# Reproductive plasticity in an Amazonian palm

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## ABSTRACT

**Question:** How plastic is the reproductive strategy of palm trees?

**Hypothesis:** The onset of reproduction and sex allocation depend on both the size and the type of environment that determines the availability of resources.

**Organisms:** The palm tree *Attalea speciosa* Mart. ex Spreng. It grows in both primary forests and disturbed sites, in a wide range of edaphic and climatic conditions.

**Field site:** The Brazilian state of Pará near the town of Marabá, on the commune of Benfica. The pioneer front, i.e. where primary or slightly degraded rain forest is turned into pastures by recently settled farmers.

**Methods:** Deforestation was used as a large-scale experiment. The effect of size (number of leaves or total height) on the onset of reproduction and sex allocation was compared in three environments: a forest, a partially invaded pasture and a pure stand of palm tree (babassual).

**Conclusions:** Reproduction starts at smaller sizes in the pasture and the babassual than in the forest, with height being a better predictor of reproduction than number of leaves in the forest. Male reproduction starts at smaller heights than female reproduction in the pasture and the babassual but not in the forest.

*Keywords*: Amazon, palm tree, phenotypic plasticity, rain forest, reproduction, sex allocation.

## INTRODUCTION

The size of a plant aerial system is positively correlated with the amount of resource the plant has stocked, with the amount of photosynthetic tissues which produce these resources, and with the size of the root system which absorbs the water and the nutrients necessary for this production. Moreover, in certain cases large individuals are able to absorb a disproportionate share of a resource. This is typically the case for light: the taller plants of a stand shade smaller plants and thus absorb much more light than smaller ones (Weiner and Thomas, 1986; Weiner, 1990). In other words, if plants of a given height absorb a certain amount of light, plants twice as tall absorb more than two times this amount of light. This asym-

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metric competition is likely to increase initially small differences in size and to shape size hierarchies between individuals (Weiner, 1985). For these reasons, size should be a good predictor of fecundity and mortality. Finally, since the timing of the onset of reproduction should evolve according to the pattern of variations and co-variations in fecundity and mortality (Charlesworth and Leon, 1976; Stearns, 1992), plant size is often assumed to be a good predictor of the onset of reproduction (Lacey, 1986). Size is probably a better predictor of the onset of reproduction than age, especially for long-lived perennials, because plants are modular organisms (Watkinson and White, 1985), with very plastic growth, so that the correlation between age and size decreases with age.

Size is also expected to be linked to the relative allocation of resources to male and female reproduction (Charnov, 1977; Klinkhamer *et al.*, 1997), which can lead to continuous gender adjustment according to size, to phase choice (at each reproduction opportunity an individual 'chooses to be male or female') (Lloyd and Bawa, 1984) or, eventually, to dioecy with no sex reversal, with one sex being taller than the other (Lloyd and Webb, 1977). Plants are predicted to have evolved such strategies for two reasons: because size can shape male and female fitness-gain curves in different ways (Charnov, 1977; Klinkhamer *et al.*, 1997) and because the production of pollen and production of fruits are likely to have different costs (Lloyd and Webb, 1977; Freeman *et al.*, 1980; Bierzychudek and Eckhart, 1988). The latter case should arise in perennial species for which allocating resources to a costly, most likely female, reproduction might increase mortality and compromise subsequent reproduction (Charlesworth and Morgan, 1991; Charnov and Dawson, 1995). Changes in fitness-gain curves with individual size might occur because size modifies the efficiency of seed and pollen dispersal as well as the intensity of competition between seedlings (De Jong, 1994; Klinkhamer *et al.*, 1997). Hence, in a wind-pollinated species, tall individuals might disperse pollen over greater distances than smaller ones (Burd and Allen, 1988). In the same vein, large plants that produce more fruits than smaller plants might attract more fruit-dispersing animals (Thomson and Brunet, 1990).

Thus, size is expected to be strongly correlated both with the onset of reproduction (Lacey, 1986) and the proportion of resource allocated to male and female reproduction (Klinkhamer *et al.*, 1997). Using height and the number of leaves as a measure of size, we tested these predictions, with an Amazonian palm tree species, the so-called babassu, *Attalea speciosa* Mart. ex Spreng. This species occurs in the Amazonian primary forest (Uhl and Dransfield, 1987) at low densities (Peters *et al.*, 1989). However, when forest is cut down and replaced by pastures or secondary forests, the babassu tends to portray a unique behaviour. Unlike forest tree species, it is resistant to fire, which is used for the management of pastures, and unless concerted efforts are made to suppress young individuals, pastures often turn into monospecific stands of babassus within a few decades. Thus, the babassu seems to be adapted to two different types of ecosystems – primary forests and much more open formations, which can be considered as artificial savannas.

This suggests that the species is very plastic and is able to adjust its resource allocation to the available resources. Competition within the plant community, at least for light, should be higher in the forest than in the pastures. More resources should be available in open environments, which is likely to modify the babassu growth pattern. The palm tree is likely to have evolved particular strategies of resource allocation to reproduction, of sex allocation and possibly of size-dependent sex allocation (Klinkhamer and de Jong, 1993; Klinkhamer *et al.*, 1997). We tested four hypotheses: (1) the onset of reproduction depends on size; (2) the link between size and onset of reproduction varies according to the type of vegetation; (3) sex allocation depends on size; (4) the link between size and sex allocation varies according to the

type of vegetation. The comparison of the reproduction pattern of the babassu in different environments gave clues as to the proximate causes of potential size-dependent reproduction and helped determine whether this pattern is adaptive or not.

## METHODS

The study was conducted in June 2003, in the Brazilian state of Pará. We worked near the town of Marabá, on the commune of Benfica on the pioneer front (i.e. where primary or slightly degraded rain forest has been turned into pastures by recently settled farmers). The climate is characterized by a mean annual temperature of 26°C and about 1800 mm of rain annually, with a marked dry season between July and October. Because the four genuses *Attalea, Maximiliana, Orbignya* and *Sheelea* have been merged, the study species, formerly called *Orbignya phalerata* Mart., is now called *Attalea speciosa* Mart. ex Spreng (Henderson, 1995). It grows in the Amazon in both primary forests and disturbed sites, in a wide range of edaphic and climatic conditions (Anderson, 1983). However, it seems to prefer well-drained zones and is replaced by the palm *Euterpe oleracea* in the swampy parts of the study area (personal observation). It is a large, single-stemmed palm. Female and male flowers grow on the same hermaphrodite individuals but on separate inflorescences. In the study site, fruits weigh about 200 g each (maximum of 350 g) and contain between one and six seeds; most fruits contain three seeds (personal observations). Germination is remote-tubular and hypogeal (Uhl and Dransfield, 1987). Thus, the terminal meristem is below ground during the first stages of the palm life cycle. On the one hand, the invasion of pastures by the babassu is detrimental to cattle ranching because grass production decreases when palm density increases (above a threshold). On the other hand, the palm tree is very useful to local populations: stipe and leaves are used for construction, seeds can be used to make cooking oil and to make cosmetics, either for personal use or at an industrial scale in the state of Maranhão (Anderson and May, 1985; Peters *et al.*, 1989).

Three plots were chosen as being representative of three types of vegetation (VT): forest, pasture and mono-specific dense stands of babassu – that is, a babassual. The first two plots are roughly $400 \times 100$ m, while the third plot (B) is $100 \times 50$ m. In the babassual and pasture plots, the forest was cut down about 20 and 8 years ago respectively.

Five stages were distinguished: entire-leafed seedling (ELS), slit-leafed seedling (SLS), juvenile with fully developed leaves but with the terminal meristem underground (Juv1), juvenile with fully developed leaves and with the terminal meristem above the surface (Juv2), and reproducing individuals [i.e. adults (Adt)]. SLS encompasses all individuals that have at least one leaf that is only partially slit, whereas the leaves of adults and juveniles are fully slit. To limit a time-consuming process, adults were censused over the entire plots, while in the forest and pasture plots young stages (ELS, SLS, Juv1, Juv2) were only censused across a 20 m wide band. This was not necessary for the monospecific stand of babassus, since this plot is smaller than the other two.

For each individual, the number of leaves (NbL) was counted and the total height (H), from the ground to the top of the last leave, was measured. Heights up to 3 m were measured using 3 m long poles. Heights in excess of this were assessed without an instrument using the 3 m poles as reference marks. Using 25 palm trees measured with a clinometer, we checked that the estimation of height would not bias our results, although the height of the tallest palm trees, especially in the forest, was underestimated: estimated and measured heights were well correlated ($R^2 = 0.75$).

Because reproduction was only documented through binary variables (i.e. presence/absence of female or male inflorescence), most statistical models analysed were logistic regressions (Collett, 1991). To determine whether interactions involving the sex of inflorescences were significant, observations on individual palm trees were split so that each observation corresponded finally to the presence/absence of one type of inflorescence, one variable documenting the sex of the considered inflorescence. For a given adult, the production of female inflorescences is not independent of the production of male inflorescences. Therefore, the validity of standard tests is disputed for the logistic model testing for a difference between the effect of size and vegetation type on male and female reproduction. Consequently, we applied randomization tests (Manly, 1991). First, the logistic regression model was applied to the original data set. Second, the sexes were randomly permuted between observations to create randomized data sets in which any relation between the sex of the inflorescence and other variables (NbL, H, VT) would only be due to chance. For each of the 1000 randomized data sets, the logistic regression model was applied and the chi-square value distributions obtained (one for each tested effect) were compared with the original chi-square values: a test was considered significant if less than 5% of the values obtained for the randomized data sets were higher than the values computed for the original data set.

## RESULTS

Stage distributions of palm trees (Fig. 1) differ significantly in the three vegetation types (log-likelihood $\chi^2$ test, d.f. = 8, $G = 856.5$, $P < 0.001$). Seedling density is higher in the forest than in the other two vegetation types, about 3000 ELS and 500 SLS per hectare, while there are at most 200 ELS and SLS per hectare in the other two types of vegetation. In the babassual, densities of palms in the different stages are roughly equal, in the forest there are more individuals in the first stages, while in the pasture there are more individuals in the intermediate stages (SLS and Juv1). Densities of Juv1 and Juv2 are higher in the pasture (about 500 and 50 individuals per hectare respectively) than in the forest (about 100 and 10 individuals per hectare respectively). In both the babassual and the forest, there are more adults than tall juveniles (Juv2).

In the three vegetation types, height increases with the number of leaves (Fig. 2). The relation is roughly linear for the first stages and displays a horizontal plateau (at a height of 10 m) for adults in the pasture and the babassual. In the forest, there are many taller adults, up to 28 m high, and the relationship between the number of leaves and height is no longer linear: height appears to increase more quickly with the number of leaves for adults than for the non-reproductive stages. Palms appear to start reproducing at smaller heights in the pasture and the babassual than in the forest (Fig. 2).

We analysed more precisely the differences between reproducing and non-reproducing individuals. Both the height and the number of leaves have a positive significant effect on the probability of being mature (Table 1): larger palms are more likely to reproduce (producing male or female flowers) than smaller ones (see also Fig. 2). This effect is significantly different in the three vegetation types (interaction between size and vegetation type). Estimated parameters show that the effect of the number of leaves on the probability of being mature is relatively homogeneous across the vegetation types, while the effect of height increases with the density of palms (i.e. palms mature smaller from the forest to the babassual) (see also Fig. 2). To test specifically that palms mature at smaller sizes in the babassual and the pasture than in the forest, we applied the same logistic models pooling
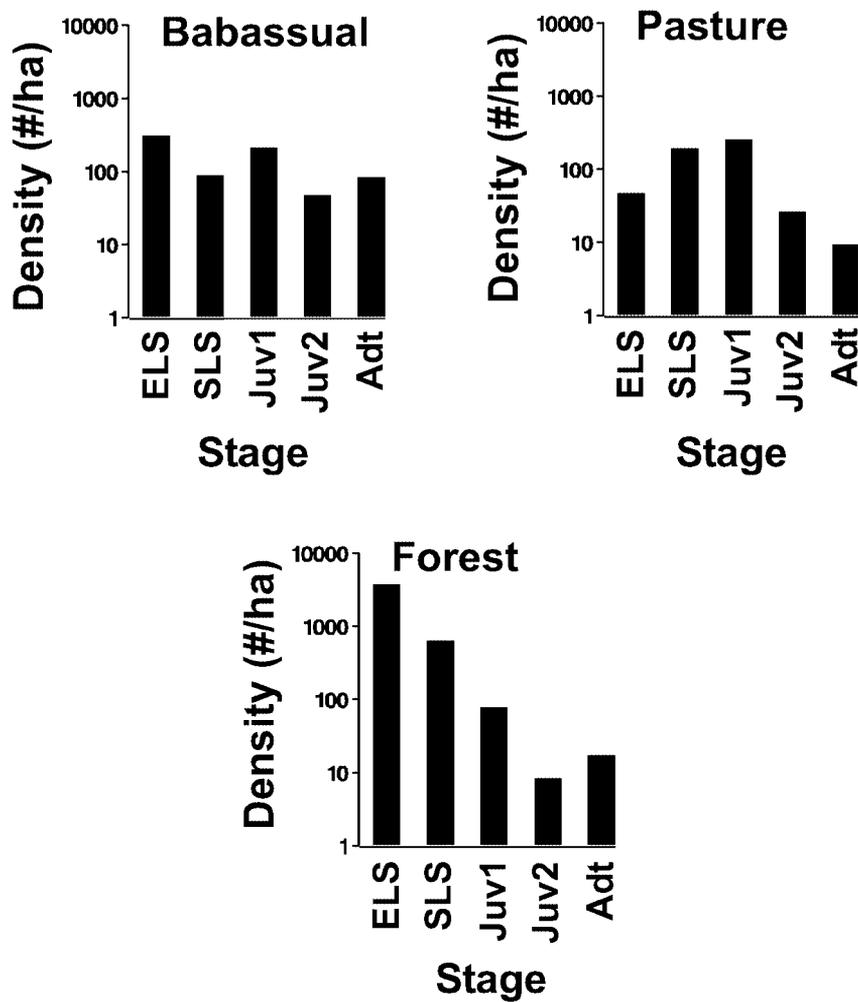
**Fig. 1.** Densities of palm trees by stage and plot. The scale is logarithmic. ELS, entire-leafed seedling; 2 SLS, slit-leafed seedling; Juv1, juvenile with terminal mersitem underground; Juv2, juvenile with terminal meristem above ground; Adt, reproducing adults.

together observations of the babassual and the pasture. The interaction between size and type of vegetation was not significant for the number of leaves but was significant for height. Three other models were used to assess the relative influence of height and the number of leaves: we tested simultaneously for an effect of height and the number of leaves, independently for the three vegetation types. In the babassual and the pasture, only the number of leaves had a significant effect ($\chi^2$ test, $P < 0.001$), whereas the reverse was true for the forest. That is, in the forest height is a better predictor of the probability of reproduction than the number of leaves. The opposite holds for the babassual and the pasture. It should be noted that the underestimation of the height of forest palms cannot account for the difference observed in the heights of reproducing and non-reproducing palms: this bias in
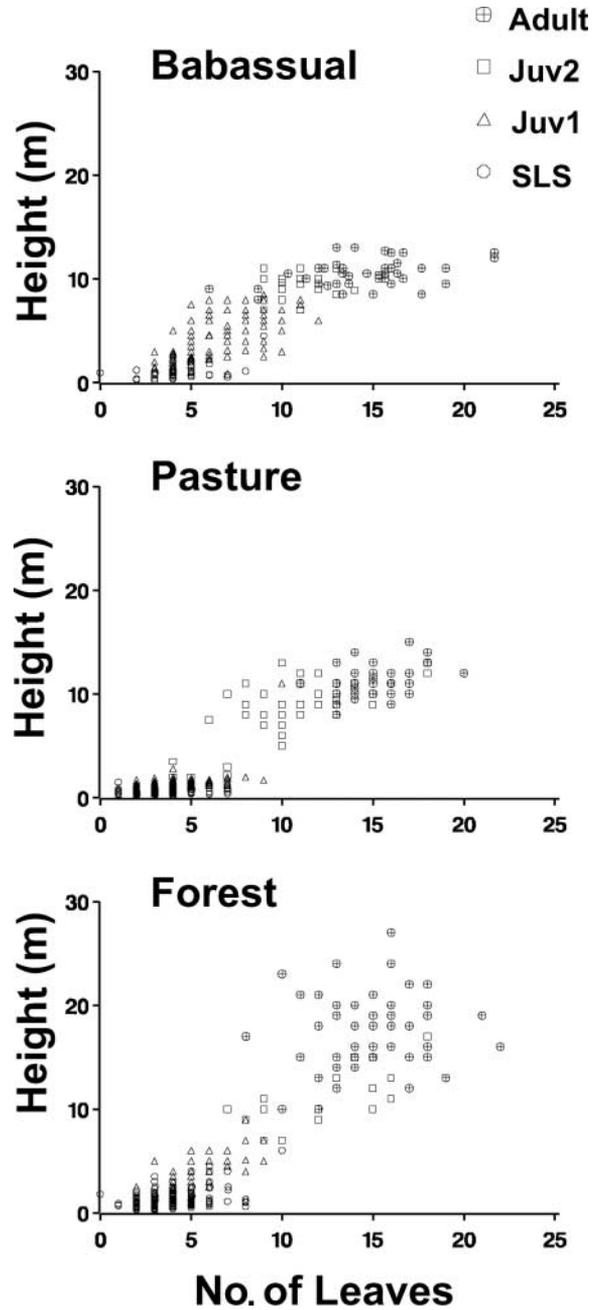
**Fig. 2.** Number of leaves plotted against total height. A different symbol is used for each stage. Entire-leafed seedlings are not plotted because they are too numerous and all occupy roughly the same position in the number of leaves–height plane. Sometimes, all leaves of a palm tree have been cut or damaged, which results in individuals with a height and no leaf.

measurement can only diminish differences between forest and pasture/babassual and lead to more conservative tests.

Looking only at reproducing individuals (Fig. 3), we distinguished adults producing both male and female flowers (MF), only female flowers (F) or only male flowers (M). In the pasture and the babassual, the percentages of adults with only female flowers are much lower than the percentages of adults with only male flowers. In the pasture, the percentage of adults with only male flowers is so high (about 60%) that the percentage of adults with both male and female flowers is about 30%, while in the babassual and the forest most

**Table 1.** The probability of being mature, denoted either by the production of male or female flowers

|  | d.f. | $\chi^2$ | Babassual | Pasture | Forest |
|---|---|---|---|---|---|
| Model | 3 | 97.0** |  |  |  |
| NbL | 1 | 89.4** |  |  |  |
| NbL × VT | 2 | 10.1* | 0.570 | 0.473 | 0.541 |
| Model | 3 | 99.67** |  |  |  |
| H | 1 | 82.6** |  |  |  |
| H × VT | 2 | 18.9** | 0.811 | 0.692 | 0.608 |

*Note*: The probability is first modelled through a logistic regression (logit link function) testing for the effect size and the interaction between the type of vegetation (VT) and the size of the palm trees (either the number of leaves, NbL, or height, H). Only individuals of stage 4 and 5 are taken into account. The first columns provide the results of likelihood ratio $\chi^2$ tests (Allison, 1999) both for the global assessment of the model and for the effects included in the model. The last three columns give the estimated parameter for the effect of size in each type of vegetation.
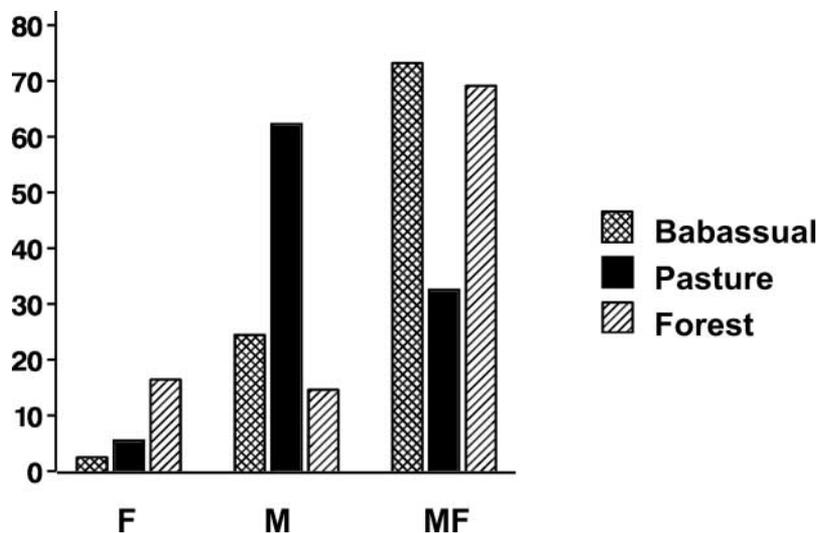** $P < 0.0001$; * $P < 0.05$.



**Fig. 3.** Percentages of reproducing palm trees that have both male and female flowers (MF), only male flowers (M), or only female flowers (F). Percentages are given separately for each type of vegetation.

**Table 2.** Logistic regression (logit link function) of the probability of producing flowers as a function of size (either height or number of leaves)

|  | d.f. | $\chi^2$ | Babassual | Pasture | Forest |
|---|---|---|---|---|---|
| Model | 6 | 155.8** |  |  |  |
| NbL | 1 | 109.2** |  |  |  |
| NbL × S | 1 | 12.0*## | M > F* | M > F** | N.S. |
| NbL × VT | 2 | 29.4** |  |  |  |
| NbL × VT × S | 2 | 8.3*# |  |  |  |
| Model | 6 | 183.5* |  |  |  |
| H | 1 | 124.8** |  |  |  |
| H × S | 1 | 9.8*## | N.S. | M > F* | N.S. |
| H × VT | 2 | 52.4** |  |  |  |
| H × VT × S | 2 | 9.4*# |  |  |  |

*Note*: All interactions between size, type of vegetation (VT) and sex (the fact the flowers are male or female) are tested but not the direct effect of the type of vegetation or sex (S). Only adults and taller juveniles (Adt and Juv2) are taken into account. The first columns provide the results of likelihood ratio $\chi^2$ tests both for the global assessment of the model and for the effects included in the model. The probability of producing flowers was also analysed, separately for each type of vegetation, using a logistic regression that included only the effect of size and the interaction with sex. The significance of this interaction is given in the last three columns together with an indication of the relative importance of the size effect for male (M) and female (F) inflorescences (the parameter for the interaction between size and sex is higher for male than female inflorescences or the reverse). The effect of sex, whether size has the same effect on female and male inflorescences, was also tested using a randomization test. The results of the tests based on 4000 permutations are given in parentheses for the interaction between sex and size and the triple interaction (see text for details).
** $P < 0.0001$; * $P < 0.05$; ## randomization test highly significant: $P < 0.0001$; # randomization test significant: $P < 0.05$.

adults have both male and female flowers (about 70%). The distributions of adults according to presence/absence of male and female flowers differ significantly in the three vegetation types (log-likelihood $\chi^2$ test, d.f. = 4, $G = 29.47$, $P < 0.001$).

Using logistic regressions, we tested for differences in the relation between reproduction and size, between male and female reproduction. The model included all interactions between size (either height or number of leaves), vegetation type and sex. All these interactions are significant for the height and the number of leaves model (Table 2). This shows that male and female inflorescences start to be produced on palms of different sizes (size × S), and that this difference in the relation between size and the production of male and female inflorescences varies with the type of vegetation (size × VT × S). We ran, separately for each type of vegetation, a logistic model testing only for the effect of size (either height or number of leaves) and the interaction with sex. The interaction was never significant for the forest, was significant both for height and the number of leaves in the pasture and only for the numbers of leaves in the babassual (Table 2, three last columns). In all significant cases, the estimated parameters were higher for male flowers than for female inflorescences – that is, male flowers start to be produced on palms that are smaller and which have less leaves than female flowers. We checked that the interactions (size × S, size × VT × S) involving the nature of inflorescences (male or female) are really significant using randomization tests as described above.

## DISCUSSION

### Invasion of pastures

The stage distribution in the forest plot is typical of perennial plant populations at equilibrium: the frequency of individuals decreases from the first seedling stage to the adult stage and this decrease is steeper for the first stages. This should be due to high mortality rates in the first stages and to low recruitment rates at more advanced stages (Crawley, 1996). In contrast, the density of adult palms is slightly lower in the pasture than in the forest, while densities of intermediate stages are much higher in the Pasture. This suggests that most adults have been cut during the process of deforestation so that the invasion of pasture starts with the younger stages. This is confirmed by our observations on recently deforested areas and is further confirmed by the fact that the height structure is truncated in both the pasture and the forest (Fig. 2): deforestation has occurred too recently for newly recruited adult palms to have grown as tall as the tallest palms in the forest. The higher densities of adults than of Juv2 in both the babassual and the forest suggest the existence of a demographic bottleneck, at least in the forest where the population is likely to be at equilibrium. Few juveniles manage to grow enough to have an above-ground terminal meristem and to reach the Juv2 stage, most likely because of the competition for light with other trees (or babassus in the babassual). Yet, these juveniles probably have high survival and growth rates so that they are quickly recruited in the adult stage and hence represent a small percentage of the population. Reproducing palms should also have high survival rates and accumulate in the adult stage. In this sense, this feature of the population structure would be due to different times of residence in the different stages and not to temporal variations in the recruitment rates. Such patterns arise commonly in palms (Savage and Ashton, 1983; Enright, 1985; Barot and Gignoux, 1999; Silva Matos *et al.*, 1999).

The low densities of entire-leafed seedlings in the pasture and the babassual might be because the corresponding palm populations have not yet reached equilibrium. These densities might also be caused by higher mortality rates and lower fecundities in the pasture and the babassual than in the forest. This could be due to environmental changes linked to deforestation. Exposure of fruits to the sun, which only occurs in pastures, seems to decrease the germination rate (Mitja and Ferraz, 2001). Fire is used to manage the pastures and might be a source of extra-mortality for seedlings as well as competition with the introduced grasses. Trampling and grazing by cattle might also be a source of mortality. Besides, effective fecundity might be reduced by human exploitation of fruits in the babassual and the pasture: the babassual is very close to a village and fruits are easier to collect in the babassual and in the pasture than in the forest.

### Onset of reproduction

Our statistical analyses support the four hypotheses presented in the Introduction about the allocation of resource to reproduction. Hence, reproduction is size dependent but is seen in smaller palms in the babassual and the pasture than in the forest. Size dependence of reproduction is a general result of plant reproductive biology, and is due to the fact that size is well correlated with the amount of resource available for a plant individual (Lacey, 1986). The key point is that total height is a better predictor of reproduction than the number of leaves in the forest, while it is the reverse in the other two vegetation types. This suggests that light

is the main limiting factor: in the forest, the taller a babassu is, the more likely it is to reach the canopy and to get the necessary light to store enough energy to trigger reproduction, while in the pasture all babassus have full access to light since they do not have any competitor tree species. In this case, the number of leaves, well correlated *a priori* with the photosynthetic surface, is also correlated with the amount of light absorbed. The babassual and the pasture follow the same pattern, which is surprising since the high density of adults and tall juveniles in the babassual provide a dense cover which should limit the available light underneath. A possible explanation is that the babassual palm population is not yet at equilibrium. A size hierarchy has not yet been established, and all palms which now reproduce began to reproduce during the same few years in a period when the plot was a pasture with no trees and no tall palms. Individual height might become a good predictor of reproductive maturity in mature babassuals.

The effect of the availability of light on the timing of reproduction has been studied in a few species. In contrast to our study, Callahan and Pigliucci (2002) found that shaded plants started to reproduce at smaller sizes. This was probably due to the species studied, which was an annual. In such species, delaying maturity until individual size permits access to more light is not an option and reproducing at a small size cannot jeopardize subsequent reproduction events.

### Sex allocation

In the babassu, the production of male flowers is seen on smaller palms than the production of female flowers (and fruits) in the pasture and the babassual, but not in the forest. Three types of interpretation are possible.

The first (A) is based on the assumption often verified (Freeman *et al.*, 1980) that female reproduction is more costly than male reproduction. This should be the case in the babassu, which produces big fruits, and big seeds with high lipid content (Anderson and May, 1985). Babassus in pastures have unrestricted access to light at small height and thus start to reproduce smaller than in the forest, but female reproduction is so costly that starting to produce fruits at the height at which male inflorescences start to be produced would reduce the probability of survival in the following years because less resource would then be available for maintenance and growth. This could happen because small reproducing babassus have access to light but have not stored as much resource in their stem as taller ones (Tomlinson and Jeffrey, 1990). Alternatively, small reproducing babassus have probably a smaller root system than taller ones. The importance of the horizontal extension of the root system is supported by the development of a particular root foraging strategy in a savanna palm (Mordelet *et al.*, 1996).

A second interpretation (B) is based on the theory of fitness-gain curves – that is, curves describing how male and female fitness (here defined as the number of offspring dispersed) vary with the proportion of resource allocated to male or female function (Klinkhamer *et al.*, 1997). Since we do not find a radical switch from maleness to femaleness, a direct effect of size – that is, for equal absolute investments the fitness return is higher for larger individuals (Klinkhamer *et al.*, 1997) – is unlikely. Non-linear gain curves and a budget effect of plant size are then to be invoked: the absolute amount of resource invested would determine the fitness return irrespective of plant size, but larger plants can invest more resource into reproduction which can lead to differences in fitness return. Here a possible mechanism would be that large palms have a larger crop of fruits which would attract more fruit-dispersing

frugivores (Bawa, 1980; Thomson and Brunet, 1990). No data are available to test this hypothesis but the epicarp and starchy mesocarp are eaten by rodents (personal observation), which might disperse fruit efficiently. In this context, it would be primordial to measure precisely the relation between male and female fecundity with the size of babassus in the different vegetation types, while we have only documented here the presence/absence of male and female reproduction.

A third interpretation (C) of the environment-dependent relation between sex allocation and size cannot be excluded. As explained above, babassus are able to invest more resource in reproduction at smaller heights in the pasture than in the forest because of easier access to light. The optimal strategy would then be to start reproduction at a smaller height, equal for male and female functions, in the pasture than in the forest, but optimal strategies do not always evolve (Gould and Lewontin, 1979). Hence, plasticity is probably a cost and is constrained by the development paths (Coleman *et al.*, 1994; DeWitt *et al.*, 1998) and might be more constrained for female than male reproduction, for example because of the larger amount of resource involved in femaleness.

Monoecy facilitates the independent allocation of resource to male and female functions. This has fostered the study of sex allocation in many monoecious plants (see review by Fox, 1993). Of nine studies, only two reported a significant change in sex allocation with size, and in both cases maleness increased with height. Fox explained this pattern by the shape of fitness-gain curves and a possible increase in the efficiency of pollen dispersal with size for wind-pollinated species. In conifers, an increase in femaleness with height is often found (Smith, 1981), which is due either to an increase in seed dispersal efficiency with height or to allometric constraints (Fox, 1993). A review of monocarpic plants found that femaleness increases with size in 28 of 34 species, which was explained by a model based on the levelling of the male fitness-gain curve with increasing size (De Jong and Klinkhamer, 1989). An alternative hypothesis is possible: small plants do not gather enough resources for female reproduction which is more costly, or unfavourable environments lead to small individual sizes and restrain seed development. Taken together, all types of sex allocation predicted by fitness-gain curves have been documented but testing for underlying mechanisms is much more difficult.

Many studies highlight the dependence of sex allocation on environmental variation. In most cases, environmental stresses (for example, dry soils, low light intensity) induce maleness (Freeman *et al.*, 1980). In the same vein, patchy environments have been shown in many cases to lead to spatial segregation of the sexes in dioecious species, with males being generally more common in less favourable patches (Bierzychudek and Eckhart, 1988). Such patterns arise because female functions are more costly than male functions. Our first interpretation (A above) of sex allocation in the babassu is based on the same hypothesis and leads to a counterintuitive pattern: the best environment (i.e. pasture) appears to be more favourable to males than to females, since male reproduction starts at smaller heights in the pasture than in the forest. This is only an apparent paradox because our study deals at the same time with the effect of environment and size on sex allocation, because different resources might be involved and because different measures of size might influence the accessibility of different resources.

Few studies have tested for changes in sex allocation with both size and environment. This was possible in the present study because of deforestation, which can be considered a large-scale experiment. The sex allocation of a monocarpic perennial *Cynoglossum officinale* has been thoroughly studied. It was found that the threshold size for reproduction

depends on environmental quality (Wesselingh *et al.*, 1997; De Jong *et al.*, 1998) and that femaleness increases with size (Klinkhamer and de Jong, 1993). However, size had the same effect on sex allocation irrespective of the environment, as measured by different levels of watering, and although water was limiting for seed production (Klinkhamer and de Jong, 1993). General predictions are difficult to make based on our findings, but any difference in the processes shaping fitness-gain curves and the relative cost of female and male functions could lead to this result.

### Ultimate causes

We have shown that both size at maturity and sex allocation are plastic in the babassu. The next step is to determine whether this plasticity is adaptive. Although it is difficult to prove that a given example of plasticity is adaptive, maturation at smaller heights in pasture than in the babassual fits Stearns' definition of adaptive plasticity (Stearns, 1989): 'The criterion for identifying an adaptation is a change in phenotype that occurs in response to a specific environmental signal and that has a clear functional relationship to that signal. The relationship must result in an improvement in growth, survival, or reproduction'. The change in sex allocation from a close to an open vegetation type might be adaptive (hypotheses A and B above) or non-adaptive (hypothesis C). Deciding between these possibilities implies testing for the underlying mechanisms: assessment of the cost of male and female function, assessment of sex-allocation changes with size (after the first reproduction) and its consequences on pollination efficiency, seed dispersal and germination. To allow a better interpretation of our results requires the description of the life cycle (survival and growth rates) of the babassu in the forest, the pasture and the babassual.

Sexual maturity is reached at smaller heights in the pasture than in the forest, but the switch from one environment to the other is also likely to change growth rate and age at maturation. Growth rates should increase with the availability of light, so that palms would also mature at an earlier age (about 8 years according to the age of the pasture, to which must be added the age of the older juveniles or seedlings surviving to deforestation) in the pasture than in the forest. Methods have been developed to describe such environmental variations in the relation between maturation, age and size – that is, reaction norms for age and size at maturation (Stearns, 1992). New estimation methods of maturation reaction norm could be applied to the babassu (Heino *et al.*, 2002; Barot *et al.*, 2004). They require an estimation of age, which could be achieved using counts of leaf scares and studying leaf dynamics (Tomlinson, 1963) or using a matrix model (Cochran and Ellner, 1992; Barot *et al.*, 2000), which would at least be a good way to describe the babassu life cycle in the different vegetation types (Caswell, 1989).

One might ask why a palm tree growing in primary forests has developed a strategy enabling the invasion of open vegetation. A key point of this invasion is the fact that the terminal meristem of the babassu, due to its germination type (common in palm trees), is below ground during its establishment phase (Tomlinson and Jeffrey, 1990). This confers a high resistance to fire, used to manage the pastures and which impedes the regrowth of tree species, and to trampling by cattle. Furthermore, as for many other palm species (Tomlinson and Jeffrey, 1990), the stem of adult babassus is also resistant to fire. The babassu also changes its maturation schedule when more light is available, which suggests that the species has evolved in an environment where light is sometimes available at low heights. Three non-exclusive interpretations can be made: (1) This could be the result of natural clearings of

various sizes due to the heterogeneity of tree cover and the fall of branches and whole trees. This is supported by studies highlighting the importance of heterogeneity in light availability for tropical forest palms (Chazdon, 1986; Svenning, 1999). It would then be useful to study maturation and sex allocation in such clearings to determine whether they provide enough light to induce the plasticity detected in a pasture. (2) It could be that there is a long history of cohabitation between men and the palm tree. Men have used palm trees for a long time in South America (Kahn, 1986; Balée, 1988; Morcote-Rios and Bernal, 2001) and the babassu might have become adapted to artificial clearings used for villages and cultivation. (3) Amazonian vegetation changed during the Quaternary period and the babassu might have encountered natural, more open formations such as savannas, and the adaptation to such conditions would still be built into the babassu phenotypic plasticity. Although the hypothesis that large parts of Amazonian lowlands were covered by savannas during glaciations now seems to have been rejected (Colinvaux *et al.*, 2000), the limit between rain forest and savanna has changed (Desjardin *et al.*, 1996; Behling and Hooghiemstra, 2000; de Freitas *et al.*, 2001).

## ACKNOWLEDGEMENTS

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