Available online at www.sciencedirect.com

ScienceDirect

Forest Ecology and Management 242 (2007) 185–194

Forest Ecology and Management

www.elsevier.com/locate/foreco

Forest structure and productivity of palmiteiro (*Euterpe edulis* Martius) in the Brazilian Mata Atlântica

Alfredo C. Fantini [a,*], Raymond P. Guries [b]

[a] Departamento de Fitotecnia, Universidade Federal de Santa Catarina, Cx. Postal 476 Florianópolis, SC 88040-900, Brazil

[b] Department of Forest Ecology and Management, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA

Received 21 August 2006; received in revised form 8 January 2007; accepted 8 January 2007

Abstract

Palm heart from *Euterpe edulis* (palmiteiro) is one of the most important non-timber forest products (NTFP) exploited from the Mata Atlântica region of southeastern Brazil. In this paper, we examine the structure of natural forests and its impact on regeneration, growth and yield of palmiteiro in the Mata Atlântica region. Flowering and seed production of mature palmiteiros are variable but approximately one-half of all 'seed-bearing' palmiteiros flower and produce seed in any given year. Our results suggest that as the density or abundance of other woody plants increases, regeneration, survival and growth of palmiteiro is usually reduced. High densities of palmiteiro itself appear to suppress growth, while harvesting of mature palmiteiro leads to a marked increase in the growth of smaller size classes of palms. A reduction in the density or abundance of trees, lianas and tree-ferns would appear to benefit palmiteiro, but the differences in forest structure between the study sites suggests that successful management strategies may differ depending upon site conditions. A native bamboo (*Guadua tagoara*) limits the regeneration of many woody plants, but it appears to have only a limited effect on the survival, regeneration and growth of palmiteiro.

Keywords: *Euterpe edulis*; Palmito; Forest conservation; Mata Atlântica; Non-timber forest products

1. Introduction

Conversion of forests to other land uses has reduced the once extensive Mata Atlântica of southeastern Brazil to small fragments thereby endangering endemic flora and fauna (Fonseca, 1985; Gentry, 1992; Mittermeier et al., 1998; Thomas et al., 1998). This trend has prompted a search for alternatives to present land uses that provide greater economic and ecological values from remaining forests. Production of non-timber forest products (NTFPs) may provide a basis for improving conservation of some forest remnants while providing a small but continuous source of income for land owners (Lopez et al., 2004; Peters, 1996; Shanley et al., 2002). *Euterpe edulis* Martius, locally known as 'palmiteiro', is one such NTFP that is exploited for palm heart (sold locally as 'palmito') in the Mata Atlântica region (Fantini et al., 2004; Galetti and Fernandez, 1998; Orlande et al., 1996).

Constraints to managing palmiteiro have ecological as well as social and economic roots. *E. edulis* is a shade-tolerant, slow-growing palm (Carvalho, 1994; Paulilo, 2000), making it largely unsuitable for plantation monocultures. Seeds are dispersed by birds and small mammals (Pizo and Simão, 2001) and can form dense seedling populations with clumped distributions centered on putative parent plants (Reis et al., 1996). Mortality within cohorts can be quite large during the first few years but declines once sapling size is achieved (Conte et al., 2003). Early growth is strongly influenced by light environments, with optimal growth achieved between 20 and 70% full sunlight; full sun appears inhibitory to growth (Paulilo, 2000). With repeated cycles of exploitation, natural populations of *Euterpe* can experience sharp declines and local extinctions are common (Nodari et al., 2000).

Ecological and genetics research on *E. edulis* includes studies of population structure and regeneration dynamics (Freckleton et al., 2003; Reis and Kageyama, 2000; Reis and Reis, 2000; Reis et al., 1996, 1999), population genetics (Conte et al., 2003; Reis, 1996), plant productivity (Bovi et al., 1991; Fantini et al., 1997) and management systems (Reis et al., 1991, 1999, 2000b,c). However, no research is available to guide

* Corresponding author. Tel.: +55 48 3721 5320; fax: +55 48 3721 5330.
E-mail addresses: afantini@cca.ufsc.br (A.C. Fantini), rpguries@wisc.edu (R.P. Guries).

0378-1127/$ – see front matter
doi:10.1016/j.foreco.2007.01.005

development of silvicultural practices for natural forests to improve *Euterpe* regeneration and early growth, especially in the degraded forest fragments held by private owners throughout the Mata Atlântica. In southeastern Brazil, these fragments are frequently invaded by bamboo following disturbance, *Guadua tagoara* being the most important species. The labor required for bamboo control is important in shaping farmers' perceptions that the remnant forests are 'worthless ecosystems.' Management guidelines that promote regeneration, growth and harvesting of palmiteiro are needed if NTFP such as palmito are to prove useful for conserving existing forest remnants (Reis et al., 2000b,c).

In this paper, we examine some forest structure and stocking parameters such as density and abundance of woody plants that appear to influence regeneration, growth and yield of palmiteiro in natural forests in the Mata Atlântica region. A secondary objective was to examine specifically the apparent impact of bamboo on restricting regeneration and growth of palmiteiro.

2. Methods

2.1. Study site

The study was conducted at the Nova Trieste Forest, a 30,000 ha privately owned forest near Eldorado do Sul, São Paulo State, Brazil (24°22′S, 48°15′W). This area is adjacent to several state parks that contain more than 400,000 ha of contiguous forest, the largest remnant patches of the Mata Atlântica. The climate of the region is characterized by average summer and winter temperatures of 24 and 18 °C, respectively. Annual precipitation ranges from 1600 to 2000 mm, without a distinct dry season (Brasil, 1979). Elevation varies between 50 and 400 m, while soils in the region are predominantly red-yellow podzols (Ultisols) (Brasil, 1979) with low natural fertility and high rates of erosion. Forest cover is classified as a Moist Dense Forest (Atlantic Coastal Forest, Brazão et al., 1993), with the average canopy trees reaching 25–30 m in height.

We divided the study area into two sites, called Eldorado 1 and 2. The two sites are contiguous, but Eldorado 1 appears to have experienced greater disturbance in the past based on the number of plots containing an abundance of bamboo (*G. tagoara*). Eldorado 1 also has wetter soils than Eldorado 2 and essentially no topographic relief. Palm heart has been exploited in the past at both sites with the last harvest completed during the late 1960s. The traditional recommendation for palmiteiro harvesting in the region, and likely the one used at that time, was to cut any palmiteiro that contained a palm heart; in practice, this led to harvesting any palmiteiro greater than 5 cm diameter at breast high (DBH).

2.2. Data collection

2.2.1. Forest structure and woody plant regeneration

Data were collected from 27 existing 40 m × 40 m permanent plots, 15 at Eldorado 1 and 12 at Eldorado 2, distributed over an area of 430 ha. In order to relate *Euterpe* regeneration and growth to the density and abundance of other woody plants on the plots, in 1995 we measured to the nearest 1 cm all woody plants greater than or equal to 5 cm diameter at breast high (measured at 1.37 m above ground), including trees, lianas and tree-ferns. Size class frequency distributions were constructed by pooling woody plants into 10 cm diameter classes except for the smallest class that contained stems between 5.0 and 9.9 cm DBH. These data also were used to estimate plot basal area (m^2 per ha), the sum of the cross sectional areas at breast height of all woody plants having a diameter greater than 5 cm DBH. Basal area was used as a measure of stand density that takes into account the size or volume of trees as well as their abundance (Husch et al., 2003). The number of stems was also recorded as a simple measure of abundance. Woody species were assigned to one of two classes, a common threshold used in many tropical forests to distinguish between mid-canopy trees (<10 cm DBH) and canopy trees (≥10 cm DBH) (Gentry and Terborgh, 1990; Lieberman et al., 1990). No attempt was made to identify woody plants to species. Other woody plants less than 5 cm DBH were counted on the same subplots used to assess palmiteiro regeneration, and were divided into two categories; seedlings (up to 1.3 m high) and saplings (taller than 1.3 m).

2.2.2. Plot sampling for palmiteiros

Data were collected between 1994 and 1998 from the same plots used to inventory woody plants to determine forest structure. As part of a long-term study, all *E. edulis* greater than 5 cm DBH in these plots had been mapped, individually tagged and measured to the nearest 1 mm DBH during 1994. Plots were re-measured 12 months after the first inventory (1995), including new palms resulting from recruitment of saplings into diameter classes greater than or equal to 5 cm. Following this second measurement, all palmiteiros greater than 9 cm DBH were harvested (1995), except 50 seed palms per hectare were retained, a legal mandate established to provide for adequate regeneration. The plots were re-measured again approximately 24 and 48 months after harvesting, in late 1996 and 1998, respectively.

2.2.3. Palmiteiro reproduction

The reproductive status of each palm in these plots was recorded in 1994 and 1995 to estimate the number of individuals of reproductive age. Palmiteiros were identified as 'seed-bearing' by the presence of inflorescence or fruits, the presence of dry panicles or scars left in the trunk by previous inflorescences. Such scars permit the identification of palmiteiros that have borne fruit during the past several years.

2.2.4. Palmiteiro structure, regeneration and growth

Young palms (<5 cm DBH), called 'natural regeneration', were inventoried in 1994, 1995, 1996 and 1998 on two 40 m × 2 m perpendicular subplots, crossing at the center of each of the 27 plots. Young palms were divided into three categories according to size; seedlings (≤10 cm height), small saplings (between 10 and 50 cm in height), and large saplings (taller than 50 cm). Palmiteiros greater than or equal to 5 cm DBH were measured for construction of size class frequency distributions using 2 cm diameter classes beginning with the 5.0–6.9 cm class. Palmiteiro growth was expressed as a percentage of an individual palm's basal area growth per unit time, usually one year. In this paper, we equate diameter growth of young palms to 'the secondary thickening' of the palm stem (Tomlinson, 1961, p. 20). Natural regeneration and recruitment estimates for young palms are based on their plot averages during the period of the inventories.

2.2.5. Bamboo
A native bamboo (*G. tagoara* (Ness) Kunth), an indicator of past disturbance, was common on some plots, especially at Eldorado 1, and was considered as a factor that could impact regeneration and growth of young palms. The number of culms of bamboo in each plot was counted, and the DBH of a random sample of 116 culms was used to estimate basal area as a measure of local density.

2.3. Analyses

Size class frequency distributions using 10 cm diameter classes were constructed for both areas as one measure of forest structure. Differences in selected measures of forest structure between the two sites were examined using Pearson product-moment correlations (SAS, 1989), e.g., to test the association between the basal area (hereafter referred to as 'density') and abundance of canopy trees, lianas and tree-ferns and the reproduction and growth rates of palmiteiro. The significance of a calculated correlation coefficient was determined using tabled 'critical values' (Snedecor and Cochran, 1989). Pearson product-moment correlations were also used to test the association between density, abundance and reproduction of palmiteiro cohorts. At Eldorado 1, where 11 of 15 plots contained bamboo, we examined the correlation between the density of bamboo and the density and abundance of woody plant seedlings and saplings, as well as the correlation between the density of bamboo and estimates of palmiteiro basal area, regeneration and growth.

A regression model (PROC GLM of SAS) was used to test the relationship between forest structure variables and the growth of palmiteiro.

$$Y = a + bX + e$$

where Y is the dependent variable (e.g., above ground growth of palmiteiro for a specified interval of time) and X the independent variable (e.g., density or abundance of woody plants, vines and tree-ferns), a and b are coefficients that specify the fit of the regression to the data and e is the residual. The utility of regressions to account for any observed difference was determined by examining p-values, the mean square of the error (MSE), the coefficient of determination (R^2) and a plot of residuals. A t-test (Snedecor and Cochran, 1989) was performed to test the departure of the linear coefficient from zero.

3. Results

3.1. Forest structure

In general, the plots at Eldorado 2 had a greater abundance and density of woody plants than those at Eldorado 1 (Fig. 1). The number of trees smaller than 10 cm DBH was significantly greater at Eldorado 2 ($F = 13.5$; d.f. = 25; $p = 0.001$), as was total density of trees smaller than 10 cm DBH ($F = 14.6$; d.f. = 25; $p = 0.001$). The number of trees greater than 10 cm DBH was significantly greater at Eldorado 2 ($F = 35$; d.f. = 25; $p < 0.001$), but there was no significant difference in plot densities between Eldorado 1 and 2 for trees greater than or equal to 10 cm DBH (Fig. 1). At both sites, the size class frequency distributions for all woody stems approximates a reverse J-shaped curve (Fig. 2), characteristic of many uneven-aged temperate and tropical forests (e.g., Gentry and Terborgh, 1990; Rankin-de-Morona et al., 1990). However, it is quite likely that at least some of the species included in these distributions are essentially even-aged although the pooled populations appear to be all-aged. We can only speculate that the plots at Eldorado 2 are probably slightly older than those at Eldorado 1 based upon a slightly greater number of large trees, lianas and tree-ferns. Palmiteiro can grow under a range of forest stocking conditions but sustainable management for NTFP production will only prosper if forest management, including appropriate stocking conditions and canopy densities, are carefully managed.

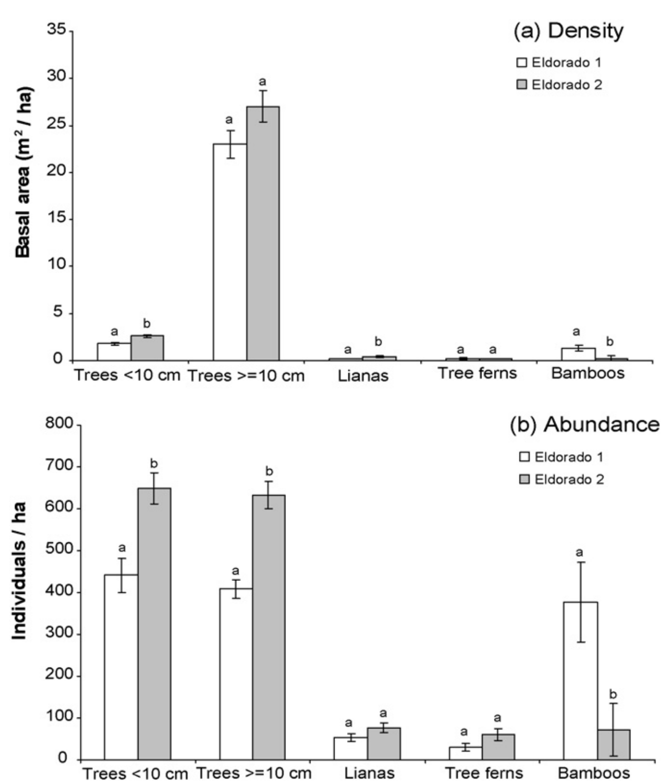

Fig. 1. (a and b) Density ($m^2\ ha^{-1}$) and abundance (individuals ha^{-1}) of trees, lianas, tree-ferns and bamboo at Eldorado 1 and 2. Bars are ±1 SE. In each pair of columns, values followed by the same letter do not differ statistically ($p < 0.05$).

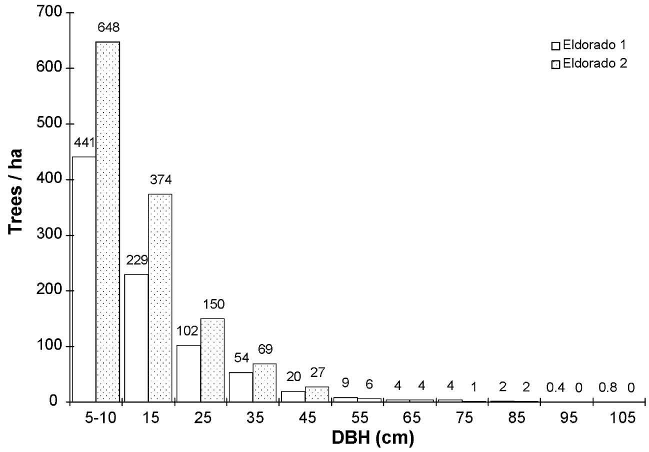

Fig. 2. Size class frequency distribution of trees, excluding lianas, tree-ferns, bamboo and palmiteiro by 10 cm classes, at Eldorado 1 (open columns) and 2 (solid columns).

The average number per ha of woody plant seedlings and saplings at Eldorado 1 was 25,865 (±2443) and 3540 (±319), respectively, and 35,286 (±4927) and 4105 (±290) at Eldorado 2. There was a larger number of young trees at Eldorado 2, but there was no statistically significant difference between the sites owing to large between-plot variation at each site.

The density of lianas was significantly higher at Eldorado 2 ($F = 4.61$; d.f. = 25; $p = 0.042$), another indication that plots at this site have a history of disturbance despite the presence of a few large trees, but there was no significant difference in the number of lianas between the sites. Tree-ferns had about the same density at both sites, and although their abundance at Eldorado 2 averaged twice that of Eldorado 1, there were no statistically significant differences between the sites for either variable (Fig. 1a).

3.2. Bamboo

The abundance of bamboo was higher at Eldorado 1, where the average number of culms per hectare was five-fold greater than at Eldorado 2 ($F = 6.36$; d.f. = 25; $p = 0.018$) (Fig. 1b). However, the distribution of bamboo within the forest was very heterogeneous, expected for an invasive species with a clonal habit. The DBH of each culm averaged 7.2 cm (±0.91, $n = 116$), resulting in an average basal area of 1.3 m^2 ha^{-1} (Fig. 1a); the most dense plot had a basal area (density) of 3.6 m^2 ha^{-1}.

At Eldorado 1, there was a strong negative correlation between the number of culms of bamboo and the basal area of trees smaller than 10 cm DBH ($r = -0.70$; $p = 0.004$), but no correlation existed with larger trees ($r = -0.11$; $p = 0.70$), perhaps because they were established before the bamboo was introduced. Bamboo density and the abundance of large trees was negatively correlated ($r = -0.65$; $p = 0.009$), suggesting that canopy trees probably limit the local establishment of new patches of bamboo. Bamboo appeared to have some negative impact on woody plant regeneration as the correlation between bamboo density and abundance was significant for small trees ($r = -0.72$; $p = 0.003$) but not for seedlings ($r = -0.32$; $p = 0.25$) or saplings ($r = -0.48$; $p = 0.07$).

3.3. Stand structure of palmiteiro

At Eldorado 1, the number of palmiteiros greater than or equal to 5 cm DBH per hectare prior to harvesting averaged 342 (±26), with a density of 2.9 m^2 ha^{-1} (±0.25), whereas at Eldorado 2, there was an average of 366 (±22) palmiteiros per ha, with a density of 2.5 m^2 ha^{-1} (±0.20). The abundance of palmiteiros and their densities at Eldorado 1 and 2 were not significantly different. At both sites, the size class frequency distribution for palmiteiro approximated a normal distribution characteristic of even-aged stands, suggesting an origin as one or a few cohorts (Fig. 3a).

Correlations between density and abundance of palmiteiro and density and abundance of woody plants were only significant at Eldorado 2 (Table 1). Both density and abundance of palmiteiro declined as the density and abundance of trees increased, particularly the density of small trees and the abundance of large trees.

3.4. Reproductive structure of palmiteiro

Based on the presence of inflorescence (panicle) scars, the average number of 'seed-bearing' palms per hectare in 1995 was 187 (±15) and 185 (±18) at Eldorado 1 and 2, respectively (Fig. 3b). At both sites, 'seed-bearing' palms approximated a

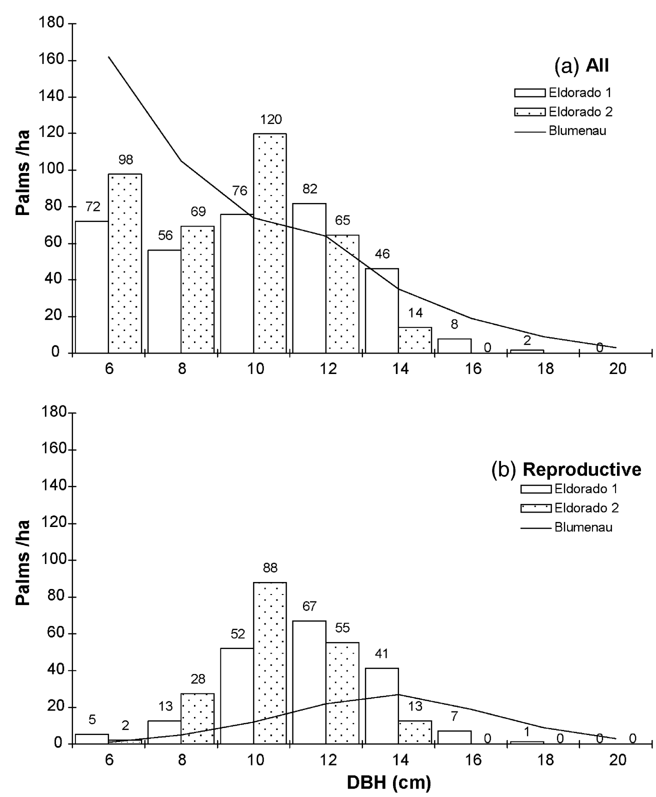

Fig. 3. Size class frequency distribution of all palmiteiros ≥5 cm DBH (a) and reproductive palmiteiros (b) at Eldorado 1 and 2. Data from Blumenau-SC, a 'natural' forest essentially undisturbed, was used to generate the reference line.

Table 1
Correlations between forest structure (density and abundance of trees, lianas and tree-ferns) and density and abundance of palmiteiro at Eldorado 2

	Density of palmiteiro ($m^2 ha^{-1}$)	Abundance of palmiteiro (individuals ha^{-1})
Density of trees, lianas and tree-ferns ($m^2 ha^{-1}$)		
<10 cm dbh	−0.36*	−0.42*
≥10 cm dbh	−0.28*	−0.34*
Abundance of trees, lianas and tree-ferns (individuals ha^{-1})		
<10 cm dbh	−0.30*	−0.36*
≥10 cm dbh	−0.51*	−0.47*

* $p < 0.05$, $n = 12$.

Table 3
The number (±SE) of palmiteiro seedlings, small and large saplings and recruitment into the seedling class, at Eldorado 1 and 2

Size class of palmiteiro	Eldorado 1	Eldorado 2
Seedlings	13,618 (±2,322)	9,152 (±1,479)
Small saplings	3,220 (±450)**	1,683 (205)
Large saplings	477 (±68)	682 (±58)*
Recruitment	19 (±2)	20 (±3)

Recruitment represents the number of seedlings growing into the small sapling class per hectare each year.
* $p < 0.05$.
** $p < 0.01$, $n = 12$.

normal distribution with respect to size class frequency distributions, and represented 51–55% of the larger palms. During the first two inventories (1994 and 1995) conducted before palmiteiro harvesting, a total of 82 ‘seed-bearing’ palmiteiros per ha (44% of all ‘seed-bearing’ palms) were identified at both sites as having produced seeds in either 1994 or 1995, while 31 (17%) produced seeds in both years (Table 2). The number of seed-bearing palmiteiros in the second inventory (1995) was 53% higher than in the first, reflecting a high year-to-year variation in seed production. The number of seed-bearing palmiteiros was not correlated with the density or abundance of other woody plants.

3.5. Natural regeneration and ‘recruitment’ of palmiteiro

The abundance of palmiteiro seedlings was not significantly different between sites, while the abundance of small saplings was significantly higher at Eldorado 1 ($F = 8.18$; d.f. = 1, 25; $p = 0.008$), and the number of large saplings was significantly higher at Eldorado 2 ($F = 4.96$; d.f. = 1, 25; $p = 0.035$) (Table 3). Over a 4-year period, the average ‘recruitment’ of seedlings into the small sapling class at Eldorado 1 was 19 (±2) palmiteiros per ha per year, not significantly different from the recruitment of 20 (±3) observed at Eldorado 2. We conclude that the regeneration of palmiteiros into seedling classes is about the same at both sites regardless of other site conditions, but recruitment into the small sapling classes may be favored by the somewhat more open forest conditions that exist at Eldorado 1. The slightly greater number of large saplings at Eldorado 2 may simply be due to the long interval between harvesting, from the 1960’s to 1995.

At Eldorado 1, the abundance of seedlings and saplings and the recruitment of palmiteiro showed no association with density or abundance of existing palmiteiros. At Eldorado 2 however, the abundance of seedlings was directly proportional to the total density of existing palmiteiro, while large saplings showed a significant negative correlation with overall density. Small saplings were not correlated with either the density or abundance of the entire palmiteiro population (Table 4), and palmiteiro recruitment into the small sapling class seemed unrelated to either the density or abundance of the overall palmiteiro population.

The relationships between forest structure and natural regeneration of palmiteiro were different at the two sites (Table 5). At Eldorado 1, no class of palmiteiro regeneration (seedlings, small and large saplings) was correlated with density or abundance of other woody plants. The abundance of bamboo at Eldorado 1 also had no significant correlation with any measures of palmiteiro regeneration (Table 5). However, the abundance and density of small and large trees at Eldorado 1, while not significantly different from Eldorado 2, were 15–30% lower in every size class except for bamboo. At Eldorado 2, several significant correlations between palmiteiro regeneration and the density and abundance of other woody vegetation were noted (Table 5). Palmiteiro seedling abundance was negatively correlated with the abundance of both small and large trees, while seedling and small sapling palmiteiro were negatively correlated with the abundance of large trees. Finally, the recruitment of seedling palmiteiro into the small sapling class at Eldorado 2 was

Table 2
Total number and proportion of seed-bearing palmiteiros per ha at Eldorado 1 and 2 that flowered and produced seed in 1994 and/or 1995

Class of palm	Abundance of palmiteiros (individuals ha^{-1})	Reproductive palmiteiros (%)
Average number of palmiteiros ≥5 cm	354	
Seed-bearing palmiteiros (from scars)	186	53
Seed-bearing in 1994 and/or 1995	82	44
Seed-bearing (1994 only)	16	9
Seed-bearing (1995 only)	35	19
Seed-bearing (both years)	31	17

Table 4
Correlations between abundance of palmiteiro regeneration (number of seedlings and small and large saplings per ha) and ‘recruitment’ (number of seedling palmiteiros per ha growing into the small sapling class) and the density and abundance of the total existing palmiteiro at Eldorado 2

Size class of palmiteiro	Existing palmiteiros	
	Density ($m^2 ha^{-1}$)	Abundance (individuals ha^{-1})
Seedlings	0.62*	0.52
Small saplings	−0.01	−0.08
Large saplings	−0.62*	−0.51
Recruitment	0.20	0.42

* $p < 0.05$, $n = 12$.

Table 5
Correlations between forest structure (density and abundance of trees, lianas and tree-ferns and bamboo abundance) and regeneration (number of seedlings and saplings per ha) and recruitment of palmiteiro at Eldorado 1 and 2

Forest structure variables	Class of palmiteiro regeneration (Eldorado 1)				Class of palmiteiro regeneration (Eldorado 2)			
	Seedlings	Small saplings	Large saplings	Recruitment	Seedlings	Small saplings	Large saplings	Recruitment
Density of trees, lianas and tree-ferns (m^2 ha^{-1})								
<10 cm dbh	0.32	−0.09	−0.09	−0.31	−0.49	−0.55	−0.38	−0.62*
≥10 cm dbh	−0.47	−0.35	0.18	−0.10	−0.69*	−0.26	0.05	0.01
Abundance of trees, lianas and tree-ferns (individuals ha^{-1})								
<10 cm dbh	0.40	−0.04	−0.02	−0.34	−0.43	−0.53	−0.38	−0.56
≥10 cm dbh	0.13	0.03	0.17	0.10	−0.71*	−0.64*	−0.20	−0.38
Bamboo abundance (culms ha^{1-})	−0.26	−0.26	−0.14	−0.02	–	–	–	–

* $p < 0.05$, $n = 15$ at Eldorado 1, $n = 12$ at Eldorado 2.

Table 6
Correlations between forest structure (density and abundance of trees, lianas and tree-ferns and bamboo abundance), and individual increment (% per year) of palmiteiro in three consecutive periods of growth at Eldorado 1 and 2

Forest structure	Period of growth (months)					
	Eldorado 1			Eldorado 2		
	Before harvesting	After harvesting		Before harvesting	After harvesting	
	12	12	24	12	12	24
Density of trees, lianas and tree-ferns (m^2 ha^{-1})						
<10 cm dbh	−0.36	−0.18	−0.28	−0.33	−0.69*	−0.68*
≥10 cm dbh	−0.36	−0.56*	−0.64*	−0.30	0.00	0.10
Abundance of trees, lianas and tree-ferns (individuals ha^{-1})						
<10 cm dbh	−0.46	−0.21	−0.34	−0.36	−0.62*	−0.65*
≥10 cm dbh	−0.14	−0.14	−0.26	−0.02	−0.53	−0.58
Bamboo abundance (culms ha^{-1})	0.24	0.06	0.14	–	–	–

* $p < 0.05$, $n = 15$ at Eldorado 1, $n = 12$ at Eldorado 2.

negatively correlated with the density of woody plants but not with the abundance of woody plants (Table 5).

3.6. Palmiteiro growth

The annual growth increment (basal area increase) of post-harvest palmiteiro saplings increased in the years following the 1995 harvesting ($F = 28$; d.f. = 1, 52; $p < 0.001$). Prior to harvest, a slightly negative but non-significant relationship was observed between the growth increment of palmiteiro and the density of other woody plants (Fig. 4). Following harvest of the larger palmiteiro stems, a marked response in the growth of remaining palmiteiro was observed, with the best growth achieved in those stands that had the lowest density of woody plants ($t = -3.08$; $p = 0.005$; Fig. 4).

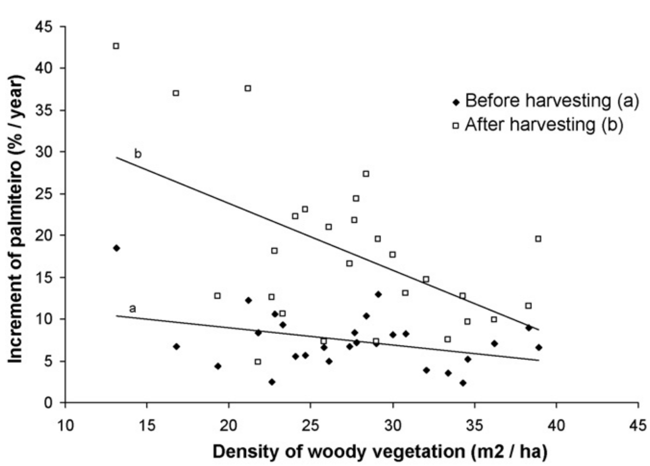

Fig. 4. Increment of palmiteiro as a function of the density of woody vegetation at Eldorado, before (a) and after (b) palmiteiro stand harvesting (average of 4 years). (a) $y = 13.13 - 0.21x$ ($t = -2.03$, $p = 0.053$), $R^2 = 0.14$. (b) $y = 39.70 - 0.80x$ ($t = -3.08$, $p = 0.005$), $R^2 = 0.27$.

In the year prior to harvest, growth of the palmiteiro was not significantly correlated with any measure of density or abundance of woody vegetation or bamboo (Table 6). However, 1 year after the harvest, significant differences in growth by the residual palmiteiro were observed at both Eldorado 1 and 2. At Eldorado 1, the more open stand, the largest growth response was achieved in plots having the lowest densities of large trees. At Eldorado 2, the denser stand, the best growth response was achieved in those plots that had fewer and less dense woody saplings and mid-story trees.

4. Discussion

4.1. Forest structure

The forest structure at Eldorado 2 appears typical of the few remaining relatively undisturbed Mata Atlântica ecosystems. Estimates of density (27 m^2 ha^{-1}) and abundance of trees

($632\ ha^{-1}$) greater than or equal to 10 cm are similar to those for two primary forests we inventoried in São Paulo and Santa Catarina (unpublished), but even higher estimates can be found for this ecosystem (Jesus et al., 1992; Veloso and Klein, 1957). The forest structure at Eldorado 1, the site having lower estimates of density and abundance of trees but numerous bamboo stems, suggests a stand with a history of moderate disturbance, probably due to past logging. The number of large trees at Eldorado 1 is below the estimates typical of mature undisturbed forest in this region (e.g., Melo et al., 2000; Kurtz and Araújo, 2000). The density (basal area) estimate at this site is close to that of Eldorado 2 only because of the presence of a few very large remnant trees (Fig. 1).

The significantly smaller number of woody stems at Eldorado 1 relative to Eldorado 2 may be the result of past invasion by the widespread bamboo, *G. tagoara*. The density of bamboo at Eldorado 1 represents the equivalent of the basal area for all other woody stems between 5 and 10 cm (Fig. 1). *G. tagoara* is a common 'pioneer' in logged forests of the Mata Atlântica and can rapidly dominate disturbed forests with its climbing habit and growth rates up to 10 cm a day (Judziewicz et al., 1999). Adult bamboo culms can completely cover a tree canopy, killing trees while opening new ground for further invasion, a process reported to occur in other forest types (e.g., Veblen, 1982; Wang et al., 2006). Any forest openings at Eldorado 1 appear to be quickly filled by bamboo thereby precluding other woody plant regeneration. Without a market, this bamboo is a growing problem for forest owners in the Mata Atlântica, as it has no current market value in this region. Other Guadua species are sold for US$ 1 per culm, and are even cultivated in Colombia (Parsons, 1991).

4.2. Stand structure of palmiteiro

At Eldorado 1 and 2, the size class frequency distribution of the palmiteiro stands suggests they are more or less even-aged and probably originated from a heavy harvest in the past. Large palmiteiro are slightly under-represented relative to other natural forests, but the large number of palms in the smaller size classes suggests that regeneration and recruitment levels are maintaining palmiteiro here (Fig. 3). The potential for future regeneration also appears adequate given the large number of seed-bearing palms, and the high number of seedlings and saplings ($>14{,}000\ ha^{-1}$) that are typical of natural forests in the region (Reis, 1995; Reis et al., 2000a).

The number of significant negative correlations between density and abundance of palmiteiros and the density and abundance of other woody plants at Eldorado 2 (Table 1) suggests that although this palm is a shade-tolerant species (Reitz, 1974), regeneration and growth are influenced by canopy conditions and other forest structures. The lack of any significant correlations between these same variables at Eldorado 1 is difficult to explain given the large variation in plot conditions between the two sites. The density and abundance of woody plants, while not significantly different between Eldorado 1 and 2 by our measures, may still be sufficient to create competitive effects (e.g., for light) that influence important determinants of growth and yield. Experiments designed to manipulate canopy conditions or light regimes would be needed to quantify those forest structure differences leading to variation in the regeneration, growth and yield of palmiteiro.

The increased growth of residual palms following harvest of older palmiteiro stems suggests that more frequent or intensive thinning of palmiteiro itself, as well as selective removal of some competing woody vegetation, may be useful management practices that provide economic benefits without creating favorable conditions for bamboo to invade.

In this study, we found no correlations between the density or number of palmiteiros and the abundance of bamboo, although the manager of the forest at Eldorado alleges that the areas invaded by bamboo have lower densities of palmiteiro. The reputation of *G. tagoara* as an aggressive, thorny bamboo, usually results in a decision that forests invaded by bamboo can no longer profitably be managed for palmiteiro. The impact of *G. tagoara* on palmiteiro reproduction and growth may have been exaggerated but trials would be needed to document the real impact of *Guadua*.

4.3. Reproductive potential of palmiteiro

The average number of seed-bearing palmiteiros per hectare (186) at Eldorado is high compared with other estimates for the region (103 palmiteiros per hectare, Fantini et al., 1993; 131 palmiteiros per hectare, Conte, 1997). However, the average number of palmiteiros greater than or equal to 5 cm at Eldorado (354) is less than that of these other forests. Estimates of 57–96 seed-bearing palmiteiro per hectare for another primary forest at Blumenau-SC (Reis, 1995) represent 49–72% of the palmiteiros in that forest. All these data suggest that seed production at Eldorado 1 and 2, while variable from year to year, appears adequate for regeneration. Our results indicate that seed production is mostly provided by different individuals each year as only 17% of the seed-bearing palms in this forest produced seeds in the two consecutive years studied. However, we did not assess the number of seeds produced by each palm, which would be essential to determine whether seedling populations represent more than a small fraction of viable seeds produced.

The lack of significant correlations between the number of seed-bearing palmiteiros and the density or abundance of small or large trees (Table 3), suggests that palmiteiro flowering and reproduction is relatively independent of the density or abundance of competing vegetation at Eldorado 1 and 2. This may be true simply because the small number of palmiteiro that survive and achieve reproductive status are in favorable positions within the forest. Reis (1995) reported an average of two inflorescences per palm within a primary forest in Santa Catarina, whereas isolated palmiteiro or those at forest margins typically may bear four or five inflorescences. It would be useful to determine the optimal forest density that would lead to an increase in flowering and seed production.

4.4. Natural regeneration and recruitment of palmiteiro

The abundance of seedling and small sapling palmiteiros at Eldorado is similar to estimates reported in other studies of long-term managed stands (Reis, 1995; Conte, 1997), suggesting that natural regeneration appears adequate to maintain economically viable populations. At Eldorado 1, the population of young palmiteiros shows no correlation with palmiteiro stand structure as measured by density or abundance. In addition, there were no consistent correlations between measures of forest structure and the number of seed-bearing palmiteiros or estimates of natural regeneration of palmiteiro (Table 5). At Eldorado 2, however, the number of palmiteiro seedlings is directly proportional to palmiteiro density and inversely proportional to the number of large sapling palmiteiros (Table 4). Recrutiment of palmiteiro into the small sapling size class is drawn from a 'bank' of seedlings only 1–2 years old (Reis et al., 2000a,b); the density of this seedling bank is a function of the number of seed-bearing palmiteiros in the stand. The number of palmiteiro seedlings and small saplings is negatively correlated with the abundance and density of large trees (Table 5), suggesting that canopies are an important factor in the success of natural regeneration of palmiteiro.

Despite some differences in the number of saplings at Eldorado 1 and 2, rates of seedling recruitment at these sites were not different. Recruitment was negatively affected by the density of small woody plants at least at Eldorado 2 (Table 5), probably due to direct competition for light at lower and mid-canopy levels.

4.5. Palmiteiro growth

Prior to harvest, no significant relationship was noted between palmiteiro growth rate and the density of other woody plants (Table 6; Fig. 4). Following harvest, the growth rates of residual palmiteiro stands increased. At Eldorado 1, palmiteiro growth 12 and 24 months after harvest was negatively correlated with the density of large trees, while at Eldorado 2 palmiteiro growth 12 and 24 months after harvest was negatively correlated with both the density and abundance of small trees (Table 6). Since the forest canopies remained unchanged by the palmiteiro harvest, any post-harvest growth response of residual palmiteiro must be related to the reduction of large palmiteiros.

Prior to harvest at both sites, the density of large palmiteiro appears to have suppressed the growth of younger size classes. However, following harvest of the larger palmiteiro, residual palms responded best on those sites with the lowest density of other woody plants (Fig. 4). At Eldorado 1, bamboo may not have the large impact on palmiteiro growth that farmers attribute to it given the lack of significant correlations between bamboo and any measure of palmiteiro regeneration and growth (Tables 5 and 6). However, the more open forest conditions at Eldorado 1 apparently provided the opportunity for residual palms to respond to improved light and competition conditions. At Eldorado 2, bamboo is largely absent but the greater density and abundance of small trees present appear to limit the ability of palmiteiro to respond following harvest, perhaps because the small trees provide strong competitive effects that parallel those of the mature palms. In the long-term, we expect bamboo to have a negative impact on palmiteiro, especially in terms of regeneration (Table 5), although more research would be needed to identify causal relationships.

5. Conclusions and recommendations for palmiteiro management

Palmiteiro is one the most abundant and valuable NTFP species in the Mata Atlântica. Data from this study suggest that it could be managed to provide adequate regeneration while permitting a sustainable harvest. All the palmiteiro parameters we studied (seed production, density of seedlings and saplings and growth rate) were reduced as the density of both palmiteiros and other woody plants increased. Following a harvest of mature palms, younger size classes were able to respond with a larger growth increment, apparently due to more favorable light conditions on those plots with the lowest density of other woody plants. Both the density and abundance of other woody vegetation, as well as the density of larger palmiteiros, appear to reduce the growth of younger size classes. These results suggest that with some modifications to overall forest structure, forest managers could expect growth rates of palmiteiro to improve.

A reduction in the density or abundance of trees, lianas and tree-ferns would appear to benefit palmiteiro, but the differences in forest structure between the two sites suggests that successful management strategies may differ depending upon site conditions. At Eldorado 1, the invasion of bamboo has already significantly reduced the density and abundance of other trees, so additional timber harvesting would likely favor the invasion of more bamboo. Interestingly, the bamboo alone does not appear to significantly reduce palmiteiro growth, but bamboo may be slowing the recruitment of both palmiteiro and other woody species. As bamboo densities increase, we believe that the current benefits to palmiteiro achieved by creating a more open canopy will be offset by increasing competition for regeneration sites. Additional research on this topic is recommended, especially studies to examine artificial regeneration of palmiteiro in the presence of bamboo.

At Eldorado 2, results suggest that forest management to favor palmiteiro productivity should include a reduction in the number of trees smaller than 10 cm DBH. Harvesting of some large trees might also improve palmiteiro regeneration. Eldorado 2 is typical of most secondary forests that have not been invaded by bamboo, so these forests have large numbers of small trees that approximate the density of unlogged forests. Without some management, especially for small trees that comprise the mid-canopy, these secondary forests may have limited potential for palm heart production.

Data for this study were gathered from natural forest stands where many factors had not been controlled experimentally. Substantial plot-to-plot variability in the data makes it difficult to generalize about management practices that involve control of shade in managed forests. Data obtained here are most useful for proposing experiments that manipulate forest structure to provide information on which to base management decisions. The main point to be drawn from these results is that an optimal stocking of both palmiteiro and other woody plants could be achieved to accomplish the goals of producing a sustainable yield of palmiteiro while retaining a forest canopy suitable for biodiversity conservation. The management of palmiteiro in the Mata Atlântica will continue to be a challenge, as current forest regulations do not allow any change in the forest structure to improve the productivity of single species like *E. edulis*.

Acknowledgements

The first author benefited from a scholarship provided by The National Council for Scientific and Technological Development (CNPq), a foundation linked to the Brazilian Ministry of Science and Technology, during the development of this study. We would like to thank Ronaldo J. Ribeiro and Joanir Odorizzi, as well as the staff from the Research Group on Tropical Forests (NTFP) at the Universidade Federal de Santa Catarina, Brazil, for their assistance with the field work. Two anonymous reviewers provided helpful comments and criticisms that improved the final version.

References

Bovi, M.L.A., Godoy Jr., G., Sáes, L.A., 1991. Correlações fenotípicas entre caracteres da palmeira *Euterpe edulis* Mart. e produção de palmito. Revista Brasileira de Genética 14, 105–121.

Brasil–Ministério da Agricultura, 1979. Aptidão Agrícola Para as Terras de São Paulo. Estudos Básicos Para o Planejamento Agrícola, no. 20. Ministério da Agricultura, Brasília.

Brazão, J.E.M., Santos, M.M., da Silva, Z.L., 1993. Vegetação e recursos florísticos. In: Caldeiron, S.S. (Ed.), Recursos Naturais e Meio Ambiente: Uma Visão do Brasil. IBGE, Rio de Janeiro, pp. 59–68.

Carvalho, P.E.R., 1994. Espécies florestais brasileiras: recomendações silviculturais. In: Potencialidades e Uso da Madeira, Embrapa-CNPF/SPI, Colombo.

Conte, R., 1997. Manejo do Palmiteiro (*Euterpe edulis* M.) no Estado de Santa Catarina. Universidade Federal de Santa Catarina, Florianópolis.

Conte, R., Nodari, R.O., Vencovsky, R., Reis, M.S., 2003. Genetic diversity and recruitment of the tropical palm, *Euterpe edulis* Mart., in a natural population from the Brazilian Atlantic Forest. Heredity 91, 401–406.

Fantini, A.C., Reis, M.S., Sgrott, E.Z., Reis, A., Portilho, W.G., Ribeiro, R.J., 1993. Demografia de *Euterpe edulis* no Vale do Rio Ribeira de Iguape. In: Proceedings from the Seventh Brazilian Forest Congress, SBS/SBEF, São Paulo, p. 757.

Fantini, A.C., Nodari, R.O., Reis, M.S., Reis, A., Ribeiro, R.J., 1997. Estimativa da produtividade de palmito em plantas de palmiteiro (*Euterpe edulis* Martius) a partir de características fenotípicas. Árvore 21, 49–57.

Fantini, A.C., Ribeiro, R.J., Guries, R.P., 2004. Palmito (*Euterpe edulis* Martius, Arecaceae) na Mata Atlantica: um recurso em declínio. In: Alexiades , M.N., Shanley, P. (Eds.), Productos Forestales, Medios de Subsistencia y Conservación: estudios de caso sobre sistemas de manejo de productos forestales no maderables. CIFOR, Bogor, pp. 141–161.

Fonseca, G.A.B., 1985. The vanishing Brazilian Atlantic forest. Biol. Conserv. 34, 17–34.

Freckleton, R.P., Silva Matos, D.M., Bovi, M.L.A., Watkinson, A.R., 2003. Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest for a tropical palm tree. J. Appl. Ecol. 40, 846–858.

Galetti, M., Fernandez, J.C., 1998. Palm harvesting in Brazil's Atlantic forest: changes in industry structure and illegal trade. J. Appl. Ecol. 35, 294–301.

Gentry, A.H., 1992. Tropical forest biodiversity: distributional patterns and their conservational significance. Oikos 63, 19–28.

Gentry, A.H., Terborgh, J., 1990. Composition and dynamics of the Cocha Cashu ''mature'' floodplain forest. In: Gentry, A.H. (Ed.), Four Neotropical Forests. Yale U. Press, pp. 542–564.

Husch, B., Beers, T.W., Kershaw Jr., J.A., 2003. Forest Mensuration, fourth ed. J. Wiley, NY, 443 pp.

Jesus, R.M., de Souza, A.L., Garcia, A., 1992. Produção Sustentável de Floresta Atlantica. Sociedade de Investigações Florestais, Vitória.

Judziewicz, E.J., Clark, L.G., Londoño, X., Stern, M.J., 1999. American Bamboos. Smithsonian, Washington DC, 392 pp.

Kurtz, B.C., Araújo, D.S.D., 2000. Composição florística e estrutura do componente arbóreo de um trecho de Mata Atlântica na Estação Ecológica do Paraíso, Cachoeiras do Macacú, RJ, Brasil. Rodriguesia 51, 69–112.

Lieberman, D., Hartshorn, G.S., Lieberman, M., Peralta, R., 1990. Forest dynamics at La Selva Biological Station, 1969–1985. In: Gentry, A.H. (Ed.), Four Neotropical Forests. Yale U. Press, pp. 509–521.

Lopez, C., Shanley, P., Fantini, A.C. (Eds.), 2004. Riches of the Forest: Fruits, Remedies and Handicrafts in Latin America. CIFOR, Bogor.

Melo, M.M.R.F., Oliveira, R.J., Rossi, L., Mamede, M.C.H., Cordeiro, I., 2000. Estrutura de um trecho de floresta atlântica de planície na Estação Ecológica Juréia-Itatins, Iguape, SP. Hoehnea 27, 299–322.

Mittermeier, R.A., Myers, N., Thomsen, J.B., 1998. Hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conserv. Biol. 12, 516–520.

Nodari, R.O., Fantini, A.C., Reis, A., Reis, M.S., 2000. Restauração de populações de *Euterpe edulis* Martius (Arecaceae) na Mata Atlântica. In: Reis, M.S., Reis, A., (Eds.), *Euterpe edulis* Martius (Palmiteiro): Biologia, Conservação e Manejo. Herbário Barbosa Rodrigues, Itajaí.

Orlande, T., Laarman, J., Mortimer, J., 1996. Palmito sustainability and economics in Brazil's Atlantic coastal forest. Forest Ecol. Manage. 80, 257–265.

Parsons, J.J., 1991. Giant American bamboos in the vernacular architecture of Colombia and Ecuador. Geogr. Rev. 81, 13–152.

Paulilo, M.T.S., 2000. Ecofisiologia de plântulas e plantas jovens de *Euterpe edulis* Mart. (Arecaceae): Comportamento em relação à variação de radiação solar. In: Reis, M.S., Reis, A., (Eds.), *Euterpe edulis* (Palmiteiro): Biologia, Conservação e Manejo. Herbário Barbosa Rodrigues, Itajaí, pp. 93–105.

Peters, C.M., 1996. The Ecology and Management of Non-Timber Forest Resources. World Bank Technical Paper 322. World Bank, Washington, DC, 157 pp.

Pizo, M.A., Simão, I., 2001. Seed deposition patterns and the survival of seeds and seedlings of the palm *Euterpe edulis*. Acta Oecologica 22, 229–233.

Rankin-de-Morona, J.M., Hutchings, H.R.W., Lovejoy, T.E., 1990. Tree mortality and recrutiment over a five-year period in undisturbed upland rainforest of the central Amazon. In: Gentry, A.H. (Ed.), Four Neotropical Forests. Yale U. Press, pp. 573–584.

Reis, A., 1995. Dispersão de Sementes de *Euterpe edulis* Martius–(Palmae) em Uma Floresta Ombrófila Densa Montana da Encosta Atlantica em Blumenau, SC. Ph.D. Dissertation, Universidade Estadual de Campinas, Brazil.

Reis, M.S., 1996. Distribuição e Dinâmica da Variabilidade Genética em Populações Naturais de *Euterpe edulis* (Palmiteiro). Ph.D. Dissertation, Escola Superior de Agricultura Luiz de Queiroz, Brasil.

Reis, M.S., Conte, R., Fantini, A.C., Nodari, R.O., 1999. Caracterização do incremento em diâmetro de *Euterpe edulis* Mart. e implicações para o seu manejo em formações florestais secundárias. Revista Árvore 23, 413–422.

Reis, A., Fantini, A.C., Mantovani, A., Nodari, R.O., Reis, M.S., Conte, R., Mariot, A., 2000a. Dinâmica da regeneração natural de *Euterpe edulis*. In: Reis, M.S., Reis, A., (Eds.), *Euterpe edulis* Martius (Palmiteiro): Biologia, Conservação e Manejo. Herbário Barbosa Rodrigues, Itajaí.

Reis, M.S., Fantini, A.C., Nodari, R.O., Guerra, M.P., Reis, A., 2000b. Sustainable yield management of *Euterpe edulis* Martius (Palmae): a tropical palm tree from the Atlantic tropical forest–Brazil. J. Sustain. Forestry 11, 1–17.

Reis, M.S., Fantini, A.C., Nodari, R.O., Guerra, M.P., Reis, A., Mantovani, A., 2000c. Management and conservation of natural populations in the Atlantic rain forest: the case study of palm heart (*Euterpe edulis* Martius). Biotropica 32, 894–902.

Reis, A., Kageyama, P.Y., 2000. Dispersão de sementes de *Euterpe edulis* Martius Palmae. Sellowia 49, 60–92.

Reis, A., Kageyama, P.Y., Reis, M.S., Fantini, A.C., 1996. Demografia de *Euterpe edulis* Martius (Arecaceae) em uma Floresta Ombrófila Densa Montana, em Blumenau (SC). Sellowia 45, 13–45.

Reis, M.S., Reis, A. (Eds.), 2000. *Euterpe edulis* Martius (Palmiteiro): biologia, conservação e manejo. Herbário Barbosa Rodrigues, Itajaí.

Reis, A., Reis, M.S., Fantini, A.C., 1991. O palmiteiro como um modelo de rendimento sustentado. Higiene Alimentar 5, 27–31.

Reitz, R., 1974. Palmeiras. Flora Ilustrada Catarinense. Herbário Barbosa Rodrigues, Itajaí.

Snedecor, G.W., Cochran, W.G., 1989. Statistical Methods, 8th ed. Iowa State Univ. Press, 508 pp.

Shanley, P., Pierce, A.R., Laird, S.A., Pierce, A.R., Guillen, A. (Eds.), 2002. Tapping the Green Market. Earthscan, London.

Statistical Analysis System (SAS), 1989. SAS User's Guide, version 8, SAS Institute Inc., Cary, NC, USA.

Thomas, W.W., Carvalho, A.M., Amorim, A.M., Garrison, J., Arbeláez, A.L., 1998. Plant endemism in two forests in southern Bahia, Brazil. Biodivers. Conserv. 7, 311–322.

Tomlinson, P.B., 1961. Palmae. In: Metcalfe, C.R. (Ed.), Anatomy of the Monocotyledons. Oxford, UK.

Veblen, T.T., 1982. Growth patterns of Chusquea bamboos in the understorey of Chilean Nothofagus forests and their influences in forest dynamics. Bull. Torr. Bot. Club 109, 474–487.

Veloso, H.P., Klein, R.M., 1957. As comunidades e associações vegetais da mata pluvial Atlântica do sul do Brasil. I.: as comunidades do município de Brusque, Estado de Santa Catarina. Sellowia 8, 81–235.

Wang, W., Franklin, S.B., Ren, Y., Ouellette, J.R., 2006. Growth of bamboo *Fargesia qinlingensis* and regeneration of trees in a mixed hardwood-conifer forest in the Qinling Mountains, China. Forest Ecol. Manage. 234, 107–115.