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Seed development, yield and quality of two palm species growing in different tropical forest types in SE Brazil: implications for ecological restoration

P.H.S. BRANCALION[1a], A.D.L.C. NOVEMBRE[2] AND R.R. RODRIGUES[3]

[1] Departamento de Ciências Florestais, Esalq, Universidade de São Paulo, Caixa Postal 09, 13418-900, Piracicaba, SP, Brazil (E-mail: pedrob@usp.br)
[2] Departamento de Produção Vegetal, Esalq, Universidade de São Paulo, Caixa Postal 09, 13418-900, Piracicaba, SP, Brazil (E-mail: adlcnove@esalq.usp.br)
[3] Departamento de Ciências Biológicas, Esalq, Universidade de São Paulo, Caixa Postal 09, 13418-900, Piracicaba, SP, Brazil (E-mail: rrr@esalq.usp.br)

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Summary

Natural forest remnants have been set as seed production fields to supply seeds of native tree species for tropical forest restoration, but the effect of different forest types on seed production has not been accessed to date for palm species. In this work, we studied seed development, yield, and quality of two palm species in different tropical forest types in SE Brazil. Seed production of palmiteiro (*Euterpe edulis*) and queen-palm (*Syagrus romanzoffiana*), which are largely used in restoration efforts due to their importance for vertebrate frugivores, were studied in natural remnants of Atlantic Rainforest, Restinga Forest, Seasonally Dry Forest, and Cerrado Forest. We studied seed development, yield, size, and germination of seed lots produced in some of these forest types, including seeds harvested in 2008, 2009, and both years. Seed yield and quality, as well as seed dry mass in 2009, were higher for palmiteiro seeds produced in the Atlantic Rainforest, while queen-palm seeds produced at the Restinga Forest showed the higher mass and yield, but the lowest physiological potential. Consequently, these natural differences of seed yield and quality have to be taken into account for establishing standards for seed commercialization and analysis, seed pricing, and seedling production in forest nurseries.

Introduction

The advance of ecological restoration efforts in recent decades has fuelled an emerging seed market: the production of native plant species (Mortlock, 2000; Smith *et al.*, 2007). This new and challenging field for seed science and technology has some particularities, many of them divergent from the traditional recommendations of seed production companies, which have to be taken into account when establishing a program for the seed production of non-domesticated plant species for environmental purposes. For instance, the production of seeds for ecological restoration has to maximize the genetic diversity of seed lots (Lesica and Allendorf, 1999; Burton and Burton, 2002), rather than constraining it to improve genetic purity.

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If the focal species for seed production takes an extended period of time to become reproductive (decades), as tropical trees do, other important challenges are also present. In these cases, it is almost impracticable to implement artificial seed production fields, due to the slow growth of mother-trees. Moreover, the complex and yet poorly studied reproductive biology of native species, especially tropical tree species which tend to be allogamous, may hamper seed production due to problems of plant-pollinator interaction (Bawa *et al.*, 1985; Bawa, 1990). Therefore, the only option currently available to produce seeds of native tree species is to use natural forest remnants as seed production fields, which do not allow for controlling the environmental production factors. Additionally, those seed production fields have to be located as close as possible to the site under restoration to increase the chances of using locally adapted genetic materials (Montalvo and Ellstrand, 2000; Hufford and Mazer, 2003; McKay *et al.*, 2005).

Given that seed development is strongly affected by the influence of light (Copeland and McDonald, 2001), photoperiod (Munir *et al.*, 2001), temperature (Donohue *et al.*, 2008), water (Kebreab and Murdoch, 2000), and nutrient availability (Cheplick and Sung, 1998), the maternal environment is an important determinant of seed yield and quality (Gutterman, 2000). A higher level of unpredictability is then associated with the production of native seeds in natural forests, which are recognized by their high levels of habitat heterogeneity. Additionally, native tree seeds can be affected differently by pathogens and seed predators in different habitat conditions. Consequently, seed companies have to face important challenges for seed production, analysis, and pricing of native tropical species. Needless to say, forest nurseries also have to consider these factors in the production planning.

In this article, we investigated important aspects of seed development, yield, and quality for two tropical palm species to supply the ecological restoration market in the State of São Paulo, SE Brazil. We aimed to illustrate the different characteristics of seed lots that may be obtained when seed production fields are set in ecologically distinct forest types. The state of São Paulo has concentrated large-scale forest restoration projects carried out mainly by agro-industry companies that wish to obtain environmental certification and financial credit (Rodrigues *et al.*, in press). As a response to this emerging market, seedling production of native shrubs and tree species in São Paulo state increased from 13 to 33 million per year from 2003 to 2008 (Barbosa *et al.*, 2009). In 2010, a total of 208 forest nurseries distributed throughout the state produced no less than 42 million tree seedlings (L.M. Barbosa 2010, Botany Institute of São Paulo, personal communication). Additionally, an ambitious program known as the Atlantic Forest Restoration Pact (http://www.pactomataatlantica.org.br/index.aspx?lang=en), which aims to restore 15 million ha of forests in this biome by 2050, will fuel the market for native tropical seeds even more in the near future (Calmon *et al.*, in press).

We used the palmiteiro (*Euterpe edulis* Mart.) and the queen-palm (*Syagrus romanzoffiana* (Cham.) Glassman) as model-species for this work; these palm species are key to tropical forest restoration due to their strong interaction with vertebrate frugivores (Fadini *et al.*, 2009; Giombini *et al.*, 2009). Palmiteiro is also important for the production of palm heart, the apical meristem and developing undifferentiated leaves of palms' stem, the most important non-timber forest product extracted from the Brazilian Atlantic Forest

(Fantini and Guries, 2007). Queen-palm is the most important ornamental palm used in Brazil, and it has also been used extensively in the United States (Lorenzi *et al.*, 2004). Considering that both species are indigenous to different types of Brazilian forest, and that their seeds have often been harvested by seed companies, study of the differences in seed development, yield, and quality among natural populations may provide important information to improve the complex production systems of tropical native tree species.

Methods

Species

Palmiteiro (*Euterpe edulis*) is a single-stemmed understory palm (5-20 m tall) endemic to the Atlantic Forest biome; queen-palm (*Syagrus romanzoffiana*) is a single-stemmed emergent palm (10-25 m tall), widely distributed in South America (central and southern Brazil, Paraguay, Bolivia, Uruguay and northeastern Argentina), and is present in the Brazilian Atlantic Forest, Cerrado (neotropical savanna), and Pampas (southern grasslands) biomes (Henderson *et al.*, 1997). Palmiteiro occurs predominantly in soils with high water availability (Matos *et al.*, 1999), while queen-palm grows both in permanently flooded soils as well as those with lower water availability (Bernacci *et al.*, 2009). Palmiteiro has recalcitrant seeds and adjacent germination (Martins *et al.*, 1999; Roberto and Habermann, 2010), and queen-palm has orthodox seeds and remote germination (Bernacci *et al.*, 2009).

Study sites

We studied palmiteiro populations in the Restinga Forest (hereafter RF), Atlantic Rainforest (AR) and Seasonally Dry Forest (SDF), and queen-palm populations in the RF, SDF, and Cerrado Forest (CF). Our studies were concentrated on populations found in 10.24-ha permanent plots established within representative portions of each forest type protected within Natural Reserves of São Paulo State, SE Brazil (figure 1; table 1). The study areas of RF, AR, SDF, and CF in which these plots are located are 22,500, 37,793, 2,178, and 1,313 ha in size, respectively. Palmiteiro is the most abundant tree species in the areas of RF and AR included in this study, accounting for 19.8 and 21.5% of the trees, respectively, while queen-palm is the most abundant palm species in the study areas of SDF and CF, accounting for 3.9 and 2.7% of the trees, respectively, in both cases considering trees with a diameter of >4.8 cm at breast height (Parcelas Permanentes, 2006).

Seed development (2008)

We initially tagged fifteen flowering mother-palms per species in each study site in 2008, maintaining a minimum distance of 50 m between mother palms, in order to evaluate seed development. However, fruit abortion and illegal palmiteiro heart palm extraction reduced the number of mother-palms studied to seven by the end of the experiment. We considered only individuals that were flowering in the same month in all three forest types per species, in such a way that the development of seeds occurred simultaneously for palmiteiro and queen-palm in the different forest types.

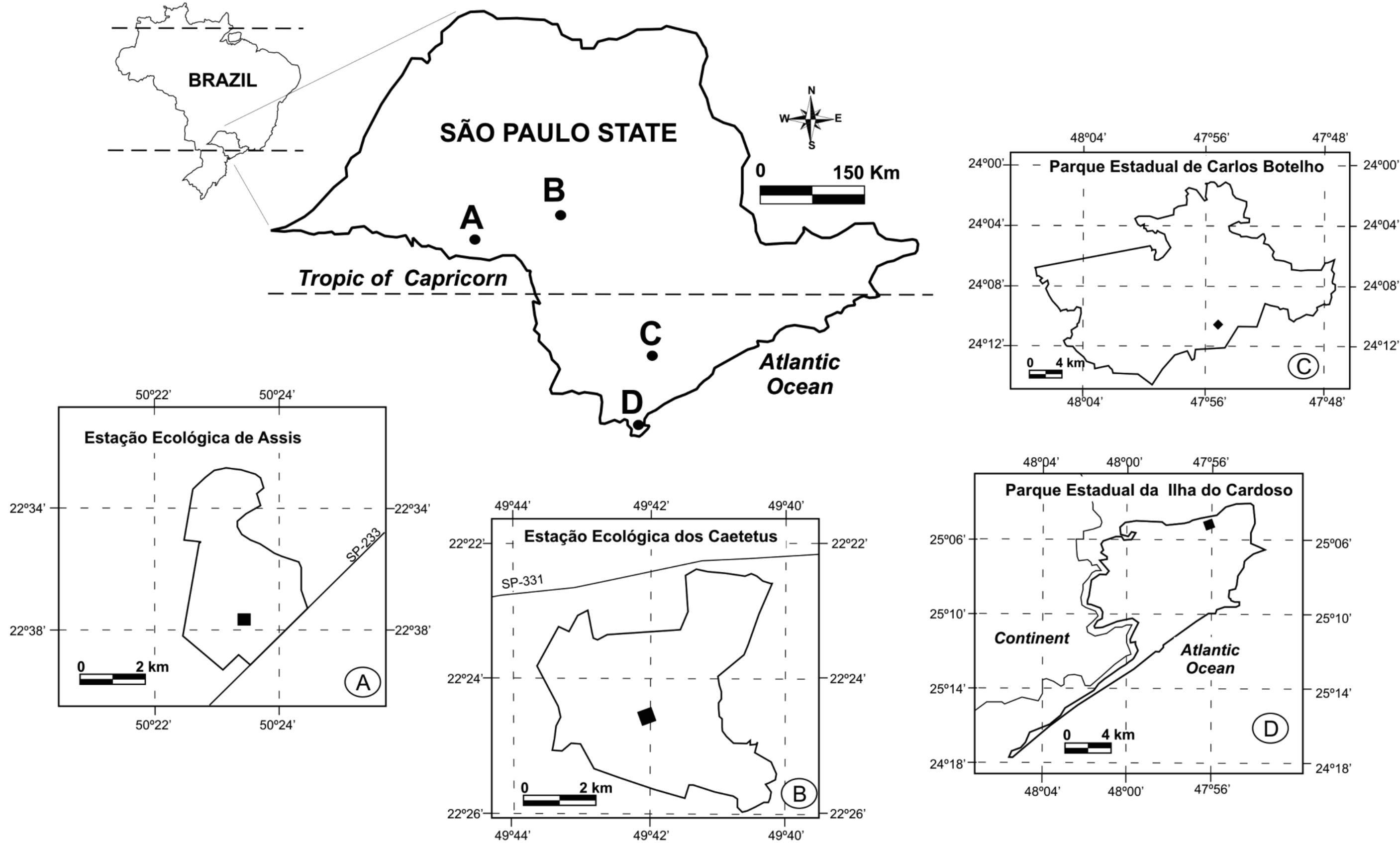

Figure 1. Study sites where palmiteiro (*Euterpe edulis*) and queen-palm (*Syagrus romanzoffiana*) populations were studied: Cerrado Forest (A), Seasonally Dry Forest (B), Atlantic Rainforest (C), and Restinga Forest (D). The black squares inside each area represent 10.24-ha, permanent parcels whose interior and surroundings were used for seed harvesting.

Table 1. Environmental characteristics of the forest types from southeastern Brazil where seed harvesting of palmiteiro (*Euterpe edulis* –Arecaceae) and queen-palm (*Syagrus romanzoffiana* – Arecaceae) populations was carried out (data obtained in 10.24-ha Permanent Parcels located in each forest type – Parcelas Permanentes, 2006).

Environmental characteristics	Forest types			
	Restinga Forest	Seasonally Dry Forest	Atlantic Rainforest	Cerrado Forest
Climate (Köepen classification)	Equatorial climate (Af), mean temperature = 22.4°C and precipitation = 2261 mm, without dry season	Humid sub-tropical climate (Cwa), with moderate dry season in the winter, mean temperature = 21.4°C and precipitation = 1303 mm	Equatorial climate (Af), mean temperature = 21.8°C and precipitation = 1582 mm, without dry season	Tropical savanna climate (Aw), with intense dry season in the winter, mean temperature = 22.4°C and precipitation = 1255 mm
Topography	Coastal-flat, close to sea level (average altitude = 7 m)	Flat to slightly mountainous (average altitude = 522 m)	Mountainous (average altitude = 400 m)	Flat (average altitude = 505 m)
Predominant soil	Ferrocarbic Spodosol: hydromorfic, sandy, high sodium and aluminum content, low pH and nutrient content	Ultisol: well-drained, sandy clay loam, low aluminum content, high pH and nutrient content	Inceptisol: clay, well-drained, high aluminum content, low pH and nutrient content	Yellow Latosol: well-drained, sandy, high aluminum content, low pH and nutrient content

From the second month after flowering onwards, we harvested immature fruits at intervals of 30 days until fruits become ripe. The pulp of immature fruits was manually removed for all evaluations by using a scalpel. The seeds were not removed from the stony endocarp in which they were enclosed, so the weights recorded express the seed plus the endocarp mass, but they are referred to in the text as "seed." Throughout maturation, each mother-palm was considered as a replicate, and ten seeds were used in each determination. Seed moisture content and dry mass were evaluated, according to the methods further described.

Mature fruits (2008 and 2009)

Seeds were harvested from 20 palmiteiro individuals from each study site in May 2008 and May 2009. Queen-palm seeds were obtained from 14 and 10 individuals from each study site in May 2008 and May 2009, respectively, except for the CF population, which did not bear ripe fruits in 2009. Seed harvesting was carried out maintaining a minimum distance of 50 m between mother palms. A plastic tarpaulin was placed at the base of each mother tree to obtain all the seeds present in the ripe bunch. Pulp was removed from palmiteiro fruits by placing them on a wire-mesh screen and rinsing thoroughly under running water. A pulp extraction machine was used for queen-palm. Fruits were processed separately for each bunch, avoiding seed mixtures among different mother palms and origins.

Seed yield was evaluated for all palmiteiro populations in 2008 and 2009, but only for queen-palm populations from SDF and RF in both years. Seed number per bunch was evaluated for each individual palm tree by extrapolating the mean weight of four samples of 100 seeds to the total mass of the bunch. Seed dry mass was determined using the oven method (105°C, 24 h; two replicates of 20 seeds).

Seed moisture content and germination

Seed moisture content was determined by the oven method (105°C, 24 h; two replicates of 20 intact seeds). Germination tests were carried out with seeds harvested in all three populations of queen-palm and palmiteiro in 2008, and with AR and RF palmiteiro populations harvested in 2009. Before germination tests, queen-palm seeds predated by weevils (*Revena rubiginosa*) were identified and removed from the seed lot by using X-ray (Brancalion *et al.*, 2011). Germination tests were carried out by sowing seeds in 300g of wet sand at 60% water holding capacity in 11×11×3 cm (H×W×D) plastic boxes. The boxes were kept at 25°C, and germination was recorded every 7 days until no further seedling emergence was observed. Germination speed was calculated according to Maguire (1962), in which:

Germination Rate Index (GRI) = $G_1/N_1 + G_2/N_2 + ... + G_n/N_n$,

where G_1, G_2, G_n = number of seeds germinated in the first, second, and last counting, and N_1, N_2, N_n = number of days after sowing when the first, second, and last counting were done.

The viability of non-germinated seeds was evaluated by the tetrazolium chloride test. The stony endocarp of queen-palm seed was initially broken with a hammer, and the enclosed queen-palm seeds and palmiteiro seeds were cut longitudinally in half with a scalpel to expose the axis. Non-rotten half-seeds were stained in a solution of 0.075% tetrazolium chloride for 24 h, at 30°C. The embryos were then classified as viable or non-viable, according to the patterns described by Moore (1972).

Data analysis

For all evaluations the mean obtained for each mother-palm was considered as a replicate in the analyses, by adopting a completely randomized design in the evaluations in laboratory. The tendency of each parameter under evaluation was graphically described using the mean ± s.e. from each evaluation. In the evaluation of seed yield and size, a two-factor ANOVA was initially applied to seed dry mass and seed number per bunch data (Log_{10} transformed data for both variables) considering forest types and years as random factors. We excluded queen-palm origin from CF from the analysis because we did not harvest seeds of this species in this forest type in 2009. However, when the effect of years was observed, a one-way ANOVA was applied to the data considering each year independently. Tukey's test ($P < 0.05$) was employed for multiple comparisons among means. The comparisons of seed moisture content, seed germination percentage, and speed were carried out by an ANOVA followed by a Tukey test ($P < 0.05$) if significant results were observed among three seed origins.

Results

Seed development

Seeds were not able to germinate before fruit ripening, so seed development was only evaluated based on seed moisture content and mass. The change in palmiteiro seed moisture content at SDF, AR, and RF followed a pattern typical of recalcitrant seed development (figure 2), while queen-palm seed development at SDF, RF and CF was typical of orthodox seeds (figure 2). Although both species showed a decline of seed moisture content and an increase in seed dry mass through maturation, they differed in the

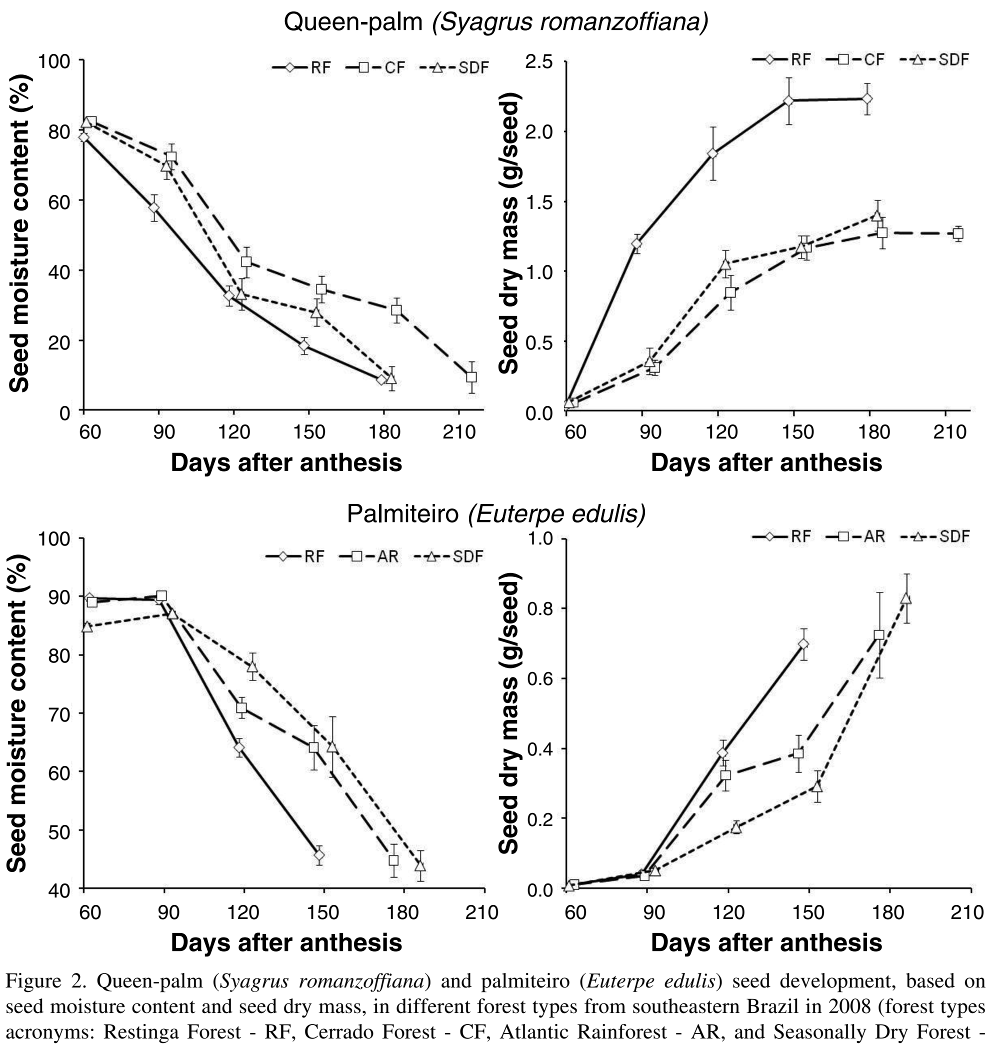

Figure 2. Queen-palm (*Syagrus romanzoffiana*) and palmiteiro (*Euterpe edulis*) seed development, based on seed moisture content and seed dry mass, in different forest types from southeastern Brazil in 2008 (forest types acronyms: Restinga Forest - RF, Cerrado Forest - CF, Atlantic Rainforest - AR, and Seasonally Dry Forest - SDF). The symbols represent the mean obtained in seven replicates (mother-palms) per harvesting moment, and vertical lines represent the standard error. The same mother-palms were used throughout the experiment.

seed moisture content attained at the end of the process. While queen-palm seeds showed 9% moisture content, palmiteiro seeds had 45% moisture content, which are typical values found in orthodox and recalcitrant seeds, respectively. The observed differences among provenances in the dynamics of the seed drying process indicate different periods of seed development, being shortest for palmiteiro in the RF population and longest for queen-palm at CF. Similarly, the period of dry mass accumulation of the seeds was shorter for palmiteiro in RF in comparison with AR and SDF (figure 2), and longer for queen-palm at CF compared with RF and SDF (figure 2). Queen-palm seeds from RF showed higher biomass than seeds from CF and SDF from 90 days after anthesis until the end of seed development.

Seed yield and size

Palmiteiro seed number per bunch differed among forest types, while seed dry mass did not differ when removing the effect of year (table 2). However, when considering the effect of forest type for each year, palmiteiro seed dry mass differed in 2009 (table 3), when palms from AR produced larger seeds (figure 3). Palms from AR also produced more seed than did palms from SDF and RF, while palms from SDF produced a larger seed crop than RF palms (figure 3). Queen-palm seed dry mass and seed number per bunch differed among forest types, with year not having a significant effect (P > 0.05;

Table 2. Two-way ANOVA results showing the effects of different forest type (Seasonally Dry Forest, Atlantic Rainforest, and Restinga Forest), and year (2008 vs. 2009), on seed dry mass (log_{10} transformed data) and seed number per bunch (log_{10} transformed data) of palmiteiro (*Euterpe edulis*) and queen-palm (*Syagrus romanzoffiana*).

Dependent variable and factors	*F*	df	*P*[a]
a) palmiteiro			
Seed dry mass			
Habitat	0.08	2,115	0.92
Year	75.34	1,115	**<0.0001**
Habitat × Year	7.95	2,115	**0.0006**
Seed number/bunch			
Habitat	35.00	2,115	**<0.0001**
Year	1.17	1,115	0.28
Habitat × Year	11.96	2,115	**<0.0001**
b) queen-palm			
Seed dry mass			
Habitat	50.68	1,44	**<0.0001**
Year	0.91	1,44	0.34
Habitat × Year	0.84	1,44	0.36
Seed number/bunch			
Habitat	27.59	1,44	**<0.0001**
Year	3.85	1,44	0.06
Habitat × Year	1.67	1,44	0.20

[a]Significant test results ($P < 0.05$) are indicated in bold

Table 3. One-way ANOVA results showing the effects of different forest type (Seasonally Dry Forest, Atlantic Rainforest, and Restinga Forest), and year (2008 vs. 2009), on seed dry mass (log_{10} transformed data) of palmiteiro (*Euterpe edulis*).

Year	Dependent variable and factor	*F*	df	*P*[a]
2008	seed dry mass			
	Forest type	3.1	2,57	0.0522
	no. seeds/bunch			
	Forest type	38.91	2,57	**< 0.0001**
2009	seed dry mass			
	Forest type	4.33	2,57	**0.02**
	no. seeds/bunch			
	Forest type	13.21	2,57	**< 0.0001**

[a]Significant test results ($P < 0.05$) are indicated in bold

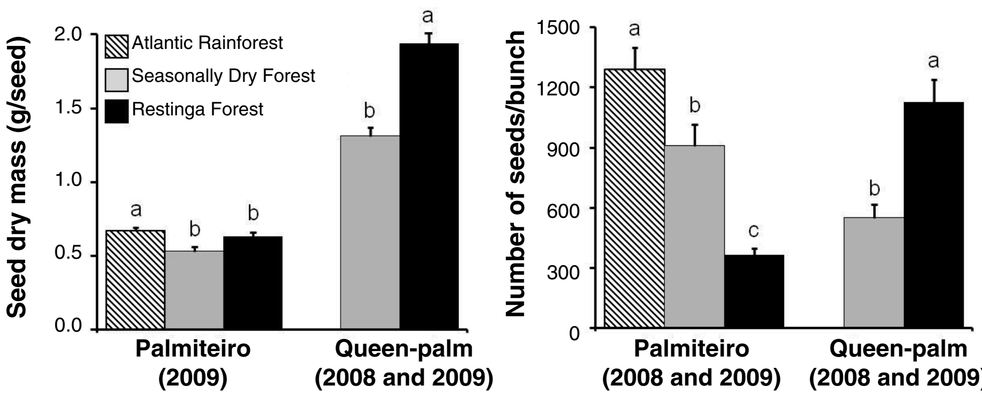

Figure 3. Effects of forest types on seed dry mass and seed number per bunch for palmiteiro (*Euterpe edulis*) and queen-palm (*Syagrus romanzoffiana*). Effects of year (2008 and 2009) were removed for palmiteiro seed number/bunch and queen-palm seed dry mass and seed number per bunch, and palmiteiro seed dry mass did not differ in 2008. Means with the same letter in the bar for a given species did not differ by Tukey's test ($P < 0.05$). (Bars represent the original means and vertical lines the standard error).

table 2). RF palms produced larger crops of heavier seeds than SDF palms (figure 3). Seed dry mass was highly variable among queen-palm (0.99 – 2.55g per seed; $N = 62$) and palmiteiro individuals (0.35 – 1.81g per seed; $N = 120$) considering together the seeds harvested in all forest types and in both years.

Seed germination and seed moisture content

Queen-palm and palmiteiro seeds remaining on the substrate at the end of the germination test were non-viable, indicating that neither of the species has seed dormancy, and that seed viability was solely defined by the germination test. Germination percentage and speed differed significantly between queen-palm populations and between palmiteiro populations in 2008 (table 4). There was greater and faster germination of palmiteiro seeds from AR compared with seeds from SDF and RF, while queen-palm seeds from RF showed the lowest physiological potential (figure 4). Although germination percentage did not differ ($F_{1,38}$ = 0.83; P = 0.34) between palmiteiro seeds harvested in 2009 at AR (86.4 ± 10.4%; mean ± 1 SD) and RF (79.9 ± 16.1%), the seeds from the former provenance germinated faster ($F_{1,38}$ = 5.79; P = 0.021), showing higher values of germination rate index (2.2 ± 0.6; mean ± 1SD) than seeds from RF (1.7 ± 0.5). Seed moisture content did not differ between queen-palm populations and between palmiteiro populations in 2008 (table 4).

Table 4. One-way ANOVA results showing the effects of forest type (Seasonally Dry Forest, Atlantic Rainforest, Cerrado Forest, and Restinga Forest) on palmiteiro (*Euterpe edulis*) and queen-palm (*Syagrus romanzoffiana*) seed moisture content and seed germination percentage and speed (seeds harvested 2008).

Dependent variable and factor	*F*	df	*P*[a]
a) palmiteiro			
Seed moisture content			
Forest type	1.79	2,27	0.1864
Germination percentage			
Forest type	4.37	2,27	**0.0228**
Germination speed			
Forest type	5.72	2,27	**0.0085**
b) queen-palm			
Seed moisture content			
Forest type	2.55	2,27	0.1479
Germination percentage			
Forest type	3.82	2,27	**0.0346**
Germination speed			
Forest type	4.23	2,27	**0.0253**

[a]Significant test results ($P < 0.05$) are indicated in bold

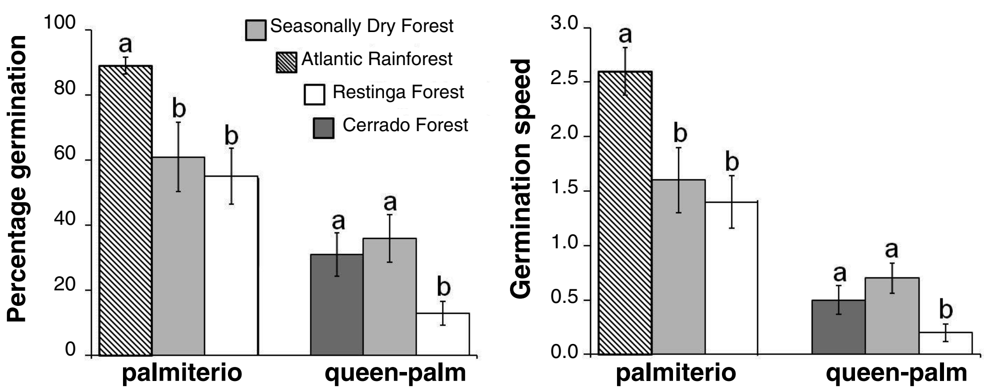

Figure 4. Effects of forest types (Seasonally Dry Forest, Atlantic Rainforest, Cerrado Forest, and Restinga Forest) on palmiteiro (*Euterpe edulis*) and queen-palm (*Syagrus romanzoffiana*) seed germination percentage and speed. Means with the same letter in the bar for a given species did not differ by Tukey's test ($P < 0.05$). (Bars represent the original means and vertical lines the SE). Seeds harvested in 2008.

Discussion

Palms represent an important group of plants not only for ornamental, fibre, and food purposes, but also for restoring tropical forests as a result of their remarkable importance in the structure and functioning of these ecosystems, for example providing food for large assemblages of vertebrate frugivores and seed predators (Henderson *et al.*, 1997). However, some particularities of palm seeds, like the recalcitrant behaviour of some species (Martins *et al.*, 1999; Wen, 2009) and the long period normally taken for germination (Tomlinson, 1990; Roberto and Habermann, 2010), constitute important obstacles for seedling production in forest nurseries. Further, our results indicate that seed yield and quality of a given palm species may vary greatly depending on seed provenance.

Palmiteiro individuals from RF showed the lowest seed yield, which is an expected response to the poor soils with high concentration of sodium present in this forest type (table 1). Contrasting with these results, queen-palm individuals showed the largest seed production in RF, which is probably attributed to the micro-habitat where this species was found. In contrast to palmiteiro, which is widespread across all habitats within RF, queen-palm individuals were found growing in ancient deposits of shells from shellfish that were consumed as food in prehistoric human settlements. These deposits have significant levels of calcium, phosphorous, and potassium in the soil, which may have resulted in enhanced seed yield. However, for both species the physiological potential of seeds produced in RF was lower, which indicates a problem for producing seedlings from seeds sourced in this forest type.

Lower germination of seeds from RF may be associated with the maternal environment, which resulted in different seed development curves both in palmiteiro and queen-palm. In contrast with the results obtained by Myint *et al.* (2010) for oil palm (*Elaeis guineensis*), for which heavier seeds showed higher germination, the heavier queen-palm seeds produced at RF in this study showed the lowest germination. The production of palmiteiro seeds at the AR was by far the most favorable situation, since its seeds showed the highest seed yield and quality.

To aggravate the problem of natural low seed germination of queen-palm, independent of the forest types, the studied seed-lots showed high rates of pre-dispersal seed predation by the weevil *R. rubiginosa.* As reported by Brancalion *et al.* (2011) for these seed-lots, queen-palm seeds from SDF, RF and CF showed, respectively, 80, 71, and 65% of seed predation by this insect, as determined using X-ray analysis. This indicates that the majority of the seeds harvested were not viable due to insect infestation.

The observed differences in seed yield and quality of palmiteiro and queen-palm in the studied forest types brings important consequences for seed trade and use. For instance, lower seed production in a given forest type could increase seed price, since greater harvesting effort would be necessary to obtain the same amount of seed, whereas lower physiological quality could reduce seed value. These particularities of seed production in different natural areas constitute an obstacle for the standardization of seed rules for native species (Elias *et al.*, 2006), and necessarily have to be taken into account when establishing standards for seed commercialization.

If seed production was established for supplying seeds for ornamental or crop purposes, the forest types where seed yield and quality are enhanced could be selected to set seed production fields. However, if the goal is to use the seeds for ecological restoration efforts, as is the case for palmiteiro and queen-palm in the state of São Paulo, these difficulties have to be faced and seed harvesting must occur in the same forest type as that which is to be restored, to ensure that the planting material consists of locally adapted genotypes (Hufford and Mazer, 2003). Therefore, seed production in natural forests has to be studied and comprehended by researchers and practitioners to improve seed quality for supplying the restoration market, but it cannot be used as an alternative to select more favorable forest types as seed production fields at the expense of the genetic origin of seeds.

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