁻¹ year⁻¹ and 1.86

Mg ha⁻¹ year⁻¹, respectively) estimated for the Atlantic Forest biome in Brazil (Martinelli *et al.*, 2017). This result showed the importance of woody vegetation for carbon cycling on inselberg, despite its small vegetation structure characterized by the predominance of herbaceous species (Couto *et al.*, 2017), which reflects the strong environmental filters, such as shallow soil, limited water and nutrient levels, and direct exposure to strong winds (Porembski, 2007; Couto *et al.*, 2016). Low soil fertility influences the lower structure of the woody plant community and, consequently, both factors are responsible for the lower primary productivity, which is reflected in lower litter production in the ecosystems (Camara *et al.*, 2018a, 2018b; Menezes *et al.*, 2020; Câmara *et al.*, 2021).

The descending order of macronutrient (N > Ca > K > Mg > P > S) and micronutrient (Mn > Fe > B > Zn > Cu) concentration observed in the inselberg litterfall was the same for a fragment of Seasonal Deciduous Forest in the municipality of Itaara, Rio Grande do Sul state (Schumacher *et al.*, 2018), and closed to that observed in litterfall from two sites of Alluvial Dense Ombrophilous Forest at different successional stages (Ca > N > K > Mg > P; Mn > Fe > Zn > Cu) in Salto Morato Natural Reserve, Paraná state (Scheer *et al.*, 2011); the concentration of S and B were not determined in the referred study. Regarding specifically the concentration of micronutrients, the decreasing order was also very similar in comparison with the litterfall of areas of Submontane Dense Ombrophilous Forest (Mn > Fe > Cu > Zn), regardless of the successional stage (initial, intermediate, advanced), in the Guaricica Natural Reserve, Paraná state (Bianchin *et al.*, 2017).

A similar pattern of micronutrient concentration (Fe > Mn > B > Zn > Cu) was observed in litter standing stock from this studied inselberg; macronutrient concentration, however, differed slightly between litter standing stock from other species (N > Ca > Mg > K > S > P) and litter standing stock from PP (Ca > N > Mg > K > S > P) (Freitas *et al.*, 2015). The Principal Component Analysis showed that mainly the concentration of N, S, and Mn, as well as the concentration of P, Ca, B, and Cu are important variables to be considered in future studies of nutrient cycling in inselberg areas, due to its greatest influence on the Principal Component 1.

The higher litterfall, C content, and concentration of N, P, Ca, Mg, S, B, Cu, Fe, Mn, and Zn in litterfall from OS (annual period and at least in two seasons) suggested that these plants probably exhibit a more efficient absorption of nutrient from soil or a greater demand for these nutrients (Scheer *et al.*, 2011). The litterfall chemical composition, i.e., the nutrient concentration of the litterfall, varies according to the plant species and, therefore, depends on the species composition in the ecosystems (Camara *et al.*, 2018b; Schumacher *et al.*, 2018). It was expected higher accumulation of litter standing

stock from PP, since the maintenance of this material is a function of the balance between the amount of litterfall and the rate of decomposition (Camara *et al.*, 2018a; Carvalho *et al.*, 2019), which tends to be slower for materials with low nutrient concentration (Liao *et al.*, 2022).

However, a previous study showed higher accumulation of litter on topsoil from OS, in comparison with the litter standing stock from PP (80.4 % and 19.6 % of the litter layer disposed on the topsoil, respectively) (Freitas *et al.*, 2015), which was influenced by the higher litterfall from OS as we detected in the present study. The lack of nutrients and high levels of Al³⁺ in the soil, in addition to lower temperatures, contribute to reducing microbial activity, which results in low rates of decomposition and, therefore, in the accumulation of organic matter on the soil that allows increasing retention of nutrients and water, which provides the establishment and development of vegetation (Benites *et al.*, 2007).

On the other hand, the lower nutrient concentration in litterfall from PP suggests that this species presents high nutrient use efficiency, i.e., redistribution of mobile nutrients from older senescent tissues, before their abscission, to younger ones, is increased under conditions of low soil nutrient availability (Scheer *et al.*, 2011). This fact, except for K concentration that was higher in litterfall from PP, could be essential for vegetation maintenance (Benites *et al.*, 2007) and responsible for the high abundance of this lithophyte tree species in the inselberg (Couto *et al.*, 2016, 2017, 2019).

This is a specific physiological plant adaptation which is frequently registered for plants in high-elevation areas, because of the low input of nutrients, such as P and N, via litterfall (Sousa-Neto *et al.*, 2017). Thus, the possible high nutrient use efficiency could be one factor that contributes to the adaptation of PP to weakly developed soils, shallow, acidic, and low nutritional quality due to leaching, that is enhanced by high drainage and lesser retention by lacking clays, besides low nutrient content of the parent material, particularly P, which is extremely limiting for plant development and show very low amounts in some soils of inselbergs (Benites *et al.*, 2007).

In the comparison between nutrients, K is the most soluble element and, therefore, the most easily released nutrient from decomposing litter (Cavalli *et al.*, 2018), available for plants in the soil during this process (Lagemann *et al.*, 2022), and has a high rate of retranslocation in the plant organism, which is lower only in comparison with P (Machado *et al.*, 2016), which is the most limiting nutrient in soil in tropical regions. According to this reasoning, it is believed that the concentration of K in the litterfall from PP would be even higher than what was recorded. Thus, the higher concentration of only one nutrient, K, in the litterfall from PP, in comparison with the litterfall from OS, is a relevant result.

Our pioneer study provided an important contribution about primary production and nutrient cycling in tropical inselberg areas, presenting and suggested that PP can be used in restoration of degraded areas where this species naturally occur, since lower litterfall nutrient concentration may be a consequence of nutrient conservation strategy that minimize the nutritional demand allowing plants to colonize low-fertility soils (Machado *et al.*, 2016), in addition to the potential of the species in soil fertilization with K. This could be a goal due to some antropic activities that threatens the inselberg diversity, which includes ornamental stone mining (Couto *et al.*, 2016, 2019), presence of invasive species such as *Melinis minutiflora* P. Beauv. (exotic Poaceae) and *Pteridium arachnoideum* (Kaulf.) Maxon (native Dennstaedtiaceae), besides coffee and *Eucalyptus* plantations (Pinto-Junior *et al.*, 2020).

5. CONCLUSIONS

Although continuous throughout the year, maximum monthly litterfall in inselberg was verified in the transition between the end of the rainy season and beginning of the dry season, probable as a negative impact of the low precipitation mainly in the previous month and in the respective month. This pattern is commonly observed in Seasonal Semideciduous Forest areas.

Pseudobombax aff. *petropolitanum* presented lower litterfall (and consequently lower C content) besides lower concentration of N, P, Ca, Mg, S, B, Cu, Fe, Mn, and Zn, which suggested higher nutrient conservation that may contribute to the high local abundance of this species, although higher K concentration, compared to litterfall from other woody species. Finally, this pattern highlighted the potential of *Pseudobombax* aff. *petropolitanum* for restoration of degraded areas by the mining of ornamental rocks in the region of occurrence of this species.

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