



ECOSYSTEMS

Spatial characterization of factors inherent in the microendemism of the dwarf pequi tree (*Caryocar brasiliense* subsp. *intermedium* (Wittm.) PRANCE & M. F. Silva)

LEANDRO DA SILVA ALMEIDA, DENISE G. DE SANTANA & EDNALDO C. GUIMARÃES

Abstract: The dwarf pequi tree, *Caryocar brasiliense* subsp. *intermedium*, is extremely restricted to ecological niches in the Cerrado biome. Thus, understanding the conditioning factors of the micro-endemism of this sub-species through its spatial distribution and the physical-chemical attributes of the soil was the objective of this research. The research was carried out in a fragment of rupestrian field. The area was divided into quadrants in which the number of pequi trees was quantified and the physicochemical characteristics of the soil were determined. The modeling of semivariograms was performed using semivariances, and ordinary kriging was used for spatial interpolation of variables with spatial dependence. The number of pequi trees, the altitude, the remaining phosphorus and the humidity showed a strong degree of spatial dependence, unlike the pH, the calcium and the magnesium, all of which had a pure nugget effect. The other variables showed a moderate degree of spatial dependence. The greater availability of bases (SB > 0.1 cmolc dm⁻³) and phosphorus (> 1.05 mg dm⁻³), the reduced percentage of moisture (< 5%) and low potential acidity (< 4.0 cmolc dm⁻³) were the factors positively related to the establishment and development of the dwarf pequi tree in the area.

Key words: ecological niches, endemic species, rupestrian field, spatial dependence.

INTRODUCTION

The *Caryocar brasiliense* Cambess. (Caryocaraceae) species is subdivided into two subspecies, *C. brasiliense* subsp. *brasiliense* of arboreal size with wide distribution in the Cerrado biome and *C. brasiliense* subsp. *intermedium* of shrubby size. The subspecies “*intermedium*”, of restricted occurrence in the biome, is popularly called pequi-dwarf or dwarf pequi tree for its small size, between 30 and 80 cm, and for having or not an apparent stem (Prance & Silva 1973, Silva et al. 2001).

A population of the dwarf pequi tree, the object of this research, is distributed in a rupestrian field with a rocky outcrop between

the altitudes of 1213 and 1258 m. These relatively high altitudes interfere in the microclimate of the place. Rock fields are found at altitudes above 900 m and experience strong daily thermal variation, high heat incidence, evapotranspiration and constant winds (Jacobi et al. 2007, Silveira et al. 2016). It is an insular ecosystem where there are restrictions to gene flow, with shallow, acidic and impermeable soils, with low water retention and rocky outcrops (Silveira et al. 2016). These unique and restrictive properties can lead plant species to endemism and speciation. It is estimated that between 15 and 60% of Cerrado plant species are exclusive to rupestrian fields (Sano et al. 2008).

A peculiar characteristic of the dwarf pequi tree is its clustered spatial distribution, which is extremely restricted to ecological niches. This reinforces the need for further studies on aspects related to its micro-endemism and, consequently, the maintenance of its germplasm. Regarding the grouping of individuals, this is not a particularity of the dwarf pequi tree. Plant species cluster as a result of their reproductive means, environmental factors or aspects of interaction with other individuals (Giehl et al. 2007). However, the grouping of the species according to the size of the plants indicates possible spatial dependence between individuals.

Geostatistical techniques are able to determine and quantify this possible spatial dependence between individuals of dwarf pequi trees, and clarify what are the conditioning factors of its restricted occurrence. Furthermore, it can map and correlate the spatial and dynamic patterns of the ecosystem and understand the factors that provide or limit the distribution. By modeling the spatial behavior of plant species, geostatistics makes it possible to outline conservation and sustainable management methods (Pelissari et al. 2014, Souza & Coimbra 2005).

Ordinary kriging is the most used geostatistical technique (Manziona et al. 2021). It provides a unique image, which is ideal for area characterization (Manziona & Castrignanò 2019), as it allows an unbiased inference with minimal variability (Silva et al. 2018). Therefore, kriging can quantify the spatial behavior of the dwarf pequi tree and the physicochemical attributes of the soil, contributing to the understanding of the conditioning factors of the micro-endemism of the subspecies.

Geostatistics has been successfully used in research aimed at understanding the behavior of species in natural environments, such as: the

study on spatial distribution and preservation of species richness in a shrub savanna (Batista et al. 2016); Spatio-temporal dynamics of tree species in a preserved mixed tropical forest (Pelissari et al. 2017); estimation of changes in the distribution of native plant species in Great Britain (Groom 2013) and; in the determination of inventory measurements and biophysical parameters of forests (Meng et al. 2009).

These researches portray how geostatistics can help in spatial dependent relationships involving species distribution in natural areas of occurrence. In this context, understanding the conditioning factors of the micro-endemism of the dwarf pequi tree (*C. brasiliense* subsp. *intermedium*), through the spatial distribution and the physical and chemical attributes of the soil obtained by geostatistical methods, was the objective of this research.

MATERIALS AND METHODS

Area of research and climate characterization

The research area of 25.2 ha is located in the municipality of Ibiá in the state of Minas Gerais, Brazil, at latitude -19.822870° and longitude -46.764410°, between altitudes of 1213 to 1258 m. The predominant soil is the dystrophic LITHOLIC NEOSOL (Santos et al. 2018), whose source material is quartzite, where the rupestrian field predominates. The terrain is quite uneven; the declivity in some points being quite accentuated (>25%). The center of the area is a divider of drainage lines mainly in the north and south directions. The area is anthropized, sporadically exploited as pasture for cattle and, for this reason, subject to fire and cultural treatments to eliminate plants that cause intoxication to cattle (Figure 1). The predominant climate in the region is Cwa, that is, subtropical with dry winters and hot summers, according to the Köppen climate classification (1948).

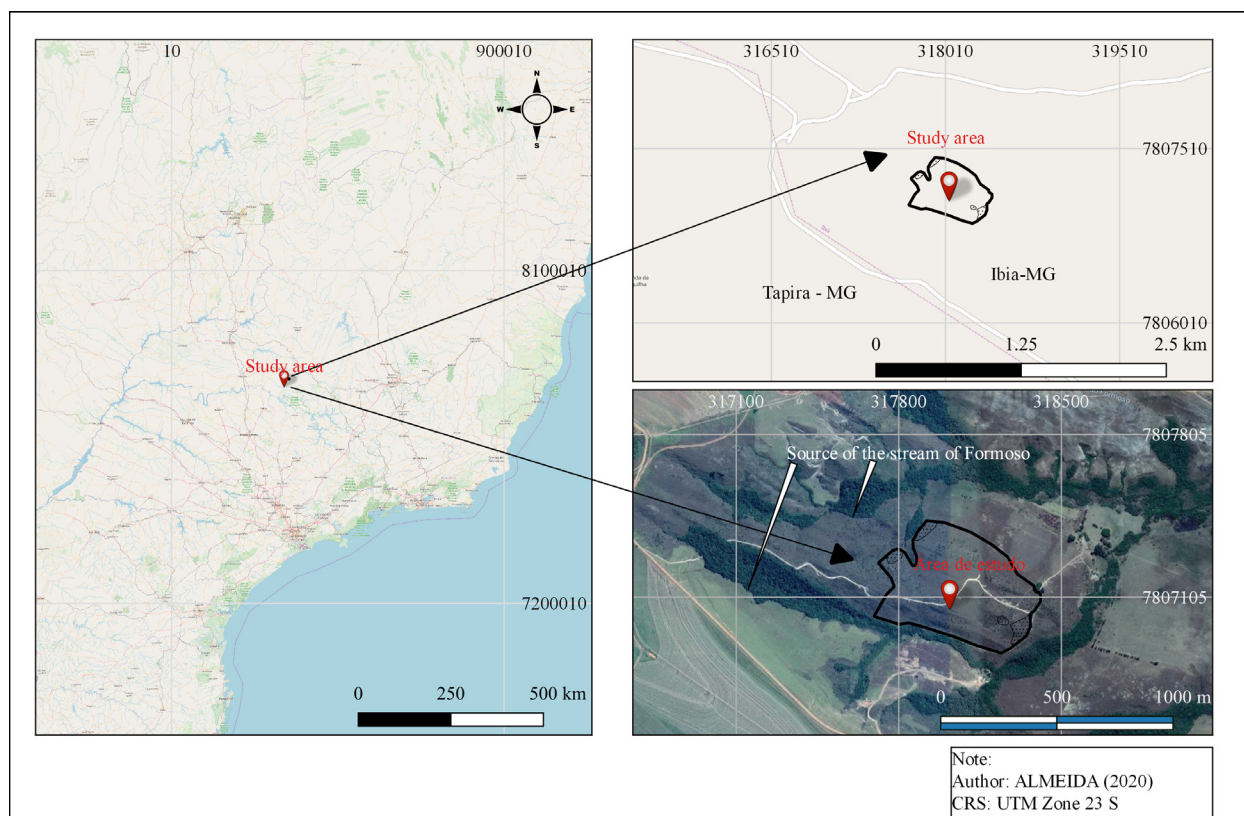


Figure 1. Location of the dwarf pequi tree occurrence area (*Caryocar brasiliense* subsp. *intermedium* (Wittm.) Prance & M. F. Silva) in the municipality of Ibiá, state of Minas Gerais. Detail for the springs of the Formoso stream adjacent to the area.

Identification of pequi trees and soil attributes

In the area, the geographic coordinates of 5256 individuals were taken (this number is practically all the individuals seen). The individuals were marked with tapes in order to minimize underestimations or overestimations, however, as many individuals present underground stems and tillers, there is no way to guarantee that two or more markings were not from the same individual, increasing the chances of overestimations.

The study area was divided into a regular grid with 60 cells or a 0.42 ha grid (50 m x 84 m). In each grid, the number of individuals was quantified, and this amount was determined as a variable to understand the behavior of the pequi tree in the area. Near the center of the grid, six soil samples were taken from the

surface layer (0.0 – 0.10 m) and mixed, forming a composite sample. The narrowest area of the grid (50 m) was along the greater slope of the terrain (northwest/southeast), where greater variability of soil attributes is expected due to erosive processes. 60 soil samples were collected for the analysis of chemical and physical attributes in June 2019. Another collection of 60 soil samples was carried out in September of the same year, the period of greatest water deficit in the region, for the determination of moisture.

Physical and chemical analyses

Chemical and physical analyses were performed by the Fertility and Soil Physics Laboratories of the Department of Soil Sciences of the Federal University of Lavras – UFLA. The pH was determined in water; phosphorus (P)

and potassium (K) by the Mehlich 1 extractor; potential acidity (H+Al) by the SMP extractor; organic matter (OM) by oxidation $\text{Na}_2\text{Cr}_2\text{O}_7$, 4N + H_2SO_4 , 10N; calcium (Ca), magnesium (Mg) and aluminum (Al) by the KCl extractor (1 mol L^{-1}); and granulometric analysis by the pipette method. For the remaining phosphorus (P.rem), a CaCl_2 10 mmol L^{-1} solution containing 60 mg L^{-1} of P in the form of KH_2PO_4 was used. Soil moisture was determined by the difference between the mass of the wet sample (0.001g accuracy) after field collection and the mass of the sample dried in an oven at 105 °C for 24 hours (Teixeira et al. 2017).

Analysis of spatial dependence

Descriptive statistics (maximum and minimum, mean, median, variance, standard deviation, coefficient of variation, coefficients of skewness and kurtosis) were used for a preliminary analysis of the general behavior of soil variables, as well as the number of individuals and altitude. For the spatial characterization, the verification of the trends was done through the dispersion of the variables in the east (x) and north (y) orientations.

The modeling of the semivariograms was performed using semivariance, a dissimilarity measurement preferably calculated by the Matheron's (1963) formula, known as the classical method. In cases of marked asymmetry on the right, presence of outliers or indications of trend in which the classical estimator did not allow the adjustment of visually reliable semivariograms, the classical estimator was replaced by the robust estimator proposed by Cressie & Hawkins (1980).

After obtaining the experimental semivariances, the variables were fitted to the spherical, exponential and Gaussian models of spatial dependence. The choice of model was based on the visual analysis known

as “a sentiment” (*sensu* Vieira et al. 1983) and on the technique of cross-validation. In cross-validation, each original value was removed from the spatial domain and a new value was estimated for the point, obtaining the graph of the relationship between estimated and observed values. The model selected was the one in which the estimated and observed values did not statistically differ at a significance of 0.01. With the semivariogram models, the degree of spatial dependence was calculated: $\text{GD} < 0.25$ indicates strong spatial dependence; $0.25 \leq \text{GD} \leq 0.75$ indicates moderate dependence and $\text{GD} > 0.75$ indicates weak dependence (*sensu* Cambardella et al. 1994).

The ordinary kriging technique was used for spatial interpolation of the variables with spatial dependence. When they did not present spatial dependence, the interpolation was performed by the inverse square method of the distances (ISD), a method of interpolation by classical statistics that is quite assertive. The methodologies adopted for the application of ordinary kriging and for the interpolation by the ISD method were according to Yamamoto & Landim (2013) and Krajewski & Gibbs (2001), respectively.

The influence of soil physical-chemical parameters on the species distribution was determined by the similarity (non-inferential) of these parameters with the density of individuals in the area. As the soil parameters are related to each other, there is a certain perception of redundancy in some variables. However, these variables were maintained for a better ability to choose factors related to the occurrence of the species.

Statistical and geostatistical analyses were performed using the R program version 3.6.1 (R Development Core Team 2019). The geoR package was used for geostatistical analysis (Ribeiro Júnior & Diggle 2018). The raster images

(dot matrix images) of the interpolation through kriging or by IDW were obtained in R, exported and inserted in the QGIS 3.8 (QGIS 2019) program for plotting thematic maps with better quality.

RESULTS

The dwarf pequi tree presented an average of 87.6 individuals per grid (0.42 ha). This value is not very representative due to the absence of individuals in some grids (minimum) and the concentration of individuals in others (grids with up to 401 individuals). Minimum and maximum altitudes of 1213 and 1258 m, respectively, depict the marked difference in level in the area. In some stretches, the declivity is greater than 25% (Table I).

The altitude, pH, Al (aluminum), t (effective cation exchange capacity), m (aluminum saturation), P_{rem} (remaining phosphorus), clay

and sand were the variables with the lowest relative dispersion (CV < 30%). The variables K (potassium), H+Al (hydrogen + aluminum), T (capacity to exchange cations at pH 7) and OM (organic matter) presented intermediate CVs, between 30 and 50%. P (phosphorus), V (base saturation), SB (sum of bases) and moisture showed high relative dispersion, CVs between 50 and 90%. The NI (number of pequi tree individuals) with CV= 125%; Mg (magnesium) and Ca (calcium) with CV of 138 and 600%, respectively, showed extreme relative dispersion (Table I).

The soil has high acidity, pH between 3.8 and 5.2 (average and median are similar, around 4.5) and, therefore, there is a deficit of bases (Ca, Mg, K), causing low saturation (V≈ 2%). Ca is scarce and practically undetected in the soil of the area ($\tilde{x} = 0.00$ and $\bar{x} = 0.005 \text{ cmol}_c \text{ dm}^{-3}$). Mg levels are very low, at an average of 0.036 cmol_c

Table I. Descriptive statistics of soil variables and distribution of dwarf pequi trees (*Caryocar brasiliense* subsp. *intermedium* (Wittm.) Prance & M. F. Silva) in the Cerrado area, in the municipality of Ibiã-MG, in 2019.

Attribute	Unit	min	\tilde{x}	\bar{x}	max	S	s ²	CV	Cs	Ck
Pequi tree	NI	0.00	38.00	87.57	401	109.57	12004	125.12	1.26	0.50
Altitude	m	1213	1240	1239	1258	11.96	143.16	0.97	-0.37	-0.93
pH		3.80	4.50	4.54	5.20	0.25	0.06	5.51	-0.22	0.70
K	mg dm ⁻³	6.88	24.75	27.61	60.31	13.66	186.56	49.47	0.54	-0.63
P	mg dm ⁻³	0.00	0.54	0.75	2.90	0.65	0.42	86.67	1.14	1.29
Ca	cmol _c dm ⁻³	0.00	0.00	0.005	0.19	0.03	0.00	600.00	6.360	41.37
Mg	cmol _c dm ⁻³	0.00	0.02	0.036	0.32	0.05	0.00	138.89	4.470	24.20
Al	cmol _c dm ⁻³	0.06	1.25	1.32	2.29	0.36	0.13	27.27	0.76	0.12
H+Al	cmol _c dm ⁻³	2.48	5.49	5.67	10.75	1.91	3.66	33.69	0.65	0.08
SB	cmol _c dm ⁻³	0.03	0.09	0.11	0.55	0.08	0.01	72.73	3.12	13.66
t	cmol _c dm ⁻³	0.84	1.33	1.43	2.41	0.39	0.15	27.27	0.66	-0.32
T	cmol _c dm ⁻³	2.70	5.55	5.80	10.83	1.91	3.66	32.93	0.67	0.08
V	%	0.55	1.56	2.03	12.55	1.79	3.19	88.18	4.16	20.23
m	%	69.44	93.86	92.31	98.67	5.24	27.50	5.68	-2.48	7.01
OM	dag kg	0.62	1.55	1.67	3.71	0.56	0.31	33.53	0.99	1.68
P _{rem}	mg L	28.08	36.16	36.10	44.68	4.36	19.01	12.08	0.03	-0.88
Clay	dag kg ⁻¹	8.00	13.00	13.48	21.00	3.20	10.22	23.74	0.47	2.57
Sand	dag kg ⁻¹	51.00	66.00	65.57	82.00	7.00	49.03	10.68	-0.01	2.72
Moisture	%	0.57	1.63	2.51	12.79	2.25	5.06	89.64	2.40	6.87

min: minimum; \tilde{x} : median; \bar{x} : average; max: maximum; s: standard deviation; s²: variance; CV: coefficient of variation; Cs: asymmetry coefficient; Ck: kurtosis coefficient. NI: Number of individuals; K: potassium; P: phosphorus; Ca: calcium; Mg: magnesium; Al: aluminum; H+Al: potential acidity; SB: sum of bases; t: effective cation exchange capacity; T: cation exchange capacity at pH 7.0; V: base saturation; m: aluminum saturation; OM: organic matter; P_{rem}: remaining phosphorus.

dm^{-3} and maximum of $0.32 \text{ cmol}_c \text{ dm}^{-3}$. K is the base with the highest availability in the area, at an average of 27.6 mg dm^{-3} ($0.07 \text{ cmol}_c \text{ dm}^{-3}$). The P concentration was low, mean of 0.75 mg dm^{-3} , to the point of not being registered on some grids, and having reached the maximum of 2.9 mg dm^{-3} . The soil has a high concentration of Al.

The average clay and sand contents of 13.48 and $65.57 \text{ dag kg}^{-1}$, respectively, characterize the soil as sandy (Table I). Humidity, measured in the $0-0.10 \text{ m}$ layer and at the height of the water deficit (after a period of 4 months without significant precipitation), was much higher in some regions (12.79%), about 22 times higher than the minimum (0.57%).

The variables NI, P, Ca, Mg, SB, V, m, coarse sand and moisture were more clearly less symmetric. The variables P, Ca, Mg, SB, V, m, OM, clay, sand and moisture showed relatively high kurtosis (Table I). The large amount of Ca values equal to zero (0) led to the predominance of only the quartile (Q1) for this nutrient and, consequently, to the asymmetry on the left. For the other variables (NI, altitude, pH, K, Al, H+Al, t, T, P.rem), the distribution of quartiles and dispersion confirmed that there was no significant trend. The variables pH, Ca, Mg showed a pure nugget effect (PNE), thus characterizing spatial independence (Table II, Figure 2).

Table II. Models, parameters, C_0/C_0+C ratio and degree of spatial dependence of semivariograms adjusted for the distribution of the number of dwarf pequi trees (*Caryocar brasiliense* subsp. *intermedium* (Wittm.) Prance & M. F. Silva), altitude and for the variables related to the physical-chemical attributes of the soil in the Cerrado area, in the municipality of Ibiá-MG, in the year 2019.

Attribute	Model	1C	2C_0	5 Practical Range (a)	$^3C_0/C_0+C$	Degree of Dependency (DD)
NI of Pequi tree	Gaussian	7652.51	1287.05	235.62	0.14	Strong
Altitude	Gaussian	177.34	11.08	294.52	0.06	Strong
pH	EPP ⁴	--	--	--	--	Absent
K	Gaussian	126.16	107.23	373.06	0.46	Moderate
P	Gaussian	0.13	0.25	255.24	0.66	Moderate
Ca	EPP ⁴	--	--	--	--	Absent
Mg	EPP ⁴	--	--	--	--	Absent
Al	Exponential	0.10	0.05	340.02	0.33	Moderate
H+Al	Spherical	1.75	1.95	113.50	0.53	Moderate
SB	Spherical	0.0014	0.0008	260.92	0.36	Moderate
t	Exponential	0.13	0.06	388.60	0.32	Moderate
T	Exponential	2.94	1.10	218.60	0.27	Moderate
V	Spherical	2.63	1.31	170.16	0.33	Moderate
m	Spherical	7.66	6.48	170.16	0.46	Moderate
OM	Exponential	0.21	0.10	339.00	0.32	Moderate
P.rem	Spherical	17.30	2.70	226.88	0.14	Strong
Clay	Spherical	8.37	3.27	272.26	0.28	Moderate
Sand	Spherical	18.95	32.74	170.2	0.63	Moderate
Moisture	Spherical	5.24	0.92	317.64	0.14	Strong

¹ C: contribution; ² C₀: nugget effect (C₀ + C = threshold); ³ method of Cambardella et al. (1994); ⁴PNE: pure nugget effect. ⁵ in the spherical model the practical range is equal to the theoretical range – exponential model the practical range is the theoretical range multiplied by 3 – gaussian model the practical range is the theoretical range multiplied by ; K: Potassium; P: Phosphor; Ca: calcium; Mg: magnesium; Al: aluminum; H+Al: potential acidity; SB: sum of bases; t: effective cation exchange capacity; T: cation exchange capacity at pH 7.0; V: base saturation; m: Aluminum saturation; OM: organic matter; P.rem: remaining phosphorus.

The number of individuals, altitude, P.rem and humidity showed a strong degree of spatial dependence ($GD < 0.25$; *sensu* Cambardella et al. 1994), and the other variables showed a moderate degree of spatial dependence ($0.25 \leq GD \leq 0.75$; *sensu* Cambardella et al. 1994) (Table II). For NI, altitude, K and P, the adjusted semivariogram

model was the Gaussian; exponential for Al, t, T and OM, and spherical for H+Al, SB, V, m, P.rem, clay, sand and moisture. The effective CTC (t) was the variable with the greatest practical range (388.6 m) and the variable H+Al, the smallest (113.5 m). These were considerable values, since

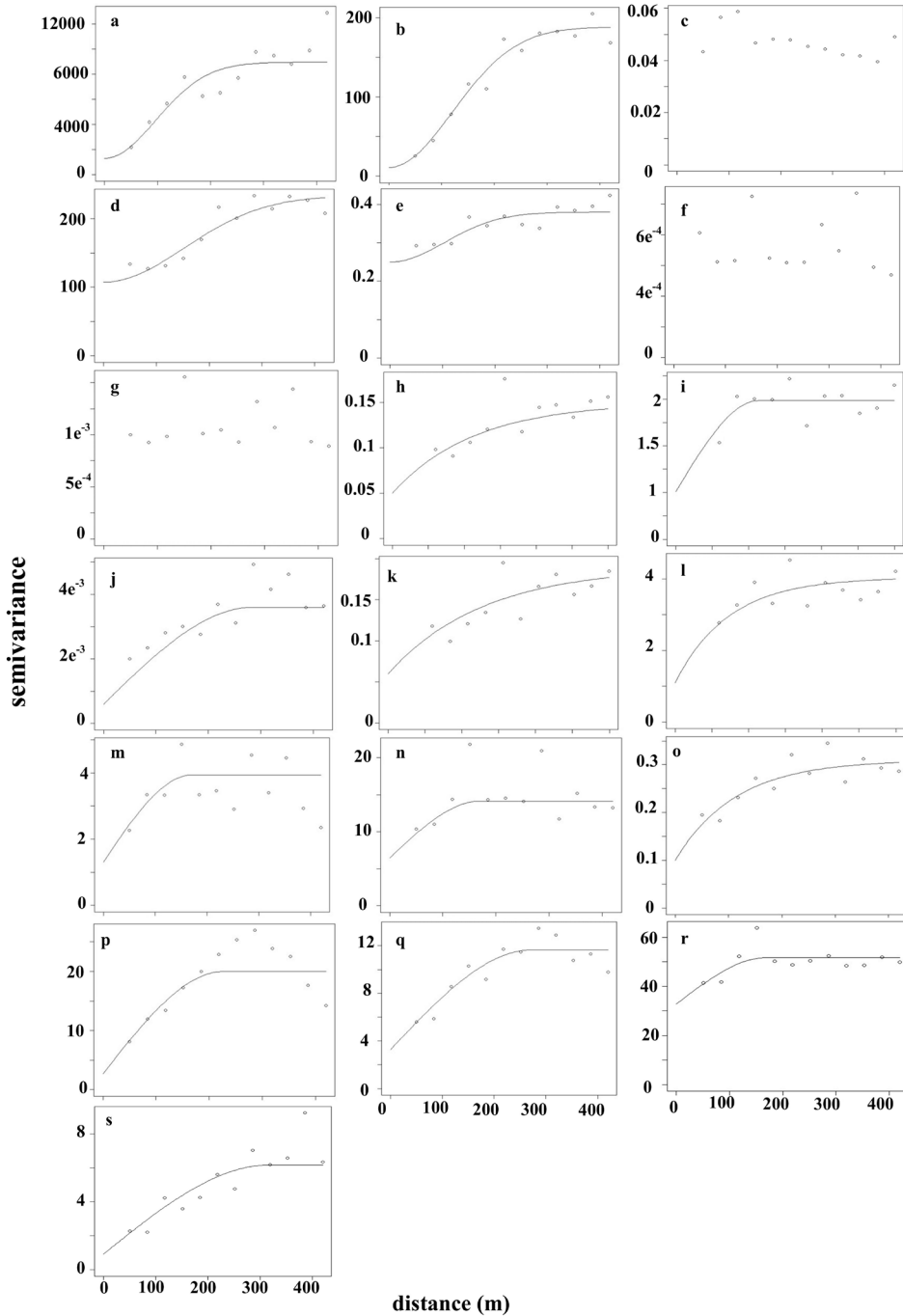


Figure 2. Semivariograms adjusted for: a: number of dwarf pequi trees (*Caryocar brasiliense* subsp. *intermedium* (Wittm.) Prance & M. F. Silva); b: altitude; c: pH; d: K (potassium); e: P (phosphorus); f: Ca (calcium); g: Mg (magnesium); h: Al (aluminum); i: H+Al (potential acidity); j: SB (sum of bases); k: t (effective cation exchange capacity); l: T (cation exchange capacity at pH 7.0); m: V (base saturation); n: m (aluminum saturation); o: OM (organic matter); p: P.rem (remaining phosphorus); q: clay; r: sand; s: soil moisture.

the minimum distance between grid points was 50 m (Table II, Figure 2).

The pure nugget effect (PNE) of pH, Ca and Mg was a consequence of the low and punctual contents of these bases in the soil, especially Ca due to the large amount of grids with the absence of this nutrient (50 of the 60 grids). These features were revealed in the thematic maps generated by ISD by some lighter or darker patches systematically distributed along the area (Figure 3c, 3f, 3g). This punctual distribution prevented more accurate inferences of the association of Ca, as well as pH and Mg, with the development of the pequi tree (Figure 3a).

The dwarf pequi tree is concentrated in the northernmost region of the area (intense green color on the map), where estimates showed a high density of individuals, with the possibility

of occurrence of more than 760 individuals per hectare (Figure 3a). The southernmost regions (lighter green tones on the map) showed a low estimate of occurrence or even absence of individuals of the species. This marked occurrence difference in regions that have similar altitudes (Figure 3b), indicated that the altitude analyzed in isolation is not related to the occurrence of the species.

The thematic map of the spatial distribution of clay showed concentration of this mineral in the northwest and southeast ends of the area, regions with availability above 14.8% (Figure 3q). In the rest of the area, the low percentages of clay (between 9 and 12%) and the high percentages of sand (average of 65.57%) indicated that the soil is quite sandy, even in places with medium texture.

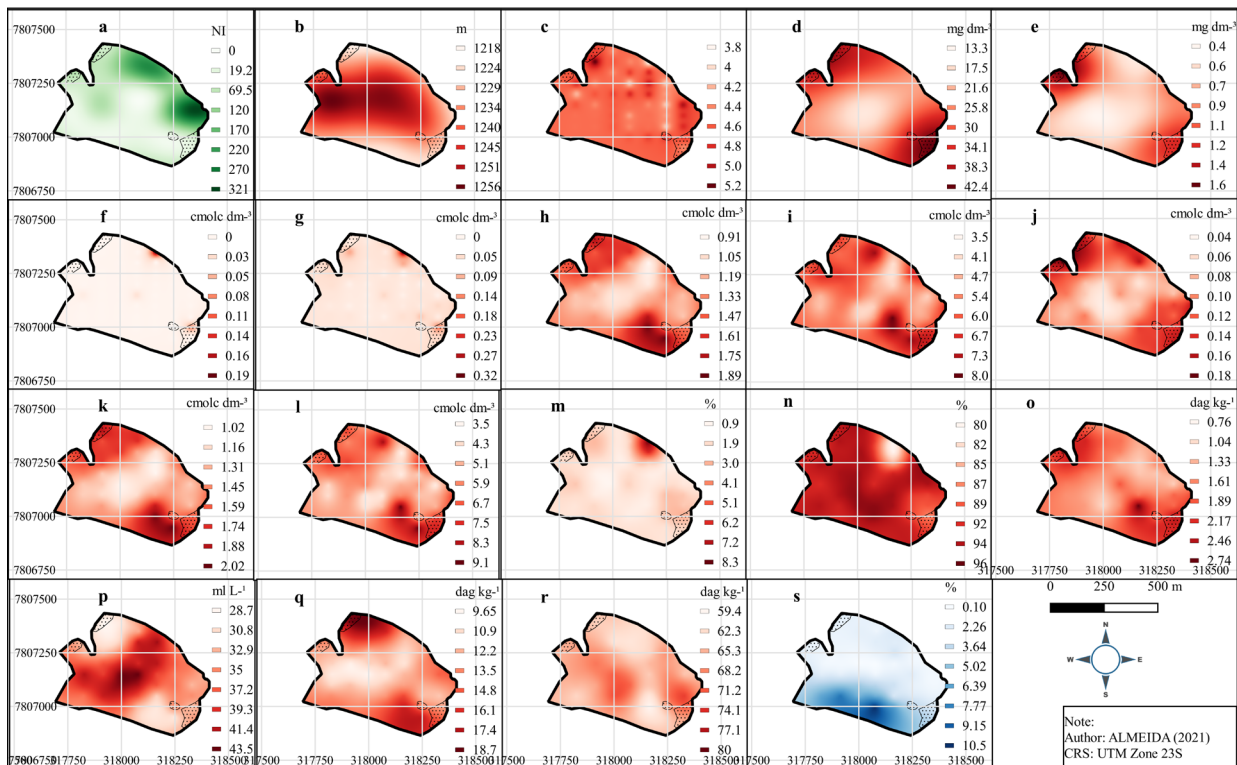


Figure 3. Maps of the spatial distribution of: a: number of dwarf pequi trees (*Caryocar brasiliense* subsp. *intermedium* (Wittm.) Prance & M. F. Silva); b: altitude; c: pH; d: K (potassium); e: P (phosphorus); f: Ca (calcium); g: Mg (magnesium); h: Al (aluminum); i: H+Al (potential acidity); j: SB (sum of bases); k: t (effective cation exchange capacity); l: T (cation exchange capacity at pH 7.0); m: V (base saturation); n: m (aluminum saturation); o: OM (organic matter); p: P.rem (remaining phosphorus); q: clay; r: sand; s: soil moisture.

One of the characteristics influenced by soil mineralogy is anionic adsorption. The central region of the area has the lowest anionic adsorption capacity ($P_{rem} > 39 \text{ mg L}^{-1}$). The two extremes (northwest and southeast) are the regions where there is greater adsorption capacity ($P_{rem} < 30.8 \text{ mg L}^{-1}$) (Figure 3p).

Potassium was distributed in bands. There are two bands in the area with the highest availability of K, one to the east and the other to the west ($> 30 \text{ mg dm}^{-3}$), separated by a central band of lower availability ($< 30 \text{ mg dm}^{-3}$). Still, in the center of the lower availability range there is an even more restricted region, with levels between 13.5 and 17.5 mg dm^{-3} (Figure 3d). The highest availability of P ($> 1.39 \text{ mg dm}^{-3}$) is in the southeastern and northwestern regions of the area, sites of occurrence of larger pequi trees (with visible stem). On the other hand, in regions with up to 0.382 mg dm^{-3} of P availability, the occurrence of the pequi tree is limited (Figure 3a, 3e). Regarding the availability of K and P, the regions where there is greater availability of both coincide with the regions in which pequi trees have greater size and visible stem (Figure 3a, hatched region on thematic map).

SB reinforces that the bases are more distributed at the extremes of the area (northwest, southeast), largely due to the weight of the element potassium (K), which is the most widely available base in the soil. The northwest extreme is the region with the highest accumulation of SB, with an availability above 0.158 $\text{cmol}_c \text{ dm}^{-3}$ reaching the maximum level found in the area of 0.177 $\text{cmol}_c \text{ dm}^{-3}$. The southeast presents SB between 0.118 and 0.158 $\text{cmol}_c \text{ dm}^{-3}$, being the second region in availability. In the center of the area (near longitude 318000 utm), there was practically no detection of bases or these were very low, with an availability between 0.04 and 0.0596 $\text{cmol}_c \text{ dm}^{-3}$, coinciding with the region

where practically no individuals of pequi trees are found (Figure 3a, 3j).

Soil moisture is a factor related to the occurrence of the dwarf pequi tree in the area. The points with the highest humidity at the height of the water deficit, above 7%, located to the south of the area, are the regions with the lowest occurrence of the pequi tree (Figure 3a, 3s). In the rest of the area the humidity is low, reaching less than 1%, and these are the areas with the highest occurrence of the species.

Al showed the highest concentration ($> 1.75 \text{ cmol}_c \text{ dm}^{-3}$) in two regions at opposite poles of the area; one to the northwest and the other to the southeast. In regions where the pequi tree is present and the availability of Al is lower, there is a higher concentration of individuals (Figure 3h). Potential acidity (H+Al) has a mottled distribution; some regions of higher concentration interspersed with regions of lower concentrations ($< 4.7 \text{ cmol}_c \text{ dm}^{-3}$) (Figure 3i). The northern region, with the highest base saturation ($V > 5.12\%$), is the region with the lowest Al saturation ($m < 86\%$), and one of the regions with the highest number of individuals (Figure 3a, 3m and 3n). The easternmost region, with base and aluminum saturations around 5 and 89%, respectively, is the other region with the highest concentration of individuals.

The OM presented greater concentration in the eastern and northwestern extremities of the area (Figure 3o), places where its concentration in the soil is greater than 1.89 dag kg^{-1} . The t and T (effective and total CEC) are quite dependent on the OM as it is the material with the greatest availability of loads in this soil. The two CEC measurements showed points of lower and higher intensities in the area, with the highest of both coinciding with the highest OM intensities (Figure 3k, 3l). It should be noted that Al is the element that occupies most of the effective CTC (t) (more than 90%; Table I). The total CEC (T) is

practically all occupied by the potential acidity, on average 97%.

DISCUSSION

Among the outstanding characteristics of the dwarf pequi tree population in the research area are the distinct density of individuals, variations in the size of the plants and very clear delimitation of the area of occurrence. In fact, the subspecies is restricted to some ecological niches of the Cerrado, and its natural occurrence is associated with the fields, especially the rupestrian fields (Silva et al. 2001), different from the common pequi tree (*C. brasiliense* subsp. *brasiliense*) distributed in dense, sparse and typical Cerrado and cerradão (Almeida et al. 1998).

In the area of 25.2 ha, although anthropized, endemic species predominate, especially from the families Eriocaulaceae, Velloziaceae, Asteraceae, typical of rupestrian fields. Species endemism is not uncommon in rupestrian fields (Conceição et al. 2015), however, the occurrence of the dwarf pequi tree is even more restricted. Possibly, the subspecies is micro-endemic (Rapini et al. 2008). Micro-endemic species are associated with spatial effects and small-scale patterns (microhabitats) (Murphy et al. 2013). Geostatistics, through ordinary kriging, quantified and confirmed this spatial dependence, especially micro-endemism. This was done by relating distribution patterns of individuals of the species to characteristics of altitude and to soil physicochemical variables.

The soil of the rocky field in the area is acidic (pH 4.5) and with high Al saturation, therefore, it has extremely low levels of nutrients, an alic soil. This nutritional limitation is also a strong speciation factor (Silveira et al. 2016), as changes in natural soil fertility levels lead to changes in species composition (Zhan et al. 2017). Even

with great nutritional limitations, the dwarf pequi tree grows and develops in the area, as well as other typical species, which leads to the understanding that these fertility levels, although low, are adequate. Thus, the species of this phytophysiognomy can be considered a source of germplasm for research aimed at improving the efficiency of cultivated plants in the use of minerals and in the resistance to environmental stresses.

The soils of rupestrian fields have characteristics similar to the poorest soils in the world, and low fertility is associated with nutrient leaching, intensified by high drainage and also by the low nutrient content of the source material (quartzite) (Benites et al. 2007, Oliveira et al. 2015). The soil texture is sandy (above 60% sand). This characteristic of the environment is considered a distinguishing factor of rupestrian fields (Silveira et al. 2016), since it directly affects the physicochemical properties of the soil and, therefore, influences the phytophysiognomy.

The nugget effect observed in the variables pH and Mg, indicate that the distribution of these variables in the area can be homogeneous or random, or that the density of the sampling points, that is, the smallest distance between the grids (50 m), was not sufficient to quantify dependence. The reduced amounts or undetectable levels of Ca do not generate variance between the observations justifying the PNE and the non-dependence. However, it is clear that the subspecies is highly adapted to a soil where there is practically no detection of Ca and Mg, being, therefore, highly efficient in the use of these bases when they are in very low concentrations.

Potassium (K) is the nutrient with the highest availability in the area and its concentration in the soil is related not only to the presence of individuals, but also to their density. Because K is related to the opening and closing of the

stomata, it is one of the elements responsible for adapting to water stress, a condition that the species suffers most of the year. The Cerrado naturally goes through a long period of drought, and as the soil is shallow and sandy, there is a low water storage capacity, increasing water stress. Research with cultivated species such as eucalyptus, corn and soybean, shows the mitigating effect of K on the damage caused by water stress (Vilela & Bull 1999, Silva et al. 2004, Serafim et al. 2012).

All area P levels are extremely low, including a maximum of 2.90 mg dm^{-3} and, even so, it was possible to observe how changes in the gradient of availability of this nutrient influenced the development of the pequi tree, since places with higher P concentration were related to larger individuals. On the other hand, places with availability tending to the minimum (0.382 mg dm^{-3}), did not show any occurrence of the species. The optimal level of a nutrient in the soil is not just a function of its chemical form and quantity, it is also a function of the species' ability to mobilize and absorb it (Lambers et al. 2008). Phosphorus (P), as well as nitrogen (N), are crucial nutrients in the composition and distribution, adaptation and survival of plant species in the environments of occurrence (Venterink 2011).

Thematic maps confirmed the positive responses of the dwarf pequi tree to the increase in exchangeable bases. Exchangeable bases are considered an influencing (selector) and determining factor in the abundance of floristic composition in rupestrian fields (Chaves et al. 2019). Even though the pequi tree is tolerant to Al, in places with reduced concentrations of this metal and increased concentration of total bases (SB), the population density was higher, indicating favorable microhabitats for the occurrence of the species.

Due to the natural cycling process of the area, sites with the highest contribution of organic matter (OM) also showed greater availability of nutrients and greater capacity for cation exchange, effective (t) and total (T). Organic matter is of paramount importance for the soil to maintain physical, chemical and biological qualities. OM gradients also condition the formation of microhabitats, important regions for species establishment and development (Conceição & Pirani 2005). Thus, the greater availability of OM is linked to greater availability of bases and, consequently, to a greater density of pequi trees. Organic matter accumulates in the soils of the rupestrian fields due to the unfavorable environment for the action of microorganisms, especially the extreme oligotrophy and the high levels of Al (Benites et al. 2007, Silveira et al. 2016).

Locations in the area with the highest concentrations of bases and, consequently, with the lowest concentrations of Al and H+Al, were the ones that presented the highest population densities, above 760 individuals per hectare. It is interesting to note that these individuals were predominantly without an visible stem. The lower level of Al may have favored cell development and, consequently, the expansion of underground stems (Echart & Cavalli-Molina 2001). It is likely that in these microhabitats there is a greater investment of the subspecies in underground stems, which may have led to an overestimation of the number of individuals, since the same individual could have received more than one marking. Clonal growth, that is, the establishment and growth of species through underground systems in rupestrian fields, is responsible for more than 50% of plant biomass (Alves et al. 2014). This vegetative development is an adaptation to environmental adversities common to rupestrian fields such as

fires and prolonged water stress (Conceição & Pirani 2005, Kolbek & Alves 2008).

Research on the dwarf pequi tree for ornamental purposes proved the relationship between soil fertility levels and plant growth and development. When the species was cultivated in a soil with pH 5.6 and good availability of nutrients, the plants reached up to 1.5 m in height and maintained the characteristic of early flowering (Junqueira et al. 2007). In these cultivation conditions, according to the authors, the association with irrigation management allowed flowering throughout the year. Another research indicated that common pequi tree seedlings submitted to increasing fertilization with slow-release fertilizers showed a linear response to leaf increment and shoot dry matter accumulation (Duboc et al. 2009).

It is important to highlight that growth and accumulation of dry matter may adaptive in nature for the species in the environment, a consequence of the creation of reserves in order to withstand periods without nutrient input (Haridasan 2008). Research in the north of the state of Minas Gerais on the common pequi tree in Cerrado, a pasture and agricultural area that has native plants, indicated higher productivity in poorer soils (acid pH=4.5 and with low availability of nutrients), that is, higher fertility did not mean higher productivity for two consecutive seasons (Leite et al. 2006).

Soil moisture at the height of the drought in most of the area was below 2%, characterizing the low water storage capacity of the soil. It is known that the soils of rupestrian fields, when developed on quartzite and sandstone, have little water retention and storage capacity (Silveira et al. 2016). The places in the area with the highest humidity at the height of the water deficit represent, in periods of high precipitation, places with seasonal elevation of the water table. The water table in the rupestrian fields

undergoes considerable seasonal fluctuations (Alves et al. 2014).

In the region of higher humidity, further south of the area, the presence of the dwarf pequi tree is limited, showing that it prefers the drier places. The southern region is adjacent to one of the springs of Ribeirão do Formoso and possibly contributes to the supply of water to the site. The wetter areas in the Cerrado are normally associated with valleys or water courses and the variation of the water table is a determining factor in the floristic and physiognomic compositions (Tannus & Assis 2004, Almeida Junior et al. 2009).

The resilience of the dwarf pequi tree to stress factors, little tolerated by other species in the Cerrado domain is undeniable. Its success is due to its ability to adapt to restrictive conditions such as an acidic environment (low pH and rich in Al), with high thermal and water stress (shallow soil, rocky outcrop and long period of water stress), in addition to low nutrient availability (Ca, Mg and P).

With unique characteristics, the rupestrian field allows the natural development of the dwarf pequi tree in some microhabitats, on the other hand, it restricts its development in others. The determining conditions for the spatial distribution of the species in the area were potassium, phosphorus and the sum of bases, that is, the highest levels of these variables are directly related to the occurrence (establishment), number of individuals and vegetative development of plants (portage). This last feature is especially correlated with phosphorus availability. Soil moisture, or rather, excess moisture is a restrictive factor for the establishment of the subspecies. It should be noted that the common pequi tree is limited by excess soil moisture (Alves Júnior et al. 2015).

Subtle changes in nutrient concentrations and soil acidity showed great influence on the

establishment, population density and size of dwarf pequi plants. These findings allow us to infer that changes in the physicochemical characteristics of the soil may lead to limitations in the establishment of the subspecies. Knowing these characteristics and their interactions with the dwarf pequi tree were important to support efforts for the preservation, conservation, management and cultivation of this subspecies, preventing its extinction.

Another fact that deserves attention is that the common pequi tree has been the object of several studies that seek to make its management viable (Carlos et al. 2014, Lima et al. 2015). Therefore, it is essential to consider the adaptive aspects of the dwarf pequi tree to take advantage of its favorable genetic characteristics for commercial purposes. These characteristics will be fundamental for the consolidation of a culture of low demand of external resources, being able to be, therefore, a very viable species for a low carbon agriculture. Evidently, all this is aiming at the benefits that the dwarf pequi tree could offer to the domestication of the species, such as small size, early fruiting, differentiated flowering period, among others that can still be identified.

Obtaining relevant information inherent to the spatial distribution of the dwarf pequi tree, through ordinary kriging, showed that geostatistics is a suitable instrument for studies that aim to characterize the natural occurrence of species, seeking preservation and sustainable management. It is noteworthy that it is a tool that allows univariate analysis, so it requires greater dedication to the interpretation of results, but it is a base technique (pillar) for the combination and or application of other geostatistical and statistical tools.

CONCLUSIONS

The micro-endemism of the dwarf pequi tree (*Caryocar brasiliense* subsp. *intermedium* (Wittm.) Prance & M. F. Silva) in the rocky field is due to the high altitudes (between 1213 to 1258 m), well-drained soil and low humidity (below 5% in the period of water deficit). Humidity above 5% at the height of the water deficit (> 5%) is a restrictive factor for the establishment of the subspecies.

Although the soil has low natural fertility, is alic, sandy (average of 65.57% of sand), shallow, with low permeability, little humidity retention and with rocky outcrops, if there are higher concentrations and availability of K (>17.5 mg dm⁻³), P (>0.55 mg dm⁻³) and sum of bases (SB>0.07 cmol_c dm⁻³), the species will establish itself successfully.

The increase in the density of subterranean stem individuals is related to higher concentrations and availability of K (>30 mg dm⁻³), higher SB (>0,099 cmol_c dm⁻³) and lower concentrations of Al (<1.19 cmol_c dm⁻³) and H+Al (<4.1 cmol_c dm⁻³).

Larger individuals with visible stems require P availability above 1.2 mg dm⁻³, but they are found at a lower density in the area. The uniqueness of the rupestrian fields and the confirmation of the spatial dependence of some soil attributes indicated by geostatistics is essential information for future conservation and management programs for the sub-species. Still, its growth and development in a soil with great nutritional limitation, transforms this sub-species into a source of germplasm for researches that aim to improve the efficiency of cultivated plants in the use of minerals and in the resistance to environmental stresses.

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LEANDRO DA SILVA ALMEIDA¹

<https://orcid.org/0000-0003-4692-9846>

DENISE G. DE SANTANA¹

<https://orcid.org/0000-0001-8328-9687>

EDNALDO C. GUIMARÃES²

<https://orcid.org/0000-0001-8932-3890>

¹Universidade Federal de Uberlândia, Instituto de Ciências Agrárias, Bloco CCG, Sala 1C 206, Rodovia BR 050, Km 78, Campus Glória, 38410-337 Uberlândia, MG, Brazil

²Universidade Federal de Uberlândia, Faculdade de Matemática, Av. João Naves de Ávila, 2121, Bloco 1J, Sala 114, Campus Santa Mônica, 38408-144 Uberlândia, MG, Brazil

Correspondence to: **Leandro da Silva Almeida**

E-mail: almeidalean26@gmail.com

Author contributions

Leandro da Silva Almeida - The research is part of the doctoral work, being the principal researcher. Responsible for writing and analyzing the article. Denise Garcia de Santana - The advisor professor of the study. Contributions in conducting the studies and writing the results. Ednaldo Carvalho Guimarães - The co-advisor professor with great contribution in geostatistical analysis. Contributions in conducting the studies and writing the results.

