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Non-biotic factors determining plasticity of the prospective oil-rich macauba palm (*Acrocomia aculeata*)

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Abstract Although macauba palm (*Acrocomia aculeata*) is a palm native to neotropics with wide distribution in Brazil and has significant potential for biofuel production, little is known regarding its variability and adaptability to environment. The aim of this study was to investigate the association of macauba palm phenotypes to soil attributes and other environmental factors. Macauba palms from 18 locations of three geomorphological provinces from the state of São Paulo, Brazil, were evaluated regarding chemical, physical and morphological soil attributes and plant morphological attributes. Data were analyzed by uni- and multivariate statistics. Univariate statistical analysis showed that there is great variability of botanical components due to soil fertility, particle size distribution and drainage and to atmospheric climate conditions. Principal component analysis identified the botanical variables fruit weight and size and palm tree circumference at chest height, and the soil variables organic matter of A horizon contents of sand and clay, and exchangeable calcium, manganese, copper, potassium and phosphorus from subsurface horizons as those with the greatest contribution in distinguishing the studied environments. Redundancy analysis identified total sand—inversely associated to water retention—pH—directly influenced by exchangeable bases—and micronutrients Zn and Mn from subsurface horizons, together with soil organic matter from A horizon, as those most associated to the botanical variables fruit weight and size. These associations show that soil fertility and particle size distribution are determining factors for the productive potential of macauba palm.

Keywords Oilseed plant · Biofuel · Soil attributes · Phenological attributes · Environmental adaptability · Genetic divergence

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Introduction

Palms (Arecaceae) constitute a group of plants common in tropical forests that can show morphological, phenological and genetic divergences among closely related species along resource gradients (Henderson et al. 1995; Svenning 2001; Savolainen et al. 2006).

Macauba palm (*Acrocomia aculeata* (Jacq.) Lodd ex Mart.) is a perennial fruit-bearing palm tree, with spines, whose stipe may reach 15 m height with 20–30 cm diameter (Lorenzi 1992), native of the savannas and open forests, distributed throughout tropical and subtropical Americas (Henderson et al. 1995). This species presents phenotypic plasticity or ability to express different phenotypes under various environmental conditions (Schlichting 1986). The macauba palm has mixed mating system (Abreu et al. 2012) with extensive genetic variability within and among natural populations (Nucci et al. 2008) expressed on the degree of germination and morpho-agronomic characters (Berton et al. 2013).

Currently, the macauba palm has drawn interest due to the possibility of its use for biofuel production. Its fruits show great potential for oil production, being able to produce over 4000 L of vegetable oil per hectare (Silva 1994; Colombo et al. 2017; Evaristo et al. 2016). The residual cake of the oil extraction from the fruit is used in animal feed and may also be employed as an effective filter in the adsorption of dye waste in chemical industrial effluents (Vieira et al. 2012). Nowadays, it is used in popular medicine, as food, and in craftwork and cosmetics, among other applications (Lima et al. 2003). There are pilot projects involving macauba palm in agroforestry systems in Brazil and planting initiatives of this species for recovery of degraded areas.

The macauba palm occurs spontaneously throughout nearly the whole Brazilian territory. However, its most dense populations are located in Minas Gerais, São Paulo, Goiás, Mato Grosso and Mato Grosso do Sul, being widespread in Cerrado (a tropical savanna typical of Brazil) areas (Bondar 1964; Silva 1994; Henderson et al. 1995; Scariot et al. 1991, 1995; Lima et al. 2003).

Despite its wide geographical distribution, little is known regarding macauba palm adaptability to environmental conditions such as those of soils, climate and vegetation formations associated to its populations within the Brazilian territory. Moreover, little is known on the association between environmental conditions and phenotypic characteristics of its populations. Nevertheless, the combination of ecological plasticity, favorable physiological attributes such as high photosynthetic capacity, and high productivity should give macauba palm great capacity of adaptation to its different natural occurring environments (Pires et al. 2013), taking Fisher's (1930) concept of adaptation, as the movement of a population towards a phenotype that best fits the present environment.

Soil is a major determinant of the composition and functioning of terrestrial ecosystems (Lambers et al. 2008). On a particular landform, the distributional pattern of plant species has been related to plant strategies, tolerance for severe stress and disturbance gradients, and biotic interactions (Levine 2000). In that sense, macauba palm is considered one of the most conspicuous palm species in Brazil, as it grows spontaneously in large populations either in degraded or intact areas and is well-adapted to different ecosystems (Motta et al. 2002; Ratter et al. 2003). Their spontaneous distribution follows naturally high fertility soils and native forest vegetation, evidencing that despite the species pioneer behavior, it avoids extremes of nutrient and water deficiencies (Motta et al. 2002), as illustrated in Fig. 1.

The present study seeks to investigate the association of macauba palm phenotypes to environmental sources of variation as factors of adaptation.

Materials and methods

Eighteen locations with native macauba palm populations were previously field-identified and selected according to their geographic distribution along the state of São Paulo (Table 1). Those locations represented three geomorphological provinces of the state of São Paulo: Basaltic Cuestas (Cuestas Basálticas), Peripheral Depression (Depressão Periférica) and Occidental Plateau (Planalto Ocidental) (Ponçano et al. 1981). Some of those palm trees occur under distinct environments regarding geological formation, relief, native vegetation associated to them, and climate, among other environmental factors, besides differing in botanical characteristics, what reinforces the need to study them separately. Soil collection was carried out by composite sampling with an auger under the projection of palm trees canopy, with samples composed of five subsamples in the years of 2008 and 2009. Soils were collected at two layers: 0–20 and 20–50 cm depth, based on the assumption that the soil profile down to 50 cm is the most important for the development of macauba palm. Nevertheless, soils were observed down to the depth of 1 m to identify other limiting soil factors and to classify soils. Soil classification at each sampling location was made according to the U.S. Soil Taxonomy (Soil Survey Staff 2010). Morphological attributes used for soil characterization and classification were color (Munsell Soil Color chart), particle-size distribution (PSD)

Fig. 1 Environments of macauba palm naturally occurring populations in the states of São Paulo (*1* to *4*) and Minas Gerais (*5*), Brazil: *1* spontaneous consortium with coffee; *2* spontaneous grazing-forestry system, *3* hill top with rock outcrops; *4* riparian; *5* grazing lands and native vegetation under regeneration

and consistency when moist, besides soil depth and drainage (Soil Survey Division Staff 1993), in addition to epipedon and soil subsurface diagnostic horizons (Soil Survey Staff 2010).

Soil particle size distribution (PSD) analysis was carried out by the densimeter (modified Bouyoucos) method (Camargo et al. 1986). Soil chemical determinations for fertility purposes were pH in $CaCl_2$, organic matter (SOM), potential acidity (H + Al), and

Table 1 Sampled macauba palm trees, coordinates in UTM (meters) and cities to which they belong

Sampled site	Abbreviation	Zone	UTM N	UTM E	City
Red	RED	23 S	7,487,684	294,269	Jaguariúna
Estância Regina	REG	23 S	7,487,539	293,839	Jaguariúna
CEC 1	CC1	23 S	7,470,776	285,118	Campinas
CEC 2	CC2	23 S	7,470,425	285,395	Campinas
CEC 3	CC3	23 S	7,469,546	285,834	Campinas
Dourado 1	DO1	22 S	7,547,275	776,455	Dourado
Dourado 2	DO2	22 S	7,547,362	776,261	Dourado
Dourado 3	DO3	22 S	7,547,633	775,760	Dourado
Santa Rosa de Viterbo 1	VI1	23 S	7,633,971	249,517	Santa Rosa de Viterbo
Santa Rosa de Viterbo 2	VI2	23 S	7,628,942	240,735	Santa Rosa de Viterbo
São Simão	SIM	23 S	7,633,915	249,644	São Simão
Barbosa	BAR	22 S	7,646,680	613,733	Barbosa
São Pedro do Turvo 1	TU1	22 S	7,488,504	631,802	São Pedro do Turvo
Piquerobi 1	PI1	22 S	7,573,953	415,871	Piquerobi
Piquerobi 2	PI2	22 S	7,574,344	415,673	Piquerobi
Piquerobi 3	PI3	22 S	7,574,314	415,604	Piquerobi
Porto X	POR	22 S	7,542,076	349,269	Teodoro Sampaio
Morro do Diabo	MOR	22 S	7,506,722	359,300	Teodoro Sampaio

exchangeable potassium (K), phosphorus (P), calcium (Ca), magnesium (Mg), boron (B), iron (Fe), manganese (Mn), zinc (Zn) and copper (Cu) (Raij et al. 2001). After chemical analysis, cation exchange capacity (CEC), sum of bases (SB) and base saturation (V%) were calculated.

Collection of botanical material was carried out in 90 plants, five productive plants for each palm tree population, from February to April, 2009. Botanical variables measured and observed in the field were circumference at breast height (CBH), plant height, number of bunches in production, dry bunches and total bunches. From each palm tree, 20 fruits from the same bunch were collected with the aid of a ladder and a pruner. Fruit weight, length and width measurements were taken in the laboratory using analytical balance and Starrett series 799-6/150 digital caliper rule.

Plant morphology data were subjected to analysis of variance, and mean values were compared by Tukey test at 5% significance through the SISVAR 4.6 program (Ferreira 2003) for the purpose of evaluating how these variables behave in relation to the environmental sources of variation (geomorphological province, climate, drainage, soil nutrients and acidity, soil particle size distribution and lithology). Number of bunches in production was standardized according to the equation: [Square root of y + 0.5 − Square root (y + 0.5)].

Multivariate statistical analysis was used to evaluate soil-vegetation relationships. Environmental and plant morphological data were initially analyzed by the principal component analysis (PCA) ordering method, and then by redundancy analysis (RDA). Data matrix for PCA analysis was composed by *n* locations and *m* descriptors of the environment and by plant morphology descriptors. There were seven plant morphology descriptors and 30 environmental descriptors, including soil chemical and physical attributes at the two sampled layers (0–20 and 20–50 cm) per palm tree location. Complementary variables, such as silt, that is the fine earth (clay + silt + sand) minus "clay + sand" and sum of bases (Ca + Mg + K + Na) as well as base saturation were eliminated for being mutually associated or supplementary. This analysis allowed evaluation of variable variances all together, thus selecting 13 environmental soil variables (physical and chemical) from the 20 to 50 cm layer, two variables from the 0 to 20 cm layer, and seven variables of plant morphology to participate in the final data matrix. As required by the RDA, two data matrices were organized, one considering plant morphological data, and another, environmental data consisting of those 22 variables previously selected by

PCA. For the RDA to be statistically valid, the number of m descriptors (botanical and environmental) must be less than the number of n locations. Monte Carlo permutation test (Ter Braak 1988) was used to evaluate the level of significance of the RDA ordination axes. Multivariate statistics were processed by FITOPAC 1.6 software (Shepherd 2006).

Results and discussion

Macauba palm trees were identified in areas corresponding to two Koeppen climatic types: C_{wa}, subtropical, with rainy summers, dry winters, mean temperature of the hottest month above 22 °C and of the coldest month below 18 °C; and A_w, tropical rainy, with dry winter, mean temperatures above 18 °C in the coldest month and above 22 °C in the most warm month. Considering all studied locations, mean annual temperatures range from 15 to 28 °C, coincident with the annual minimum and maximum reported by Motta et al. (2002). Land use associated to macauba palm populations shows large diversity, but macauba individuals under a more dense plant cover, such as forest, can hardly be found, suggesting that the species adapts more easily to environments of lower competition for light and nutrients. Considering slope and their relative position on landscape, macauba palm trees are hardly found on hill summits, but frequently found on hillsides and lowland, which is in agreement with observations of Motta et al. (2002) in three geographical regions of the Minas Gerais state, Brazil, where the palm occurs at positions from midslope to toeslope.

From 18 locations, 10 had soils with base saturation (V) $\geq$ 50% in the A horizon and eight have V $<$ 50% on the A horizon. Of the 18 sampled subsurface horizons eight had a high fertility status (V $\geq$ 50%) and 10 had a low fertility (V $<$ 50%) (Table 2). The greatest V values (51 to 70%) were found in soils from the Basaltic Cuestas province, what is in the range of moderate base saturation (Raij et al. 1996). Soil fertility was considered mainly through evaluation of the 20–50 cm layer (B or C horizon), layer less influenced by land management than those superficial. The soil's first 50-cm depth was considered the most important layer for development of macauba palm roots. Five locations had soils of very high acidity (Raij et al. 1996), located in the municipalities of São Simão, São Pedro do Turvo and Piquerobi; eight soils had high acidity, from Jaguariúna, Campinas, Barbosa and Teodoro Sampaio; four had medium acidity and were located at Campinas and Dourado; and only one was identified with low acidity, occurring in Santa Rosa do Viterbo. This shows macauba palm adaptability to a large range of soil acidity levels. Soil macronutrient content classes, as described by Raij et al. (1996), were different depending on the geomorphological region, with prevalence of low to medium macronutrient contents. Soils showed high levels of micronutrients in three geomorphological provinces. Soil B horizon particle-size distribution was mostly loamy. Although drainage of the sampled locations showed large variation (Table 3), those occurrences agree with the findings of Markley (1956) and Martin and Guichard (1979), which indicated limited distribution of macauba palm in areas of deficient drainage.

Results of univariate statistics (Table 4) showed that, except for CBH, studied botanical variables differed significantly among locations, showing a great deal of variability among macauba palm trees. This may be due to genetic variability of plants from different locations, to environmental factors variability among the three geomorphological provinces of the state of São Paulo or to the combination of these factors. Bunches in production, botanical variable related to the productive potential of the palm tree, exhibited the greatest mean values at the Dourado 1 location. Furthermore, in that location, the fruits were relatively larger and heavier. Botanical variables CBH and fruit size and weight were affected by climatic types, with greater values of these three variables under the more mild C_{wa} climate, than under the hotter A_w climate. Plants from Peripheral Depression and Basaltic Cuestas geomorphological provinces populations were taller, had greater CBHs and larger and heavier fruits than those of the Occidental Plateau.

Poor to somewhat poor drainage was also responsible for significant reduction in fruit weight and size, CBH and bunches in production, whereas plant height was not affected by soil drainage. Fruit size and weight and plant height showed greater values on soils developed from granitic rocks, whereas greater number of bunches in production was found on soils developed from basic rocks. Association of botanical variables to rock type distribution may be consequence of the influence of this factor for soil formation

Table 2 Soil Chemical properties of soils under18 macauba palm sites at the state of São Paulo, Brazil

Site	pH-A	pH-B	K-A (mmolc/dm^3)	K-B (mmolc/dm^3)	Ca-A (mmolc/dm^3)	Ca-B (mmolc/dm^3)	Mg-A (mmolc/dm^3)	Mg-B (mmolc/dm^3)	V-A (%)	V-B (%)
RED	5.1	4.7	1.8	1.9	36.0	20	9	2	60	36
REG	4.3	4.9	1.4	2.2	13.0	22	3	5	23	46
CC1	4.9	5.0	2.2	1.2	27.0	23	9	9	50	57
CC2	4.7	4.5	2.0	0.9	1.60	10	6	4	41	41
CC3	5.4	5.3	2.2	1.0	64.0	32	14	6	68	53
DO1	5.2	5.1	0.9	4.1	36.0	35	12	12	59	63
DO2	5.3	5.2	2.4	2.8	68.0	34	29	14	74	65
DO3	5.2	5.1	1.2	1.5	62.0	52	20	16	69	65
VI1	5.3	4.9	3.6	2.5	32.0	17	14	6	64	64
VI2	5.6	5.7	6.9	5.4	171.0	123	38	28	88	85
SIM	4.2	4.2	0.8	0.5	7.0	2	1	1	13	12
BAR	4.6	4.6	0.7	0.7	14.0	13	5	4	39	41
TU1	4.2	4.0	1.7	3.9	9.5	5	8	5	24	15
PI1	4.8	4.3	3.6	1.3	12.0	11	51	27	76	66
PI2	4.5	3.9	0.6	0.2	7.0	2	1	1	26	17
PI3	4.3	4.0	0.3	0.1	5.0	2	0	0	18	12
POR	5.4	5.0	0.7	0.5	12.0	6	4	2	60	44
MOR	4.7	4.4	0.7	0.6	5.0	8	3	2	37	39

A horizon depth: 0–20 cm; B horizon depth: 20–50 cm

pH-A, pH of the A horizon; pH-B, pH of B horizon; K-A, potassium of A horizon; K-B, potassium of B horizon; Ca-A, calcium of A horizon; Ca-B, calcium of B horizon; Mg-A, magnesium of A horizon; Mg-B, magnesium of B horizon; V-A, base saturation of A horizon; V-B, base saturation of B horizon

or of the broad spatial distribution of these geological formations, which cannot be dissociated from climatic, topographic or plant genetics variations. The analysis showed there is large plasticity on botanical components of macauba palm among the populations. Possible environmental causes are soil fertility and soil water availability, determined by particle size distribution, drainage and climate, with this last factor being differentiated among studied locations especially by small differences in temperatures, which are milder in the C_{wa}, and in the length of the dry season, longer in the A_w.

Soil and plant data matrix were initially analyzed by PCA, used as a selective and exploratory method, and consisted of 18 sampled locations (plant populations) and 37 variables, where 30 were soil variables of the depths 0–20 and 20–50 cm, and seven plant variables. Few available data of land use history from each studied site and the fact that subsurface soil layers carry more stable attributes for perennial plants and are less influenced by those non-controlled practices were considered, together with PCA results, to eliminate all environmental variables from A horizon, except for SOM (soil organic matter) and H + Al (potential acidity). For further analysis, all soil variables from B horizon plus SOM and H + Al from A horizon together with all plant variables were kept for final analysis, remaining a total of 22 variables. Variables were identified by the symbols "-A" for the A horizon and "-B" for the B horizon. All selected variables showed correlations greater than 0.2 with axes 1 and 2.

The new PCA analysis showed CBH, total sand, clay, SOM, pH, K, Ca, CEC, Cu, and Mn had greater correlation to axis 1, which expressed 37.91% of the total data variance. Plant height, fruit weight, fruit size, number of dry bunches, P, Mg, H + Al, B, Fe and Zn were most correlated to axis 2, which represented

Table 3 Soil Classes classes and morphological attributes of 18 soils sampled under macauba palm sites on in the state of São Paulo, Brazil

Site	Soil class[1]	Drainage class	Depth	PSD[2] class Horizon A	Color	Surface horizon	PSD class Horizon B	Color	Sub-surface horizon
RED	RLdh	Well	0–60	Loamy	7.5YR 3/3	Umbric	Loamy	7.5YR 3/3	None
REG	RLd	Well	0–40	Loamy	7.5YR 2/3	Ochric	Loamy	7.5YR 2/4	None
CC1	GXbe	Poor	100 +	Loamy	5Y 2.5/1	Umbric	Clayey	2.5Y 4/1	Kandic
CC2	LVd	Somewhat excessive	100 +	Loamy	5YR 3/4	Ochric	Loamy	2.5YR 3/4	Oxic
CC3	LVdf	Somewhat excessive	100 +	Clayey	2.5YR 3/4	Ochric	Clayey	2.5YR 3/6	Oxic
DO1	CXef	Moderate well	100 +	Loamy	2.5YR 3/4	Ochric	Clayey	2.5YR 3/4	Cambic/Kandic
DO2	CXef	Moderate well	90 +	Loamy	2.5YR 3/4	Ochric	Loamy	2.5YR 3/4	Cambic
DO3	CXef	Moderate well	95 +	Loamy	2.5YR 3/2	Mollic	Loamy	2.5YR 3/4	Cambic
VI1	PVAe	Well	100 +	Loamy	2.5YR 3/3	Ochric	Loamy	2.5YR 3/4	Kandic
VI2	RLe	Well	100 +	Clayey	2.5YR 3/2	Mollic	Clayey	2.5YR 3/3	None
SIM	RQg	Poor	100 +	Sandy	10YR 2/1	Umbric	Sandy	10YR 4/1	Cr/Btc None
BAR	LVAd	Very well	100 +	Loamy	5YR 3/2	Ochric	Loamy	3.5YR 4/6	Oxic
TU1	LVd	Well/somewhat excessive	100 +	Loamy	2.5YR 3/4	Ochric	Clayey	2.5YR 3/4	Oxic
PI1	RQo	Excessive well	100 +	Sandy	2.5YR 3/4	Ochric	Sandy	2.5YR 3/6	None
PI2	RQg	Poor	100 +	Sandy	2.5YR 4/3	Ochric	Sandy	10YR 5/3	None
PI3	RQo	Somewhat poor	100 +	Sandy	5YR 3/4	Ochric	Sandy	5YR 3/5	None
POR	RQo	Excessive well	100 +	Sandy	2.5YR 3/4	Ochric	Sandy	2.5YR 3/6	None
MOR	LVd	Somewhat excessive	100 +	Sandy loam	2.5YR 3/6	Ochric	Loamy	2.5YR 3/6	Oxic

[1]RLdh, Lithic Udorthent; RLd, Lithic Udorthent; GXbe, Typic Kandiaqualf; LVd, Rhodic Hapludox; LVdf, Rhodic Hapludox; CXef, Typic Eutrudept; PVAe, Typic Kandiudalf; RLe, Lithic Udorthent; RQg, Aquic Quartzipsamment; LVAd, Typic Hapludox; RQo, Typic Quartzipsamment; RQg, Aquic Quartzipsamment

[2]*PSD* particle-size distribution

13.09% of data total variance. Weight and size of fruits and P correlated well to both ordination axes.

PCA plot (Fig. 2) showed that distribution of macauba palm follows very closely the direction of both pH and clay vectors. The trees on soils with high pH (Viterbo 2; Dourado 1, 2 and 3; Campinas CEC 3) follow closely the pH vector, a vector with the highest score with PCA axis 1. The vectors of the basic cations K, Ca and Mg showed a similar tendency than that of the pH vector and are thus associated to the same

Table 4 - Mean values of fruit size and fruit mass, circumference at breast height (CBH), plant height and number of bunches in production of natural occurring macauba palm, collected at 18 sites in the state of São Paulo, Brazil

Site	Fruit size (cm)	CBH (cm)	Fruit mass (g)	Plant height (m)	Bunches in production
RED	4.2ab	83.0ab	45.1ab	11.3a	3.8 cd
REG	4.4a	95.4ab	47.4a	9.6a-c	6.6a-d
CC1	3.7b-f	90.6ab	29.0b-g	6.4b-d	3.2d
CC2	3.9a-d	118.2a	34.2a-f	5.6 cd	4.2b-d
CC3	4.2ab	106.8ab	40.0a-c	8.2a-d	5.0b-d
DO1	4.2ab	95.4ab	41.0ab	7.1a-d	9.8a
DO2	3.8a-e	107.4ab	37.3a-d	6.8b-d	7.4a-d
DO3	3.8a-e	107.4ab	37.7a-e	5.9b-d	8.2a-c
VI1	3.9a-d	90.8ab	33.0a-g	6.2b-d	4.8b-d
VI2	4.0a-c	94.0ab	39.1a-c	9.9ab	5.6a-d
SIM	3.8a-e	96.6ab	32.9a-g	7.9a-d	3.2d
BAR	3.8a-e	73.6b	32.8a-g	5.6 cd	6.6a-d
TU1	3.4d-f	78.6b	22.0d-g	7.5ad	4.2b-d
PI1	3.3e-f	94.2ab	18.5 fg	9.3a-c	8.0a-c
PI2	3.2f	80.4b	17.0 g	7.1a-d	3.8 cd
PI3	3.2f	75.8b	19.0 fg	8.4a-c	4.6b-d
POR	3.5c-f	92.0ab	24.6c-g	4.2d	7.4a-d
MOR	3.4d-f	92.8ab	21.2e-g	5.6 cd	8.8ab

Means with different letters in the column differ by less than 5% by the Tukey test

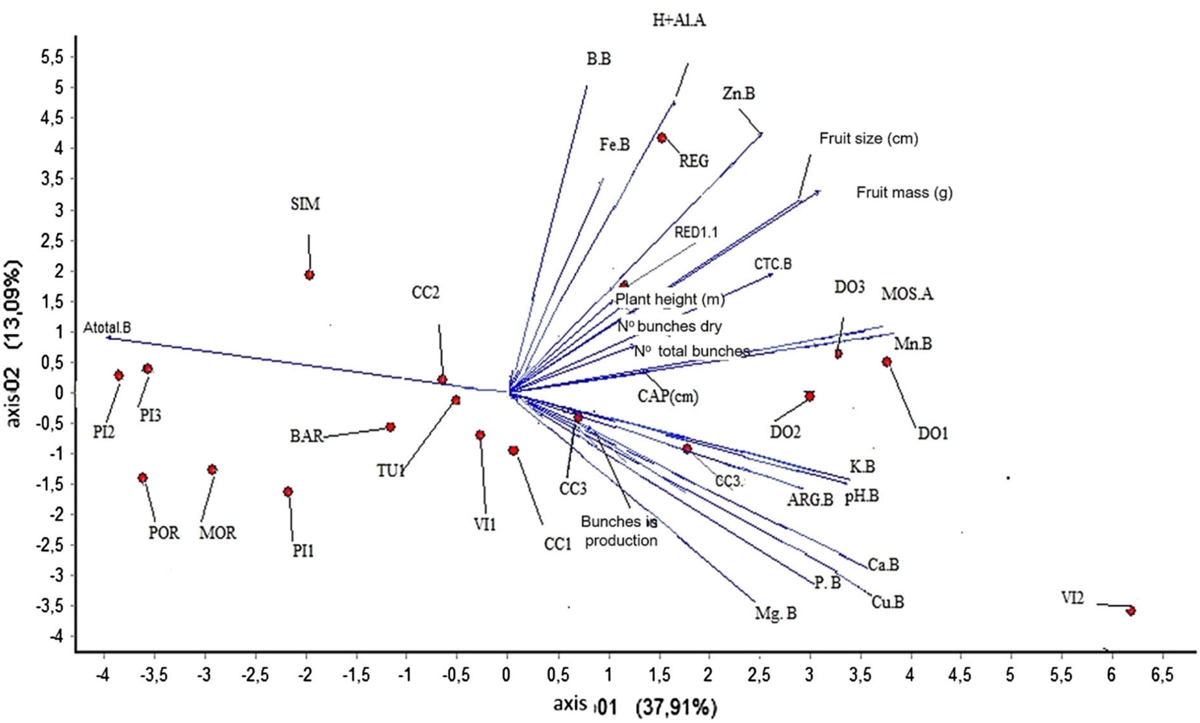

Fig. 2 Principal component analysis based on environmental variables and plant morphology and the scores of sampled 18 macauba populations in the state of São Paulo, Brazil

macaúba palm populations. On those five populations soils were developed from basic rocks (basalt and diabase). Very similar association is observed between those populations and the clay vector, another vector with high score with the PCA axis 1. In the very opposite direction the total sand vector is represented, that is closely associated to Piquerobi 1, 2 and 3, Porto X, Morro do Diabo and São Simão, all of those with soils derived from sandstones, loamy to sandy soils. Therefore, the studied macauba palm populations show a very clear gradient regarding soil fertility and particle-size distribution.

An almost inverse relationship was observed between total sand and morphological variables that indicated plant vigor (CBH, plant height, fruit size and number of bunches in production, dry bunches and total bunches). Since macauba palm populations (Porto X, Morro do Diabo and Piquerobi 1, 2 and 3) more opposed to those botanical variables, besides being more sandy, are also under a A_w climate, with warmer dry winter than populations under C_{wa}, one can associate their less favorable botanical attributes to a greater water deficit, determined by soil and climate, not neglecting the fact that soil of those sites have also lower nutrient availability.

Redundancy Analysis (RDA) was carried out using two data matrices, one of plant morphological data (7), and another of environmental data (15). Due to the high correlations between soil P and soil Ca, the program FITOPAC 1.6 (Shepherd 2006) automatically eliminated the Ca variable as redundant. Thus, the environmental data matrix was composed of 14 variables. In RDA, the first two axes explained almost 34% of total data variance, 22.59% by axis 1 and 11.17% by axis 2 (Fig. 3). This value is considered excellent in studies of ecological and environmental data due to the high number of variables that may be influencing an observation. Therefore, environmental variables of this study can explain quite well botanical attributes. Monte Carlo permutation test (Ter Braak 1988), which evaluates the level of significance of RDA ordination axes, showed significance at the level of 1% for the first three ordination axes.

In general, RDA biplot was more effective than PCA in performing ordination as function of geographical location of macauba palm trees, especially placing populations from Occidental Plateau on the plot left side, far from populations from Basaltic Cuestas or from peripheral depression (Fig. 3). RDA also captured better the relationship between environmental variables and macauba palm diversity. SOM-A, pH-B, Mn-B, clay-B, CEC-B, and Zn-B, on one end, and total sand-B, on the other end, were the environmental variables most responsible for ordering macauba palm populations on axis 1. Nevertheless, all environmental variables, except Fe-B and Mg-B, showed high correlation to axis 1 if compared to axis 2. RDA analysis confirmed evidences observed on PCA that botanical attributes that relate to favorable agronomic features are strongly influenced by soil chemical (fertility) and physical (particle size) attributes.

The high SOM-A contents on the Peripheral Depression study sites (Red, Estância Regina and CC3) (Fig. 3) is supposed to be due to the very dense macauba palm populations in those three sites, with little direct sunlight, favoring plant residues addition and SOM accumulation. Soil organic matter (SOM) is an attribute that favors plant growth due to increasing soil chemical fertility, promoting good soil physical conditions and offering a more adequate environment for soil organisms. SOM-A being the vector with the highest score with RDA axis 1 shows that macauba palm botanical features responded positively to those soil conditions and corroborated observations of Rocha (1946) and Lorenzi (1992) that this palm adapts more easily to more fertile soils.

Following SOM-A and pH-B, variables that most correlated to axis 1 were total sand-B, Mn-B, clay-B, Zn-B, CEC-B, K-B, Cu-B, B-B, P-B, and H + Al-A, what shows that more than being responsible for macauba palm ordering by RDA, these soil attributes do contribute for determining changes on macauba palm botanical features, at least on those included on the RDA botanical matrix.

Botanical variables that correlated most to axis 1 were fruit size and weight (Fig. 4). Total of bunches, bunches in production and plant height correlated better to RDA ordination axis 2, which was not associated to any environmental attribute. Dry bunches and CBH did not show high correlation to any ordination axes. Fruit size and weight were the botanical variables that explained most of data's total variance and are thereby associated to landscape stratification (with strong distribution pattern along the same RDA axis), represented in the RDA by soil fertility and particle-size attributes. The remaining botanical features may be related to plant age (height), phenological seasonality (total of bunches; bunches in production) or biannuality, or determined more strongly by plant intrinsic features, such as its genetics.

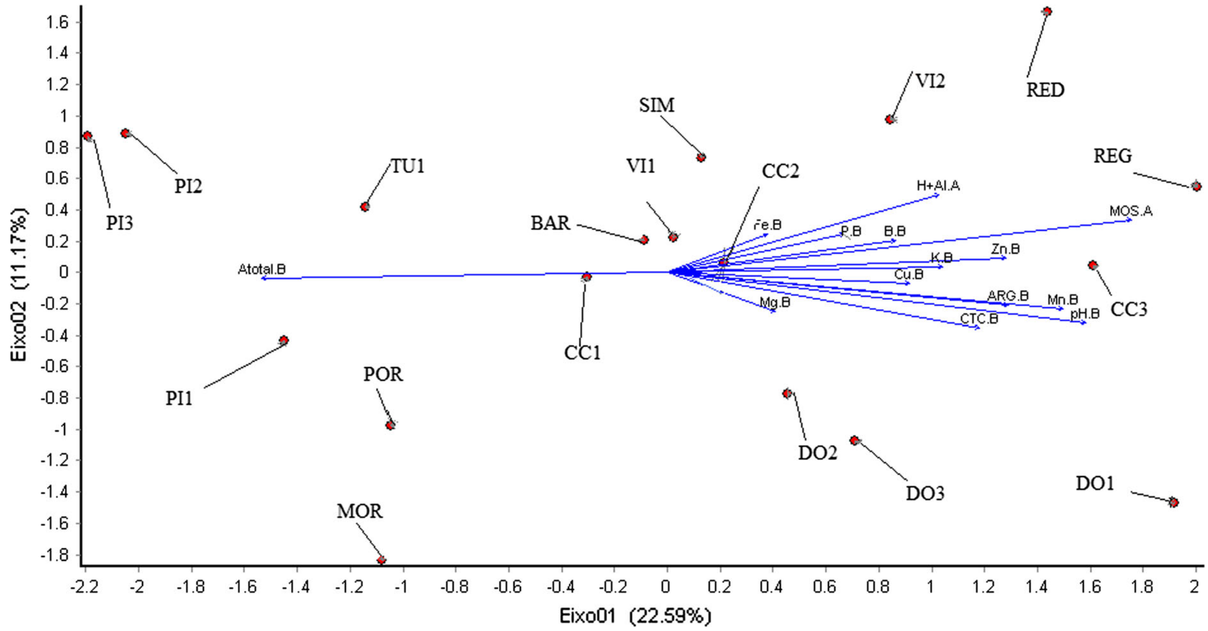

Fig. 3 Redundancy analysis based on environmental variables and plant morphology and the scores of 18 macauba sampled populations in the state of São Paulo, Brazil

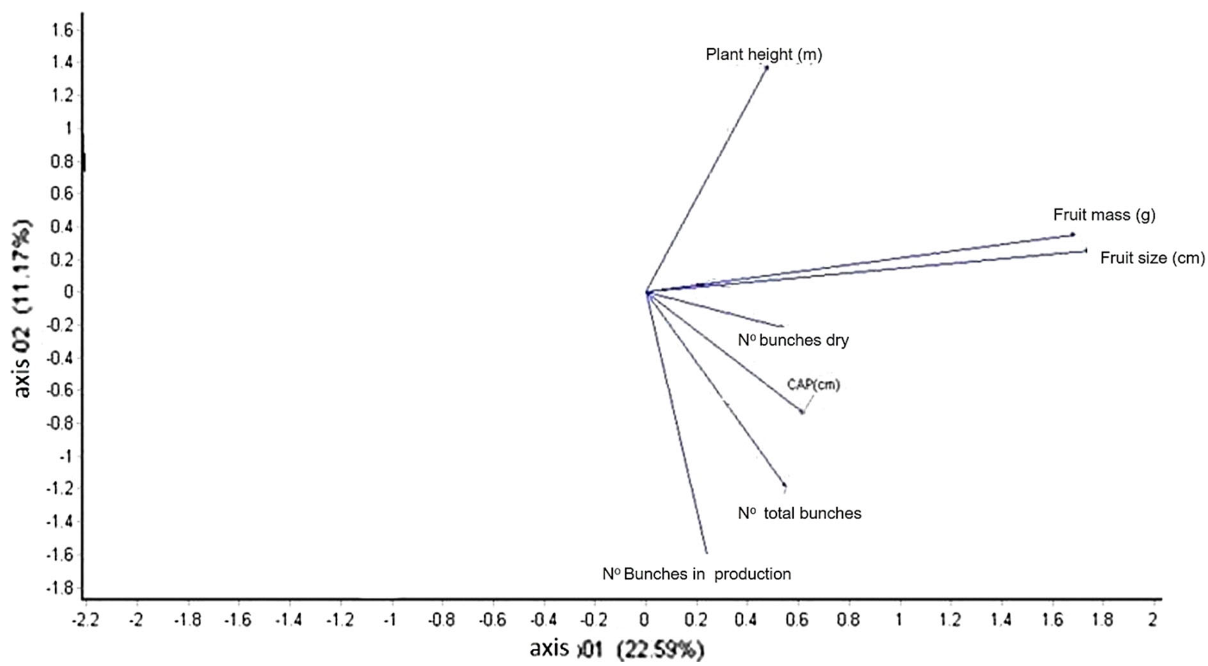

Fig. 4 Analysis of redundancy based on morphology of plant variables of macauba palm from different 18 populations in the state of São Paulo, Brazil

Conclusions

The studied sites show large variability of environmental factors, allowing stratification of macauba palm trees by different groups of variables. Soil chemical fertility—A horizon soil organic matter and B horizon pH, Ca, Mn, Cu, K and P—particle-size distribution—B horizon clay and sand—soil drainage and atmospheric climate are non-biotic factors most contributing for stratifying macauba palm in regard to its environment of occurrence.

Size and weight of macauba palm fruits, botanical features intended for agronomic purposes, are the most correlated to environmental factors, indicating that they may respond to a change in those non-biotic factors under agronomic management.

Therefore, in a prospecting approach, the study shows chemical fertility, represented by macro and micronutrients, particle-size distribution and degree of soil drainage as site-specific factors that can determine productive potential of macauba palm.

Number of dry bunches and circumference of the stem at chest height correlate very poor to all variables of the non-biotic environment.

Total bunches of macauba palm, bunches in production and plant height do not correlate to any of the studied environmental attributes, but their pattern of variation suggests that other factors such as plant age, genetics, phenology or biannuality may influence them more strongly.

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