

Growing straight versus growing decumbent: soil quality and allometry in *Syagrus glaucescens* Becc. (Arecaceae), an endemic and threatened palm of the Espinhaço Mountains, Brazil

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ABSTRACT

Syagrus glaucescens is an endemic palm found in the rupestrian grasslands of the Espinhaço Mountains in southeastern Brazil. It is highly associated with quartzitic soils and exhibits strong intra-specific morphological variation in the different areas where it occurs. Allometric traits were used to verify whether there are any significant differences in the morphological traits between populations of this species located in two distinct areas. In the region of the Serra do Cipó individuals exhibit decumbent stems whereas on the Diamantina Plateau stems are straight and perpendicular to the ground. Soil quality was related to plant morphological traits to test the hypothesis that allometric variation is influenced by soil nutritional differences. Stem shape and size differed significantly among individuals inhabiting the two different regions: individuals in Serra do Cipó were shorter and had fewer leaves compared to individuals found in the Diamantina Plateau. Water retention capacity and nutrient absorption of the soils of the two sites were markedly different. In Serra do Cipó the soils were more acid, with higher aluminum saturation and lower sand content compared to the soils in Diamantina. These traits correlated with stem shape and indicate that soil acidity and aluminum saturation influence the architecture of *S. glaucescens*.

Keywords: aluminum saturation, Diamantina, phenotypic variability, rupestrian grasslands, Serra do Cipó, soil-plant relationships

Introduction

Phenotypical variation in plant morphology may result from genetic differences among individuals and/or from the effects of environmental factors such as light, rainfall and soil quality (e.g., Archibald & Bond 2003; Ellison *et al.* 2004). Plant allometry, the study of size-correlated variations in organic form and process (Niklas 1994), is a powerful tool in understanding not only how abiotic factors cause these variations but also to investigate adaptive differences among species, competitive interactions, forest structure and dynamics, and plant life history (e.g., Niklas 1993; 2006; Weiner & Fishman 1994; Sposito & Santos 2001; Kimura & Simbolon 2002; Poorter *et al.* 2012).

Allometric studies in the Neotropics have been focused primarily on rainforest species (e.g., King 1996; Fontes 1999; Alves & Santos 2002; Kimura & Simbolon 2002; Osunkoya *et al.* 2007; Calvo-Alvarado *et al.* 2008; Rosseto *et al.* 2013) in an attempt to link the allometry of supporting and photosynthesizing structures with different life histories and light assimilation strategies (see also Lüttge *et al.* 2007).

In open vegetation, however, where light is not a limiting factor, such as in the Cerrado (savanna), shortage on water and nutrient supply, and escape from fire and herbivores may represent the most important factors selecting plant allometric variation (Archibald & Bond 2003).

The rupestrian grasslands are the most endangered and threatened physiognomy of the Brazilian Cerrado (Fernandes *et al.* 2014). The rupestrian grassland ecosystem is under the influence of seasonal climate with rainy summers and dry winters, is mostly established in quartzite-derived soils above 900 m a.s.l. The vegetation is strongly influenced by the substrate, climate and topography, with resulting high environmental heterogeneity (Carvalho *et al.* 2012; 2014). Sclerophyllous scattered shrubs and short trees form an open and poor developed canopy among the well-developed herbaceous layer. Water deficit, poor and shallow soils, and fires are important factors driving plant distribution and structure (Burman 1991; Giulietti *et al.* 1997).

Syagrus glaucescens (Arecaceae), popularly known as “coquinho-da-pedra”, is an endemic palm tree of the rupestrian grasslands of the Espinhaço mountains. Casual

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observations indicate differences in the morphology of individuals in two localities of its native range. In Serra do Cipó, the stem is strongly decumbent whereas in the Diamantina plateau its stems are mostly straight and perpendicular to the soil. Observations also indicate that while in Serra do Cipó *S. glaucescens* is found exclusively on rocky outcrops, in Diamantina it can be also found in quartzite-derived soils with well-developed vegetation. Here, we investigated the allometric variation in the two phenotypes of *S. glaucescens* and tested the hypothesis that soil nutritional traits influence such variation. We used a comparative approach to answer the following questions: (1) do stem length and shape of individuals of *S. glaucescens* vary between the two regions?; (2) are there differences in soil nutritional quality between the regions?; and (3) if so, do these differences account for allometric variation?

Material and Methods

Study area

This study was conducted in two regions of the Espinhaço mountain range, in Minas Gerais, Brazil. In Serra do Cipó the study was performed at the “Reserva Particular Vellozia” and its surroundings (43°33’W, 19°20’S to 43°39’W, 19°12’S), in the Area de Proteção Morro da Pedreira, in the municipality of Santana do Riacho. A wider studied area was examined in Diamantina plateau, including the city of Diamantina and the Parque Estadual do Biribiri (43°36’W, 18°18’S to 43°45’W, 17°54’S). Both regions are dominated by rupestrian grassland vegetation and were selected due to the high abundance of *Syagrus glaucescens* Becc. and easy access. Distance between the study sites is about 125 km.

An herbaceous layer characterizes the landscape of the rupestrian grasslands where rocky outcrops, epilithic and woody species sparsely occurs creating vegetation islands. The climate is latitude - and altitude-dependent and is classified as Cwb following Köppen, with dry winters and rainy summers and mean annual temperature varies from 17.4 to 19.8°C (Madeira & Fernandes 1999). Soils are shallow, acid, nutrient-poor, and as a result of high sand content, they are subjected to erosion and have low water retention capacity (Negreiros *et al.* 2009; Carvalho *et al.* 2012; Le Stradic *et al.* 2014).

Studied species

Syagrus glaucescens is a small palm with distribution strongly associated with quartzite outcrops that occurs in the rupestrian grasslands from Serra do Cipó to Diamantina (Miola *et al.* 2011). It was included in the list of threatened species of the International Union for Conservation of Nature and Natural Resources (Vulnerable category) as a result of its small distributional area and high destruction of its native habitat (Noblick 1998). Despite this fact, the few

studies on *S. glaucescens* are restricted the phenology (Miola *et al.* 2010; Belo *et al.* 2013) and spatial distribution (Miola *et al.* 2011). Miola *et al.* (2010) also observed resistance and increased flowering after fire.

Adults of *Syagrus glaucescens* might reach up to four meters high and are usually found aggregated in small populations. The stem may be straight or decumbent. Glassman (1987) described two closely related *Syagrus* Mart. species in the region and argued that morphological differences in plant height and leaflet number were the main criteria for splitting them. On the other hand, their distribution patterns were also different: while *S. duartei* Glassman was restricted to the quartzitic outcrops above 1300m in Serra do Cipó *S. glaucescens* was found in northern Diamantina region, always at lower elevations. Conversely, Marcato & Pirani (2001) argued that splitting *Syagrus* into two species was complicated in the field due to overlap in morphological traits. Therefore, we adopted the criteria established by Marcato & Pirani (2001), who merged the two species into *S. glaucescens*, to address our questions.

Allometric analysis

To examine differences in allometry between the two phenotypes (Serra do Cipó, and Diamantina), 42 adults (individuals with the presence of reproductive structures) in each region were randomly selected and tagged. Individuals were randomly selected during random walks, always considering a minimum distance of 20 m between marked plants. Stem length, height, and diameter, and total number of leaves were recorded for each individual to indicate the allometric parameters. Stem length was defined as the distance between stem base to the tip of the leaf apex whereas stem height was the vertical distance from ground level to the tip leaf apex. When the plant has the habit decumbent, length tends to be larger than the height, so the stem length/height ratio (L/H) was used as a measure of stem shape. The Kolmogorov-Smirnov test was used to examine data normality. We compared the L/H ratio using Mann-Whitney test, as the data were not normally distributed. Differences in stem length, height and diameter, and total leaf number between the two phenotypes were evaluated using a t-test. Data were log-transformed to better fit the linear regressions on the measured variables (Niklas 2004).

Soil analysis

To characterize the soils where the two phenotypes of *Syagrus glaucescens* were growing, 15 mixed soil samples from each population were obtained (n = 30). Mixed sample (10 soil samples collected beneath each palm individual) consisted of soil collected from 0 to 15 cm depth. The procedures for mixed samples followed Dick *et al.* (1996). Each sample was dried at room temperature under shade, homogenized, and sent to the Soil Department of the Federal

University of Viçosa for analysis. Soil granulometric analyzes (fine sand, coarse sand, silt, clay) were performed following EMBRAPA (1997).

For variables with normal distribution or log-transformed, differences in soil properties between areas were analyzed through a T-test, whereas Mann-Whitney test was applied for variables with non-parametric distribution. Soil traits that statistically differed between the two areas were correlated with plant traits using Pearson's correlation.

Results

Allometric variation

A significant difference in stem length, height, and total leaf number were observed between the two phenotypes of *Syagrus glaucescens* (Tab. 1). The phenotype found in Diamantina had consistently longer stems (ca. 21%), were taller (35%; Fig. 1) and had more leaves (19%) than the phenotype found in Serra do Cipó. Stem shape also differed between the two phenotypes ($t = 2507$, $P < 0.001$). In Diamantina stems were straight and perpendicular to the soil, whereas in Serra do Cipó stems were tortuous and decumbent. The height and length measurements of stems were significantly correlated in spite of the morphological differences found between the two phenotypes (Fig. 2). Stem diameter did not vary with stem length or height in any of the phenotypes (Tab. 2). Nevertheless, stem height and

diameter were positively correlated ($r = 0.562$, $P = 0.009$; Fig. 3). L/H ratio was negatively correlated to stem diameter ($r = -0.569$, $P = 0.008$) and height ($r = -0.650$, $P = 0.001$; Fig. 3), indicating that stem height and diameter decreased as the shoot became more decumbent.

Total leaf number (an estimation of crown volume) was also positively correlated with stem height ($r = 0.60$, $P = 0.005$), length ($r = 0.886$, $P < 0.001$), and with stem diameter ($r = 0.815$, $P < 0.001$; Fig. 3). Otherwise, total leaf number correlated negatively with the L/H ratio ($r = -0.614$, $P = 0.004$). Albeit a statistically significant correlation between total leaf number and stem height was found, there were no significant differences between the two phenotypes ($t = 1.40$, $P = 0.276$). Conversely, the linear regression between stem length and total leaf number of *S. glaucescens* differed statistically between the two populations studied ($t = 3.8711$, $P < 0.001$; Fig. 4).

Soil nutritional status

Soils colonized by *Syagrus glaucescens* were very similar in organic matter and macronutrient content in the two regions (Tab. 3). However, significant differences between the two areas were found in remanescant phosphorous, Al saturation, pH, and soil granulometry (Tab. 3), supporting the contention that water retention capacity and nutrient absorption is different in the soils of the two regions. Soils in Serra do Cipó are more acidic, alic with higher Al content compared to soils in Diamantina.

Table 1. Summary statistics (mean \pm SD) of the two phenotypes of *Syagrus glaucescens* ($n = 42$), * $P < 0.001$; ** $P < 0.005$; ns = non significant).

Plant traits	Diamantina	Serra do Cipó	t value
Height (cm)	176.61 \pm 59.68	114.26 \pm 42.89	5.442*
Length (cm)	178.71 \pm 60.36	141.09 \pm 41.94	2.990**
Diameter (cm)	53.14 \pm 15.42	50.16 \pm 20.31	1.339 ^{ns}
Total leaf number (unit)	8.97 \pm 2.00	7.30 \pm 1.47	2.212*

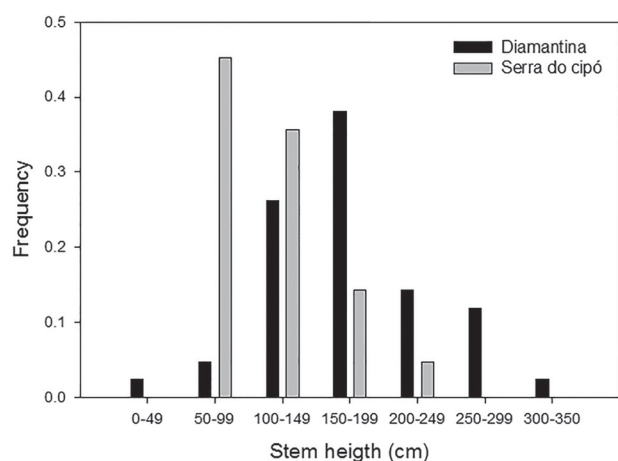


Figure 1. Stem height classes of *Syagrus glaucescens* in both studied areas.

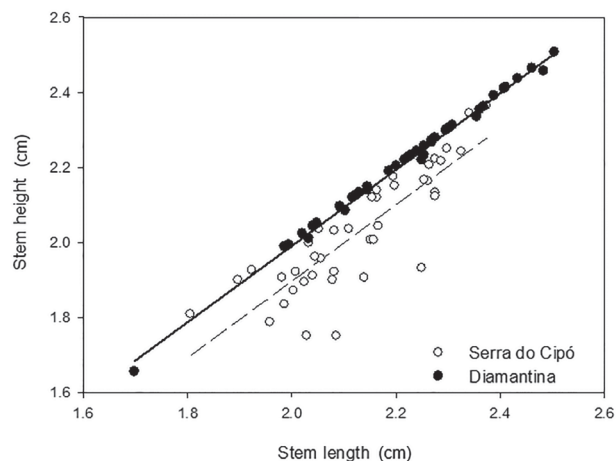


Figure 2. Linear regressions between stem length and height in Diamantina ($F = 8792.725$; $P < 0.001$; $r^2 = 0.9955$; $y = -0.0445 + 1.0174.x$) and in Serra do Cipó ($F = 103.2182$; $P < 0.001$; $R^2 = 0.7207$; $y = 0.6983 + 0.7057.x$).

Table 2. Summary of linear regression between stem diameter, stem length and height (n = 42). (Confidence interval = 95%). R² = determination coefficient, r = regression coefficient.

	R ²	r	F	P
Diamantina				
Diameter × Height	0.0154	0.171	0.627	0.433
Diameter × Length	0.0109	0.141	0.440	0.511
Serra do Cipó				
Diameter × Height	0.0335	0.155	1.388	0.246
Diameter × Length	0.0040	0.0447	0.163	0.689

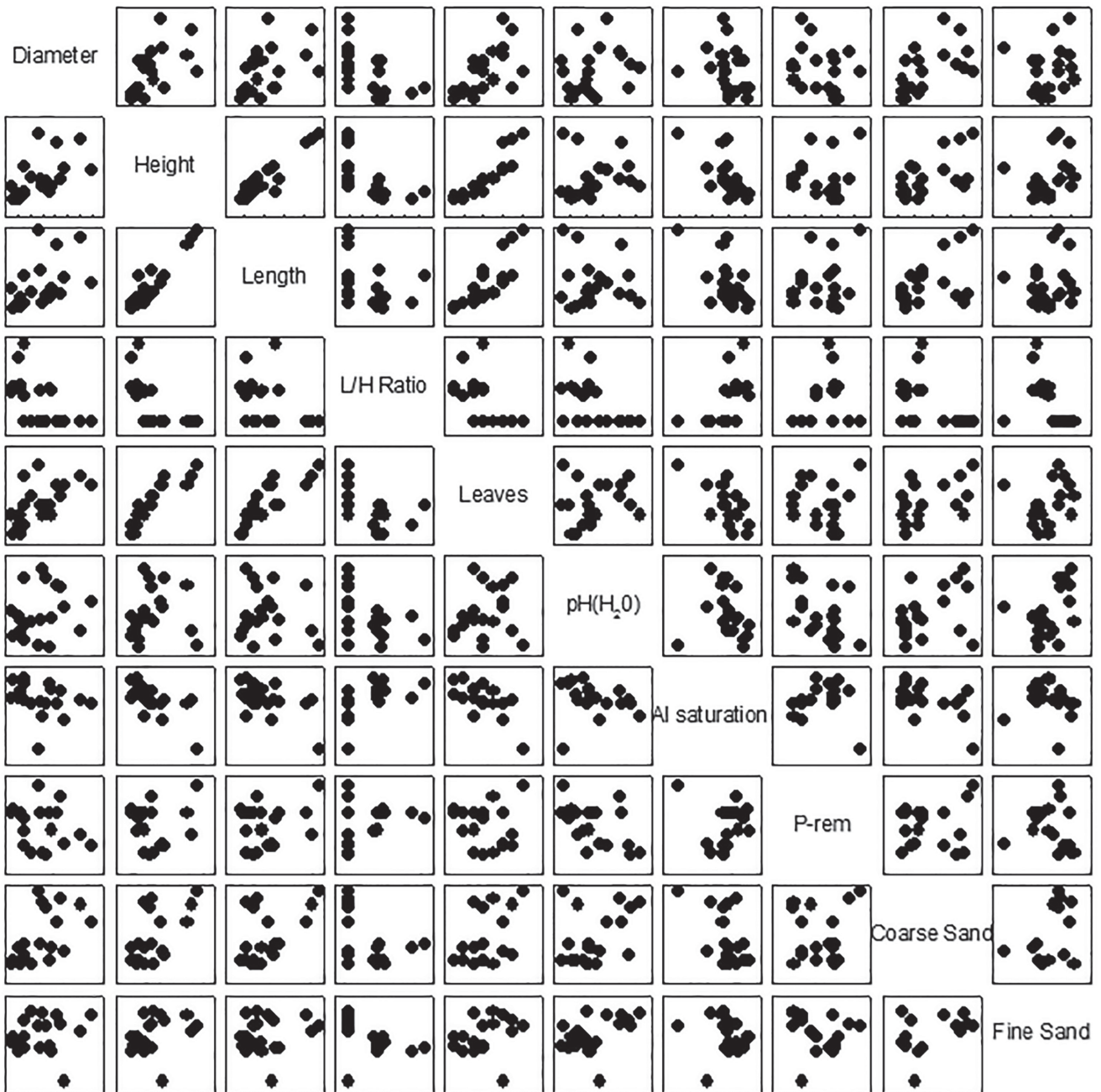


Figure 3. Pearson correlation between soil and plant traits (n = 20).

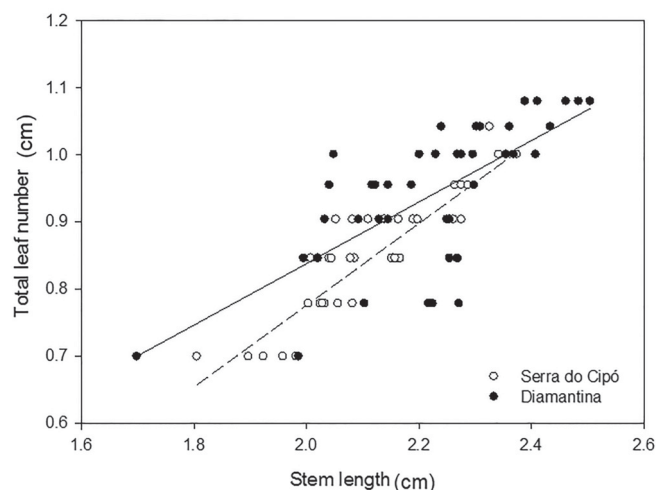


Figure 4. Linear regression between stem length and total leaf number of *Syagrus glaucescens* in Diamantina ($F_{1,40} = 37.905$; $P < 0.001$; $r^2 = 0.4866$; $y = -0.0777 + 0.4579 \cdot x$) and Serra do Cipó ($F_{1,40} = 167.245$; $P < 0.001$; $r^2 = 0.8070$; $y = -0.4426 + 0.6091 \cdot x$).

Table 3. Chemical and textural traits of soils in which *S. glaucescens* was found. Means (\pm SD; $n = 10$) for both studied areas are followed by their respective P and t values ($\alpha < 0.05$). Variables with asterisk represent statistically different means between the two phenotypes.

Parameter	Diamantina	Serra do Cipó	Statistical Test	P	t
pH (H ₂ O)*	4.46 \pm 0.30	4.14 \pm 0.14	t	0.008	2.978
P (mg/dm ³)	1.58 \pm 0.80	1.66 \pm 0.37	M-W	0.493	95.500
K (mg/dm ³)	39.00 \pm 17.76	51.00 \pm 19.48	t	0.167	-1.439
Ca ²⁺ (cmol _c /dm ³)	0.02 \pm 0.02	0.002 \pm 0.006	M-W	0.101	122.000
Mg ²⁺ (cmol _c /dm ³)	0.093 \pm 0.18	0.074 \pm 0.02	M-W	0.068	80.500
Al ³⁺ (cmol _c /dm ³)*	1.28 \pm 0.56	2.586 \pm 0.386	t	<0.001	-6.076
H+Al (cmol _c /dm ³)	10.19 \pm 3.67	11.30 \pm 2.38	t	0.433	-0.802
BS (cmol _c /dm ³)	0.22 \pm 0.17	0.19 \pm 0.08	t	0.985	0.0193
CEC _{effective} (cmol _c /dm ³)	1.53 \pm 0.67	2.810 \pm 0.396	t	0.440	-0.789
CEC _{pH7.0} (cmol _c /dm ³)	10.40 \pm 3.83	11.51 \pm 2.19	t	0.440	-0.789
Bases saturation (%)	1.94 \pm 0.72	1.80 \pm 0.82	t	0.692	0.434
Al saturation (%)*	86.72 \pm 4.95	92.75 \pm 2.57	M-W	0.001	61.000
Organic matter (dag/kg)	5.81 \pm 2.04	6.51 \pm 1.88	t	0.434	-0.799
P remanescent (mg/L)*	25.29 \pm 15.23	35.16 \pm 4.78	M-W	0.049	78.500
Coarse sand (%)*	23.900 \pm 7.866	13.600 \pm 2.547	t	<0.001	3.939
Fine sand (%)*	54.000 \pm 10.477	44.600 \pm 2.875	M-W	0.003	145.000
Silt (%)*	11.600 \pm 6.004	31.000 \pm 1.491	t	<0.001	-9.917
Clay (%)	10.500 \pm 8.695	10.800 \pm 1.687	M-W	0.126	85.000

A negative correlation was found between pH and L/H ($r = -0.528$, $P = 0.016$), whereas Al saturation correlated positively with L/H ($r = 0.540$, $P = 0.014$), strengthening the hypothesis that soil acidity and Al saturation influence the morphogenetic process of *S. glaucescens* stem growth in both areas (Tab. 3). With regards to soil granulometry in which *Syagrus glaucescens* was found, 100% of the samples in Serra do Cipó can be classified as sandy loams, while in Diamantina soils varied widely (11.1% sands, 11.1% silt loam, 33.3% sandy loams and 44.5% loamy sands).

Following the Minas Gerais State Agronomic Soil Classification (Alvares *et al.* 1999), the soils colonized by *Syagrus glaucescens* were acidic and deficient in most sampled macronutrients (Tab. 3). Organic matter levels, however, were

within the standards for the state of Minas Gerais. In respect to Al toxicity, a trend for high to very high Al³⁺ levels and Al saturation was observed.

Discussion

The stem shape was significantly different in the two phenotypes as well as were soil characteristics in sites where they occurred. Morphological differences (stem shape, height, length and total leaf number) were strongly correlated with exchangeable Al and Al saturation in the soil. The aluminum was the factor that most correlated with morphological variation in *Syagrus glaucescens*. Aluminum is known to

influence soil pH (see Goodland & Pollard 1973; Malavolta & Kliemann 1985). Aluminum toxicity is an important factor constraining Cerrado plant development; it tends to increase nutrient deficiency (Goodland & Ferri 1979) and reduce the size of the plants (Oliveira-Filho & Ratter 2002). The high concentration of aluminum result in inhibition of root growth (Delhaize & Ryan 1995), which can affect the stability of the stem. In general, root elongation is hampered through reduced mitotic activity induced by Al, with subsequent increase in susceptibility to drought (Jones & Kochian 1995). It is likely that higher Al saturation and low pH values (a consequence of high Al availability; Motta *et al.* 2002) in Serra do Cipó account for the decumbent stem shape of *S. glaucescens*. In Diamantina, low Al saturation and higher pH values were lower compared to Serra do Cipó and perhaps did not impair plant development allowing the production of higher stems with larger crown volume (as suggested by total leaf number). The low soil quality to which *Syagrus glaucescens* is associated in both areas is the result of high leaching of weathered material (Benites *et al.* 2003; 2007). Organic matter levels in the soils can be considered satisfactory according to the agronomic classification of Alvares *et al.* (1999). Low soil pH results in decreased microbial activity, reducing the ratio of organic matter decomposition (Lopes 1984). In addition, plant sclerophylly, a common feature of the rupestrian grassland's flora (Negreiros *et al.* 2014), should also account for high levels of organic matter since microbial degradation is reduced (Carvalho *et al.* 2012).

Significant differences in water retention capacity were observed between soils in the two areas. The soils of Diamantina were richer in sand compared to soils in Serra do Cipó. Nevertheless, soils in Diamantina were relatively deeper, allowing higher root development that provides higher mechanical stability, which should allow the production of a higher stem in relation to the ground. In Serra do Cipó, all *Syagrus glaucescens* plants were found on rocky outcrops, where soil depth was rarely over 10 cm. It is likely that stem shape of *S. glaucescens* in Serra do Cipó could provide lesser mechanical stability as a consequence of poor root development. However, future experimental work is needed to support these hypotheses.

Allometric relations and models of mechanical stability in Syagrus glaucescens

Three models of mechanical stability were proposed to describe the allometric relationship between stem height and diameter (Niklas 1994). The elastic similarity model states that the diameter (D) varies in the proportion of 3/2 of stem height (H), according to the relation $D \propto H^{3/2}$ (MacMahon 1973). According to the stress similarity model, the stem size at any point varies in a way that the bending stress remains constant along the stem following the relation $D \propto H^2$ (Niklas 1994). Finally, the geometric similarity model predicts that structures of different sizes retain isometric

proportions, so that increases in height causes a directly proportional increase in diameter, following the relation $D \propto H^1$ (Niklas 1994). Otherwise, these relationships are different in distinct ecological groups and in different taxa (Alves *et al.* 2004). All the eight species studied by O'Brien *et al.* (1995) at a semi-deciduous forest in Panama showed values close to the elastic similarity model. *Cecropia* species from Amazonian and from southeastern Brazil in open or disturbed habitats were all close to the geometric similarity model (Sposito & Santos 2001). For other pioneer species, the values did not fit any of the predicted mechanical stability models (Alvarez-Buylla & Martinez-Ramos 1992; Santos 2000), as it was also found for *Euterpe edulis*, an endemic palm of Brazilian Atlantic Forest (Alves *et al.* 2004). For all mentioned species, strong allometric relations between stem height and diameter were found, making *Syagrus glaucescens* an exception to the provided models along with *Metroxylon sagu* (Kjaer *et al.* 2004). The study by Goodman *et al.* (2013) also found a weak height-diameter relationships to palm species in Amazon. *Astrocaryum* and *Attalea*, for example, have a wide range of heights across a broad range of diameters with very little relationship between the two.

Niklas (1993) argued that palms tend to match the geometric stability model, but the regressions between stem height and diameter of *Syagrus glaucescens* were not significant for both phenotypes. Hence, linear regression coefficients values (an indication of stem height variation in response to diameter) did not match the values predicted by any of the three stability models. Our data on the allometry in *S. glaucescens* corroborates the study by Schatz *et al.* (1985) for tropical palms, indicating that a direct relationship between stem height and diameter may not always exist; i.e., it can change in shape during stem growth (Alves *et al.* 2004). This fact was observed in palm *Euterpe precatorea* that showed geometric similarity in individuals under one meter, whereas palms above this value did not adjust to any mechanical model (Avalos & Otárola 2010).

Although the allometric relationships between stem height and leaf number were significant, no differences between the two phenotypes were observed. A strong difference in the slope of the regression between total leaf number and stem length between the two phenotypes was observed, indicating that although an increase in stem length resulted in higher leaf production in both areas, in Diamantina fewer leaves were produced with an increasing in stem length compared to Serra do Cipó.

Morphological variation: genetic or environmental basis?

Reports on remarkable changes in plant anatomy, morphology and physiology in response to biotic and abiotic factors are widespread in the literature (Lortie & Aarssen 1996), including many Cerrado species (e.g., Marques *et al.* 2000; Cardoso & Lomônaco 2003; Rocha-Filho & Lomônaco 2006; Negreiros *et al.* 2014). Variation in plant traits

may be under the control of genetic differences with the formation of ecotypes (Cordell *et al.* 1998; Kjaer *et al.* 2004) or may be the net result production of different phenotypes in response to environmental conditions where the plants are growing with no genetic basis (phenotypic variability, Via *et al.* 1995; Agrawal 2001).

Metrosideros polymorpha (Myrtaceae) is a high polymorphic tree in Hawaii, whose traits are chiefly determined by altitude and soil nutritional status (Cordell *et al.* 1998). Plant height decreased and leaf pubescence increased with increasing elevation, where soils had low water retention capacity, low nitrogen levels and high daily temperature fluctuation. In contrast, plants growing at lower elevation have longer stems whereas anatomical leaf traits related to water economy decrease as a function of soil higher water retention capacity and higher N and organic matter availability (Cordell *et al.* 1998). Individuals of *Acacia karroo* occurring in forest, savanna and arid-shrublands in South Africa present remarkable differences in stem and branching architecture (Archibald & Bond 2003). Trees in savannas present an elongated growth form with small canopy and leaf areas and tall, thin, unbranched trunks. On the other hand, trees in arid areas showed opposite trends with wider canopies, and increased lateral branching. Archibald & Bond (2003) argued that these differences could be explained by the differential selective pressures imposed by each of the environments inhabited by this species. In savannas there is a great pressure for rapid vertical growth to escape fires, while in arid areas a defensive, lateral growth form is selected for. Plasticity in allocation can be understood as a change in a plant's allometric trajectory in response to the environment (Weiner 2004).

Though we argue that granulometry and soil nutritional differences may influence *Syagrus glaucescens* morphological traits, the morphogenetic effects caused by wind should not be discarded (Cordero *et al.* 2007). Furthermore, genetic-based differences may also play an important role. While Glassman (1987) validated two *Syagrus* species in the Espinhaço mountains, Marcato & Pirani (2001) recognized *S. glaucescens* as a single species based in morphology rather than on molecular data. According to Glassman (1987), *S. glaucescens* and *S. duartei* are similar species being only distinguishable by differences in total height (*S. glaucescens* being shorter than *S. duartei*), rachillae number (15-17 for *S. glaucescens* and 5-8 for *S. duartei*), pinnae number (38-40 for *S. glaucescens* and 60-64 for *S. duartei*). In addition, Glassman (1987) also stated the two species have very different spatial distribution: *S. duartei* is endemic of Serra do Cipó whereas *S. glaucescens* occurs not only in Serra do Cipó but also in Diamantina. Although Marcato & Pirani (2001) have fused the two species in *S. glaucescens* by overlapping morphological characters observed, our data support the evidence of two distinct species or at least ecotypes; therefore calling for molecular studies in order to evaluate the genome of these two ecotypes or species.

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