

Germination and allometry of the native palm tree *Euterpe edulis* compared to the introduced *E. oleracea* and their hybrids in Atlantic rainforest

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(With 1 figure)

Abstract

Palms are distinctive plants of tropics and have peculiar allometric relations. Understanding such relations is useful in the case of introduced species because their ability to establish and invade must be clarified in terms of their responses in the new site. Our purpose was to assess the survival and invasive capacity of an introduced palm species in the Atlantic rainforest, *Euterpe oleracea* Mart., compared to the native *Euterpe edulis* Mart. and to the hybrids produced between the two species. Considering this, we compared the allometry in different ontogenetic stages, the germination rates, and aspects of the initial development. The ontogenetic stages proposed for both *Euterpe* illustrated the growth patterns described for palm trees. *E. oleracea* and hybrids adjusted to the geometric similarity allometric model, while *E. edulis* presented a slope greater than would be expected considering this model, indicating a greater height for a given diameter. *E. oleracea* showed the same amount of pulp per fruit as *E. edulis* and a similar initial development of seedlings. The main differences observed were a lower germination rate and a faster height gain of *E. oleracea* seedlings. We conclude that *E. oleracea*, which is similar to *E. edulis* in aspects of allometry, development, seed and seedling morphology, may be an important competitor of this native palm tree in the Atlantic Forest.

Keywords: palms, hybridization, growth model, species introduction.

Germinação e alometria de *Euterpe edulis* comparadas à palmeira introduzida *Euterpe oleracea* e seus híbridos na floresta Atlântica

Resumo

Palmeiras são plantas características dos trópicos que apresentam relações alométricas peculiares. Compreender tais padrões pode ser útil no caso de espécies introduzidas, uma vez que sua habilidade de estabelecimento e invasão deve ser esclarecida em relação as suas respostas à nova localidade. Nosso propósito foi compreender a sobrevivência e a capacidade de invasão de uma palmeira introduzida na floresta Atlântica, *Euterpe oleracea* Mart. (açazeiro) comparada à palmeira nativa *Euterpe edulis* Mart. (juçara), também considerando seus híbridos. Para isso comparamos suas relações alométricas em estádios ontogenéticos, sua germinação e seu desenvolvimento inicial. Os estádios ontogenéticos propostos para ambas as *Euterpe* ilustraram os padrões de crescimento esperados para palmeiras. *E. oleracea* e híbridos apresentaram-se sob o modelo alométrico de similaridade geométrica e *E. edulis* apresentou inclinação maior do que este modelo. *E. oleracea* produziu a mesma quantidade de polpa por fruto que *E. edulis*. As principais diferenças observadas foram menor taxa de germinação e maior velocidade de crescimento em altura para as plântulas de *E. oleracea*. Em conclusão, nossos resultados indicam que *E. oleracea*, sendo similar a *E. edulis* em termos de alometria, desenvolvimento e morfologia de sementes e plântulas, pode ser um importante competidor para a espécie nativa na Floresta Atlântica.

Palavras-chave: palmeiras, hibridização, modelo de crescimento, introdução de espécies.

1. Introduction

Palms are typical exponents of tropical plants and play an important role in natural and human communities (Henderson et al., 1995; Tomlinson, 2006). They have impressive development and great ecological importance, especially as food resources. After their fruit are eaten and their seeds land on the ground, development must start quickly because most of them do not form soil seed banks (Henderson et al., 1995). Palms are also unique in the way they build long, tall lived trees entirely by primary growth, i.e., all tissues result directly from the activity of shoot and apical meristems, ensuring minimum susceptibility to fire, pathogens and wind damage (Tomlinson, 2006). This growth results in a unique allometric pattern, where height may increase almost unlimitedly by the plant diameter when compared to other tree species (Rich, 1987).

Allometric patterns of plants result from the balance of investments in support structures and photosynthetic biomass (Niklas, 1995; Niklas, 2004). Aerial parts of a plant are submitted to forces like gravity and wind, so they have to allocate energy to support themselves while growing, and must also provide photosynthetic structures to ensure biomass assimilation. Allometric relationships may change during the development of plant individuals, with each ontogenetic stage presenting a different allometry between height and diameter, as a response to dissimilar environmental, morphological and physiological conditions experienced by individuals from different stages (Gatsuk et al., 1980; Weiner, 2004).

It is already recognized that non-indigenous species are intensively dispersed for economic purposes (Levine et al., 2003), and this applies to many palm trees (Holmquist et al., 2010; Henderson et al., 1995; Svenning, 2002; Meyer et al., 2008). Although the establishment of plant populations outside their natural range of occurrence is not common (Richardson et al., 2000), some of these populations can become successfully established (Mooney and Cleland, 2001) and modify ecosystem functions, as well as the availability or quality of resources and space (Levine et al., 2003). Therefore, assessment of morphological traits can also be a tool for evaluating the status of non-indigenous species, since phenotypic plasticity indicates its ability to adapt to different environments (Tucic et al., 2006).

Amongst many examples from Brazil, two ecological and economically important palm trees with dissociated occurrence are now being cultivated in the same environments: *Euterpe oleracea*, originating from the Amazon rainforest, has been cultivated on a large scale in the Atlantic Rainforest, the natural habitat of the congener palm *E. edulis*, since the late 1970s. Fruit from both species is important in terms of food resources for birds in their original areas (Galetti et al., 1999; Moegenburg and Levey, 2003; Genini et al., 2009). When co-existing, these palms produce hybrids (Bovi et al., 1987a; Campos et al., 1991).

The objective of this study was to assess the phenotypic plasticity of the introduced species *E. oleracea* and its hybrids with the native *E. edulis* in the Atlantic rainforest.

Considering this, we compared their ontogenetic development, allometry, seed and seedling characteristics and germination. Since the two species have similar morphology when occurring in their natural ranges (Henderson et al., 1995), we expected similar allometry and germination rates when co-occurring in the same environment. This would indicate the potential competition between the two species and the potential of *E. oleracea* to invade the Atlantic forest.

2. Methods

Study area: We sampled the populations of *Euterpe edulis*, *E. oleracea* and their hybrids in Carlos Botelho State Park (CBSP), located in south-eastern Brazil, with a total area of 37,644 ha and the altitudes between 20 and 1000 m (SÃO PAULO, 2008). The vegetation is a typical tropical rainforest with Af climate (*sensu* Köppen 1948) and average rainfall from 1700 to 2400 mm (SÃO PAULO, 2008). In 1970, *E. oleracea* was planted in a floodplain area within the Park.

Seeds were collected from plants located in the experimental plantation of *Agência Paulista de Tecnologia dos Agronegócios* (APTA) (Agrarian Technology Agency of São Paulo State) in the municipality of Pariqueira-Açu, São Paulo, south-eastern Brazil. The objective of these *E. oleracea* plantations was to produce hybrids with *E. edulis* to improve the development of palm heart (Bovi et al., 1987a).

Study species: the jussara palm, *E. edulis*, occurs naturally in the Atlantic rainforest on the Brazilian coast and may also be found in Paraguay and Argentina (Henderson et al., 1995). It has an arborescent habit, with a single stem, and may reach 15 m in height in the study site. It produces globular purple-black fruit with 1-1.4 cm in diameter (Henderson et al., 1995). This species has been under threat due to indiscriminate exploitation, mostly of which is illegal, since the second half of the twentieth century (Silva Matos and Bovi, 2002). As it produces a single stem and does not resprout, the plant dies when the palm heart is extracted. Currently, the presence of *E. edulis* is restricted to remote areas of the Atlantic rainforest (Silva Matos and Bovi, 2002).

The assaí palm, *E. oleracea*, is commonly found along the Amazon river basin in the North of Brazil, and therefore it is geographically distant from *E. edulis* in the Atlantic rainforest (Henderson et al., 1995). *E. oleracea* produces multiple stems and can reach 12-20 meters in height. Its apical meristem is also exploited to produce palm heart (Henderson et al., 1995). It bears purple-black globular fruits with 1-2 cm in diameter (Henderson et al., 1995; Lorenzi et al., 2004) which are harvested for assaí cream production. The palm heart from *E. oleracea* has a lower quality than its congener but, as a plant with multiple stems, the production may be higher and the plant is not necessarily killed during palm heart extraction as occurs with *E. edulis*. The better quality of its palm heart, the increasing demand of the consumer market and the

scarcity of *E. edulis* made it one of the most expensive palm hearts in Brazil.

Experimental production of hybrids between *E. edulis* and *E. oleracea* started after *E. oleracea* was introduced into the Atlantic rainforest (Bovi et al., 1987a). The main purpose was to increase the production of high-quality palm hearts by combining the palm heart quality of *E. edulis* and the presence of multiple stems of *E. oleracea* (Bovi et al., 1987a; Campos et al., 1991). Although promising results were obtained in these experiments, data on hybrids produced under non-mediated conditions have been unavailable until present.

Data sampling. At CBSP, we measured the height and basal diameter of all individuals (except seedlings) of *E. edulis*, *E. oleracea*, and their hybrids in 35 contiguous plots (10 × 10 m). Seedlings were sampled in sub-plots (2 × 2 m) within each 100 m² plot. As each stem in the *E. oleracea* clumps is able to reproduce, we counted each stem as a distinctive individual. Individuals from each population were divided into ontogenetic stages according to their morphology (Gatsuk et al., 1980; Silva Matos et al., 1999). Taking this into account, besides height and diameter, we also observed leaf and leaflet shape, stem exposure, and presence of inflorescences, infrutescences or signs of previous reproduction such as the presence of scars on stems.

At APTA, we randomly selected 10 individuals of *E. edulis*, *E. oleracea*, and their hybrids, from which we collected one infrutescence and obtained its total fruit mass. We arbitrarily selected 50 pieces of mature fruit per infrutescence and obtained the mass and diameter of each fruit and seed using a digital scale and a digital caliper. Finally, for the experiment on seed germination, each seed was sown in compost soil and watered daily under greenhouse conditions. Due to differences in the time of fruiting, seeds of *E. edulis* were planted in April, 2010 and seeds of *E. oleracea* were planted in June, 2010. We followed the germination and seedling growth for eight months. After the seeds germinated, we removed the seedlings and measured their diameter, height and the wet and dry weight (70 °C for 48 hours) of their shoots and roots. Germination rate was considered as the percentage of seeds that germinated during the study.

Data analysis: We classified the individuals into ontogenetic stages, which we defined according to the distributions of height and diameter, their coefficient of variation (CV), and also their morphological characteristics. Depending on the normality of data, we used either Student's t-test or Mann-Whitney to test for differences between stages and populations considering the mean or median diameter and height. The analyses were performed in the Past 2.05 statistical program (Hammer et al., 2010).

The allometry in terms of diameter and height was tested using the model (Equation 1)

$$H = b \cdot D^a \quad (1)$$

(McMahon and Kronauer, 1976), where H is the plant height, D is the diameter, *b* is the intersection value, and

a is the slope value that represents the proportionality between the two variables (McMahon and Kronauer, 1976). Allometric relationships between stem height and diameter usually follow one of the three different models: the geometric, elastic, and stress similarity, characterized by their slope values (respectively 1.0, 0.66, and 0.5) (McMahon and Kronauer, 1976; Dodonov et al., 2011). We calculated Pearson's correlation coefficient and performed a standardized major axis regression (SMA) (Warton et al., 2006) between log H and log D for the pooled data and for each ontogenetic stage separately, for the two species and their hybrids. We then compared the obtained slopes to the values expected from the three allometric models, and evaluated the differences in the slopes between populations and between stages of each population. We used a likelihood ratio test (Warton et al., 2006) for these comparisons. We used the *smatr* package (Warton, 2007) in R (R Development Core Team, 2011) for the SMA regression and for the comparisons.

For the germination and seedling comparisons, we first used a permutation t test, in Past 2.05 (Hammer, 2010), to compare the number of germinated seedlings per parental plant and the weight and amount of fruit per infrutescence between the two species and their hybrids. We then used a permutation analysis of variance (ANOVA) (Manly, 2007) to check for homogeneity of means between the seeds and seedlings originated from different parental plants within each species (intra-specific comparisons). We performed this comparison for the following variables: fruit and seed weight and diameter and pulp weight (calculated as fruit weight – seed weight), for all fruit and for the germinated fruit only; root, shoot and total weight of the seedlings (wet and dry); shoot:root ratio (wet weight only); and water proportion, calculated as (1 – wet weight / dry weight). Afterwards, we compared the two species for the same variables, by means of restricted permutation tests (Manly, 2007). In these restricted permutations, all seedlings originated from the same parental plant were permuted together, and the mean difference between the two species was compared to the distribution of differences in 5,000 permutations. We used Bonferroni correction (SISA 2011) to correct multiple comparisons.

We calculated Pearson's correlation coefficient between the dry weight of each seedling and the original weight of its former seed and between the height and diameter of seedling stems, and assessed their significance by means of restricted permutations. Permutation tests for significance of regression and correlation coefficients consider the random rearranging the pairs of variables (Manly, 2007). To account for the non-independence, we rearranged the variables only between seedlings originating from the same parental plant. Finally, we performed SMA regressions between log H and log D for seedlings of the two species, and compared them with a likelihood ratio test (Warton et al., 2006) in the *smatr* package (Warton, 2007) in R (R Development Core Team, 2011). We performed all the restricted permutation analyses and the permutation ANOVA in R (R Development Core Team,

2011), and the code developed for this is available from the authors on request.

3. Results

We determined five ontogenetic stages for both species of *Euterpe* and hybrids: (i) seedling: individual with up to three leaves with palmate leaflets; (ii) sapling: individual with pinnate leaves, without exposed stem; (iii) juvenile: individual with pinnate leaves and exposed stem; (iv) immature: individual with pinnate leaves, exposed stem and with no signs of reproductive events; (v) adult: individual with pinnate leaves, exposed stem, and signs of reproduction such as infrutescences or their scars on the stem. Mean height and diameter were significantly different between all ontogenetic stages of the three populations (Table 1). Younger stages had higher CVs for diameter, and older stages had higher CVs for height (Table 1).

All three populations presented high Pearson's determination coefficients (R^2) between the log height and log basal diameter for the pooled data. The SMA regression for *E. edulis* populations presented slopes higher than expected for geometric similarity (Table 2), while *E. oleracea* and hybrids fitted the geometric similarity model (Table 2).

Saplings and juveniles of *E. edulis* fitted to the geometric similarity model; the immatures of this species, however, did not fit to any of the three models, presenting a slope much greater than would be expected under geometric similarity (Table 2). Hybrids presented a geometric

similarity model for saplings, while juveniles could be described by both geometric and elastic similarity models (Table 2). Likewise, saplings and juveniles of *E. oleracea* fitted to both the geometric and the elastic similarity models (Table 2).

The likelihood ratio test indicated significant differences between the three species (LR = 11.96, $p = 0.002$). However, after an *a posteriori* analysis, we identified that this difference occurs only between hybrids and *E. oleracea* (LR = 4.49, $p = 0.03$) and between hybrids and *E. edulis* (LR = 20.98, $p = 4.63 \times 10^{-6}$). There was no difference between *E. edulis* and *E. oleracea* (LR = 0.45, $p = 0.49$), as also observed by the overlap in the 95% confidence intervals of these two species. Analyzing each population separately, we found different slopes between the ontogenetic stages of *E. edulis* (LR = 43.15, $p = 4.25 \times 10^{-10}$), but not between the stages of *E. oleracea* and the stages of hybrids (*E. oleracea*, LR = 1.16, $p = 0.56$; hybrids LR = 3.08, $p = 0.21$).

For both species and their hybrids, we observed significant differences between the individuals of the same species with regards to the size of their fruits and seeds (permutation $p < 0.001$ in all analyses), indicating large intra-species variability. Infrutescences of *E. edulis* were four times heavier than those of *E. oleracea* (2222 ± 961 g and 526 ± 260 g respectively, permutation $p < 0.0001$) and had five times more fruits (1667 ± 708 and 329 ± 142 , permutation $p < 0.0001$). The fruits and seeds of *E. oleracea* were slightly larger than of *E. edulis* (permutation $p < 0.02$), but the pulp weight did not vary significantly between

Table 1. Diameter and height distributions of ontogenetic stages of *E. edulis*, *E. oleracea* and hybrids at Carlos Botelho State Park (CBSP), SP, Brazil. In each population, different superscript letters indicate significant difference between distributions according to a t-test or a Mann-Whitney test, considering $p < 0.05$. Letters used for height and for diameter are independent of each other. We only considered ontogenetic stages that had sufficient data for the analysis. Min: minimum, max: maximum, avg: average, sd: standard deviation, cv: coefficient of variation.

Population	Ontogenetic stage	N	Relative frequency	Diameter (cm)					Height				
				min	max	avg	sd	cv	min	max	avg	sd	cv
<i>E. edulis</i>	Seedling	3	0.18	-	-	-	-	-	-	-	-	-	-
	Sapling	240	0.60	0.21	3.41	0.93 ^a	0.54	0.58	0.01	0.29	0.12 ^a	0.06	0.51
	Juvenile	49	0.12	2.11	6.33	3.83 ^b	1.18	0.31	0.30	0.98	0.48 ^b	0.19	0.39
	Immature	34	0.08	5.99	19.75	12.06 ^c	3.98	0.33	1.00	9.00	3.85 ^c	2.22	0.58
	Adult	2	0.005	-	-	-	-	-	-	-	-	-	-
<i>E. oleracea</i>	Seedling	0	-	-	-	-	-	-	-	-	-	-	-
	Sapling	35	51.47	0.69	3.97	1.77 ^a	0.87	0.49	0.05	0.29	0.21 ^a	0.07	0.31
	Juvenile	25	36.76	1.74	9.24	5.25 ^b	1.94	0.37	0.31	0.97	0.43 ^b	0.21	0.48
	Immature	7	10.29	6.05	23.89	10.83	6.20	0.57	1.23	4.50	1.39	1.41	1.01
	Adult	1	1.47	-	-	-	-	-	-	-	-	-	-
Hybrids	Seedling	0	-	-	-	-	-	-	-	-	-	-	-
	Sapling	35	48.61	0.86	1.88	1.32 ^a	0.67	0.51	0.03	0.29	0.18 ^a	0.06	0.36
	Juvenile	32	44.44	2.75	8.73	5.08 ^b	1.69	0.33	0.30	0.88	0.44 ^b	0.16	0.35
	Immature	5	6.94	5.36	14.33	12.10	3.43	0.28	1.01	3.75	2.00	1.09	0.55
	Adult	0	-	-	-	-	-	-	-	-	-	-	-

Table 2. Sample size (N), regression data and allometric model for the pooled data and ontogenetic stages of *E. edulis*, *E. oleracea* and hybrids at Carlos Botelho State Park (CBSP), SP, Brazil, according to a Standardize Major Axis regression. We only considered ontogenetic stages that had sufficient data for the analysis.

Population	Stage	N	SMA Regression				R ²	p-value	Allometric model
			Slope <i>a</i>	Lower limit	Upper limit				
<i>E. edulis</i>	Pooled data	323	1.16	1.12	1.20	0.89	<0.05	None	
	Sapling	240	0.94	0.86	1.02	0.57	<0.05	Geometric	
	Juvenile	49	1.11	0.95	1.30	0.70	<0.05	Geometric	
	Imature	34	1.82	1.57	2.09	0.84	<0.05	None	
<i>E. oleracea</i>	Pooled data	67	1.09	0.98	1.19	0.80	<0.05	Geometric	
	Sapling	35	0.82	0.69	0.98	0.41	<0.05	Geometric/Elastic	
	Juvenile	25	0.88	0.63	1.22	0.50	<0.05	Geometric/Elastic	
	Imature	7	-	-	-	-	-	-	
Hybrids	Pooled data	72	0.98	0.89	1.08	0.84	<0.05	Geometric	
	Sapling	35	1.04	0.82	1.32	0.53	<0.05	Geometric	
	Juvenile	32	0.81	0.65	1.02	0.62	<0.05	Geometric/Elastic	
	Imature	5	-	-	-	-	-	-	

Table 3. Comparisons between fruits, seeds and seedlings of *E. edulis*, *E. oleracea* and their hybrids (mean \pm SD). Significance tests refer only to comparisons between *E. edulis* and *E. oleracea*. Their hybrids were significantly different ($p = 0.0002$) from both species for all characteristics. Significance tests performed by restricted permutation, significant differences highlighted in bold.

Variable	<i>E. edulis</i>	<i>E. oleracea</i>	Hybrids	<i>p</i> (<i>E. edulis</i> = <i>E. oleracea</i>)	
				Uncorrected	Bonferroni- corrected
Fruits and seeds					
Fruit diameter (mm)	12.74 \pm 0.79	13.64 \pm 0.77	8.10 \pm 0.78	0.0026	0.0035
Fruit weight (g)	1.34 \pm 0.24	1.59 \pm 0.26	0.33 \pm 0.15	0.0114	0.0155
Seed diameter (mm)	11.45 \pm 0.79	12.26 \pm 0.77	5.63 \pm 0.83	0.0026	0.0035
Seed weight (g)	1.02 \pm 0.19	1.23 \pm 0.22	0.14 \pm 0.11	0.0060	0.0082
Pulp weight (g)	0.32 \pm 0.08	0.36 \pm 0.08	0.20 \pm 0.06	0.1432	0.1949
Seedlings					
Stem wet weight (g)	0.81 \pm 0.23	0.88 \pm 0.44	n.a.	0.3128	1.0000
Root wet weight (g)	0.50 \pm 0.16	0.39 \pm 0.22	n.a.	0.0134	0.0734
Total wet weight (g)	1.31 \pm 0.36	1.27 \pm 0.61	n.a.	0.7280	1.0000
Stem dry weight (g)	0.24 \pm 0.07	0.26 \pm 0.13	n.a.	0.5802	1.0000
Root dry weight (g)	0.15 \pm 0.04	0.11 \pm 0.07	n.a.	0.0018	0.0099
Total dry weight (g)	0.39 \pm 0.10	0.37 \pm 0.18	n.a.	0.3810	1.0000
Stem:root ratio	1.66 \pm 0.43	2.53 \pm 1.16	n.a.	0.0002	0.0011
Water proportion	0.70 \pm 0.04	0.70 \pm 0.17	n.a.	0.9988	1.0000

the species (permutation $p = 0.19$) (Table 3). The results were the same for the analysis considering all fruits and considering only the fruits that germinated. Fruits and seeds of hybrids were significantly smaller than both other species for all variables ($p = 0.0002$, Table 3).

The percentage of germinated seeds was higher for *E. edulis* than for *E. oleracea* (mean \pm SD per individual: 66.0 \pm 17.2% for *E. edulis*, 13.0 \pm 8.1% for *E. oleracea*; permutation $p < 0.0001$). None of the hybrid seeds germinated, however 17 seedlings of *E. oleracea*, originated from six different individuals, they presented abnormal leaf forms and

leaflet numbers (1 to 6 leaflets), unlike *E. edulis* (always 6 or 8 leaflets) and *E. oleracea* (always 2 leaflets). Probably these seedlings originated from the breeding of *E. edulis* and *E. oleracea* (see Figure 1).

When comparing seedlings originating from different parental plants, we observed significant differences for all features in seedlings from *E. edulis* and for no features in seedlings from *E. oleracea*. Thus, the morphometry of seedlings of *E. oleracea* seems to be more homogeneous between parental plants than observed for *E. edulis*. There were significant differences between the two species only

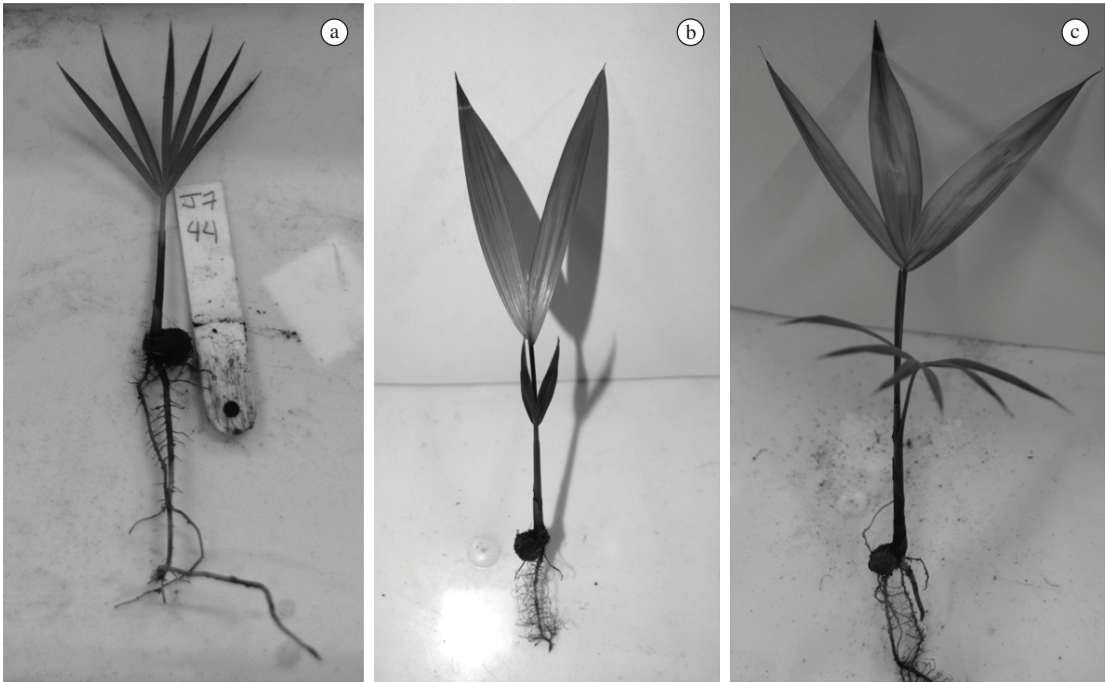


Figure 1. Seedling leaves of (a) *E. edulis*, (b) *E. oleracea* and (c) hybrids between *E. edulis* and *E. oleracea*. Seedlings considered hybrids emerged from seeds of *E. oleracea* and presented a variable number of leaflets (1-6). For more information see text.

for dry root weight, which was slightly greater in seedlings of *E. edulis* (permutation $p = 0.01$), while the shoot:root ratio was greater for *E. oleracea* (permutation $p = 0.001$) (Table 3). The shoot and the total weight, as well as water proportion, did not vary between the two species (Table 3).

The final weight of seedlings was correlated with original seed weight for *E. edulis* ($r = 0.55$, $p = 0.0002$), but not for *E. oleracea* ($r = 0.23$, $p = 0.07$). We observed significant correlations between the height and diameter of seedlings for both species, but the regression slope was significantly higher for *E. oleracea* (*E. edulis*: $r = 0.39$, slope = 1.1; *E. oleracea*: $r = 0.30$, slope = 1.8; LR = 7.8, $p = 0.005$; Figure 1).

4. Discussion

The ontogenetic stages as defined in this study seem to correlate with plant morphology, as we observed differences between the stages with regards to their allometry and variability in height and diameter, especially for *E. edulis*. This indicates that our classification is a useful tool for studying *E. edulis* and *E. oleracea* populations and their hybrids, thus enabling us to understand individual responses to their environment throughout their ontogeny. Young palms are usually overbuilt with respect to diameter growth before investing in height (Rich, 1987; Tomlinson, 2006), and, conversely, older palms cannot grow significantly in diameter as monocotyledon species do not have secondary growth (Rich, 1987). This is reflected in the allometry of

our species, with older stages presenting higher allometric coefficients. It also explains the changes in variability of diameter and height, with younger stages being more variable for diameter than older stages, which are more variable for height.

Growth limitations also explain why allometric models proposed for neotropical and temperate forests (Dean and Long, 1986; Niklas, 1995) apply only partially to these palm trees. We observed that pooled data of *E. edulis* presented slopes higher than expected under geometric similarity. In order to maintain the elastic similarity, a safe proportionality against mechanical failure, stem diameter is expected to increase as a $3/2$ power of height (McMahon and Kronauer, 1976). Palms are not able to significantly increase in stem diameter, even though they keep growing in height. Alternatively, these species present a combination of attributes to ensure mechanical support: initial development of stem diameter for future support requirements, sustained cell expansion, and increasing stiffness and strength with age (Rich et al., 1986).

The absence of differences in the allometric model of the two *Euterpe* species indicates similar growth characteristics. The native *E. edulis*, the introduced *E. oleracea* and their hybrids presented allometric relationships either in accordance with the geometric growth model or more than it, i.e. taller than would be expected for this model. This supports our hypothesis that congener species tend to have similar characteristics of growth when they occur in the same environment. However, the allometric model

observed for the population of *E. oleracea* introduced into the Atlantic rainforest is different from that observed for its populations in the Amazon Rainforest. In its original range, *E. oleracea* tends to present elastic similarity (Cole and Ewel, 2006). Therefore, although *E. oleracea* is able to establish in the Atlantic rainforest, there is clear evidence of environment-related phenotypic plasticity.

Size, pulp availability and amount of fruits produced are important in determining the plant's attractiveness to dispersers (Jordano, 2000). While our results indicate a higher production of fruits per stem by *E. edulis*, *E. oleracea* often has more than one reproductive stem at the same time, which may counterbalance the difference observed. In addition, the introduced palm, *E. oleracea*, produced the same amount of pulp per fruit as the native palm species, but had slightly larger fruits and seeds and this could influence the disperser's choice (Jordano, 2000). Although hybrids also produced fruit, these fruits were significantly smaller than that of the original species and had significantly less pulp.

As expected from the similarity between the congener palm trees, *E. edulis* and *E. oleracea* (Henderson et al., 1995), both species produced similar seedlings, except for root weight and shoot:root ratio. With regards to intra-parental variation in seedling morphometry, individuals of *E. oleracea* are more similar among them than those of *E. edulis*. This could be a result of the reduced genotypic variation of seeds of *E. oleracea* planted in the Atlantic rainforest. This can probably be explained by them having originated from a reduced sample of the original Amazonian population that was introduced in the Atlantic Rainforest, resulting in reduced genetic variability. This reduced variability could also be responsible for the lower germination rate of the exotic species.

Unlike *E. edulis*, the final size of *E. oleracea* seedlings was uncorrelated with the original size of the seed. This indicates that this species stops depending on the seed and starts using soil nutrients earlier, which is also shown by the higher production of roots by *E. oleracea*. Although the larger size of *E. oleracea* seeds did not result in improved growth, it seems to result in faster height gain. Two pieces of evidence confirm this hypothesis. First, the shoot:root ratio of *E. oleracea* was 50% larger than for *E. edulis*, meaning that for the same total weight, *E. oleracea* will have more shoot biomass and less root biomass than *E. edulis*. At this stage, it is expected that the seedling stops using seed resources for carbohydrate production and starts their production by its own photosynthesis (Green and Juniper, 2004). This would also explain the lack of correlation between seed and seedling weight. Second, as shown by allometry, seedlings of *E. oleracea* of a given diameter will be proportionally taller than seedlings of *E. edulis*. Larger seeds may also confer an advantage for growing in suboptimal circumstances, such as beneath the dense forest canopy. In this situation, having more reserves may allow a larger growth before the seedling runs out of reserves and starts depending uniquely on photosynthesis (Green and Juniper, 2004). Under deep

shade conditions the taller *E. oleracea* would have some competitive advantage over *E. edulis*.

Our results indicate that *E. oleracea*, which is similar to *E. edulis* in aspects of allometry, development, seed and seedling morphology, may be an important competitor of this species. The similarity between the congener species, native *E. edulis* and introduced *E. oleracea*, may give the latter a greater ability in the use of resources than would be expected for an unrelated species. Fruits and seeds of *E. oleracea* were larger than those of *E. edulis*, but had a similar amount of pulp, and the faster height gain of its seedlings may confer them a competitive advantage in the field in spite of their lower germination rate. In conclusion, as *E. oleracea* is able to establish and also compete with the native *E. edulis*, the introduction of this species into the Atlantic rainforest should be discouraged.

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