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QUANTIFICATION OF RAMET PRODUCTION IN THE NEOTROPICAL PALM *EUTERPE PRECATORIA* (ARECACEAE) IN COSTA RICA

Gerardo Avalos[1,2] & Rachel A. Schneider[3]

[1]Escuela de Biología, Universidad de Costa Rica, 2060 San Pedro, San José Costa Rica
[2]The School for Field Studies, Center for Sustainable Development Studies, 10 Federal St., Salem, MA 01970 USA
[3]Wellesley College, 106 Central Street, Wellesley, MA 02481 USA

Abstract. We document the capacity of the neotropical palm *Euterpe precatoria* var *longevaginata* for vegetative propagation by measuring the number and size of ramets attached to mother palms and associating ramet frequency with the size of mother palms. *Euterpe precatoria* is subjected to intensive extraction for its edible palm-heart. Being single-stemmed,extraction results in the death of the palm. The study took place at Quebrada González in Braulio Carrillo National Park, Costa Rica. We measured the incidence of ramets with at least 10 cm in stem height in 192 palms from 30 plots of 15 x 15 m established in a primary forest without extraction (Las Palmas trail, 10 plots), in a primary forest exposed to illegal extraction (La Botella trail, 10 plots), and in a secondary forest without extraction (El Ceibo trail, 10 plots). All measured palms had at least one leaf with a minimum lamina length of 50 cm, and ramets were at least 10 cm in stem height. Of the palms examined 22.8% had attached ramets (average = two ramets per individual). The majority of the mother palms were 40-90 cm tall, with the number of ramets decreasing logarithmically with increasing mother palm height. Ramet production was limited to small, young palms. During the early stages of seedling establishment, when biomechanical limitations for increasing height are more intense, investment in ramet production spreads out mortality risks, and facilitates the acquisition of leaf area to survive in the light-deprived understory. The production of ramets in *E. precatoria* is a relict of its phylogenetic history, where clonal reproduction is common and precedes sexual reproduction. Since ramets do not develop into adult palms, conservation policies must concentrate on the control of extractive activities and the creation of incentives and certification plans to stimulate the cultivation of this species outside protected areas.

Resumen. Documentamos la capacidad de la palma neotropical *Euterpe precatoria* var *longevaginata* para la propagación vegetativa mediante la medición del número y tamaño de los rametes adjuntos a las palma madre y la asociación de la frecuencia de rametes con el tamaño de la palma madre. *Euterpe precatoria* sufre una extracción intensiva de palmito. Ya que es una especie de tallo individual, la extracción resulta en la muerte de la palma. El estudio se llevó a cabo en Quebrada González en el Parque Nacional Braulio Carrillo, Costa Rica. Se midió la incidencia de rametes con al menos 10 cm de altura en 192 palmas encontradas en 30 parcelas de 15 x 15 m ubicadas en un bosque primario sin extracción (sitio Las Palmas, 10 parcelas), en un bosque primario expuesto a la extracción ilegal (sitio Botella, 10 parcelas), y en un bosque secundario sin extracción (sitio Ceibo, 10 parcelas). Todas las palmas medidas tenía por lo menos una hoja con una longitud de lámina de 50 cm, mientras que los rametes tenían por lo menos 10 cm de altura del tallo. De la palma examinadas el 22,8% presentaba rametes (promedio = dos rametes por palma). La mayoría de las palmas madre tuvieron 40-90 cm de altura, con el número de rametes disminuyendo de forma logarítmica al aumentar la altura de la palma madre. La producción de rametes se limitó a palmas pequeñas. Durante las primeras etapas del establecimiento de la plántula, cuando las limitaciones biomecánicas para el aumento en altura son más intensas, la inversión en la producción de rametes reduce los riesgos de mortalidad y facilita la adquisición de área foliar para sobrevivir en el sotobosque bajo dosel cerrado. La producción de rametes en esta especie es una relicto de su historia filogenética, en donde la reproducción clonal es común y precede a la reproducción sexual. Ya que los rametes no se convierten en palmas adultas, las políticas de conservación deben concentrarse en el control de las actividades extractivas y en la creación de incentivos y planes de certificación para estimular el cultivo de esta especie fuera de las áreas protegidas.

Key words: Arecaceae, Costa Rica, Braulio Carrillo National Park, clonality, Euterpe precatoria*, heart of palm, palm ecology, ramet production, vegetative reproduction.*

* e-mail: faetornis@yahoo.com

INTRODUCTION

The Neotropical palm *Euterpe precatoria* (Arecaceae) is subjected to intensive extraction for its palm-heart throughout its latitudinal range from Belize to Bolivia (Stoian 1994). The palm-heart or "cabbage" is obtained from the apical meristem, plus the rolled, developing leaves clustered inside a section of approximately 1 m in length at the apex of the stem in a mature palm. Being single-stemmed, the extraction of palm-heart results in the death of the genetic individual without the possibility of regeneration (Galetti & Fernandez 1998, Reis 2000). In Braulio Carrillo National Park (BCNP), Costa Rica, extraction concentrates on the tallest reproductive individuals of this species (19-22 m in height; Avalos 2007), causing significant changes in the structure of the forest understory and potentially leading to genetic erosion and the eventual extirpation of the species in areas close to human habitation. Although commercially produced palm-heart from *Bactris gasipaes* (peach palm) is available, *E. precatoria* continues to supply most of the demand for the black market, since consumers attribute a putative superior taste and quality to this species. The extraction of wild palm-heart is also an old tradition embedded in the culture of rural communities, making it difficult to implement alternatives that, although economically effective, are not culturally sound. Poachers have developed a profitable black market that evolved from a traditional, small-scale, intermittent extraction concentrated in rural communities, to a year-round permanent process of extraction that targets major cities and expensive restaurants. Records from the National System of Conservation Areas of Costa Rica indicate that in BCNP in 2003 alone park rangers seized 2000 illegally extracted stems, a tendency which continued into 2011. However, much of the extraction goes unnoticed by park officials, and it is likely that its impact is severe, consequently increasing the potential extirpation of *E. precatoria* from reserve areas close to human communities.

The genus *Euterpe* belongs to the subfamily Arecoideae and the tribe Euterpeinae, along with 5 other genera (*Prestoea*, *Neonicholsonia*, *Hyospathe*, *Oenocarpus*, and *Jessenia*). Henderson & Galeano (1996) recognize seven species in this genus, all with variable vegetative reproductive capacity. The species *E. precatoria* is divided into two varieties by Henderson *et al.* (1995), *longevaginata* (stems solitary or cespitose, low and high elevations in the Andes and Central America) and *precatoria* (stems solitary, low elevations in the Amazon). In Costa Rica, *E. precatoria* var *longevaginata* is commonly described as a single-stemmed, solitary subcanopy palm (Grayum 2003). Only occasionally is it referred to as *rarely clustered* or *cespitose* (Henderson *et al.* 1995), but more often than not the vegetative reproductive capacity of *E. precatoria* var *longevaginata* is overlooked. We have observed that the production of ramets (i.e., new sprouting shoots connected to the genet or mother palm, *sensu* Harper 1977) emerging from the base of the stem, or from established, mature stilt roots (similar to the related species *E. oleracea*) is relatively common. This is congruent with the phylogenetic relationships of the *Euterpe* clade, in which clonality is frequent (Henderson 2002) and with the considerable morphological plasticity displayed by *E. precatoria* var *longevaginata* in the structure and distribution of stilt roots and the types of substrates it can colonize. We have observed tall palms growing on fallen, decomposing logs, as well as on the buttresses of dead, snapped-off canopy trees up to three meters above the ground. Under these circumstances, the stilt root cone can rise up significantly above the ground, and the roots that are usually clustered can separate, in the same way as those of *Socratea exorrhiza* (Fig. 1). Although the phylogeny and classification of palms has made significant progress (Asmussen *et al.* 2006, Baker *et al.* 2009), and the *Euterpe* clade is well known (e.g. Henderson 2002), it is likely that a more comprehensive study of this species across its latitudinal range will produce a classification that better reflects this plasticity.

In this study, we document the capacity of *E. precatoria* var *longevaginata* for vegetative propagation by quantifying the frequency of ramets attached to mother palms in BCNP, Costa Rica. Commercial palm-heart from *Bactris gasipaes* is obtained by harvesting only ramets, which poses no major threat to the mother palm (e.g. Mora-Urpí & Gainza-Echeverría 1999). Similar harvesting practices could be used on *E. precatoria* if its vegetative reproductive capacity is quantified and potentially manipulated by means of genetic modification.

METHODS

The study was implemented in 2006 at Quebrada González in BCNP, Costa Rica (48000 ha, 10°09'44"N, 83°56'15"W, 400-500 m a.s.l.) on the Caribbean slope of the central mountain range. The forest is classified as a tropical premontane rain forest, receiving more than 4000 mm of rain per year (Holdridge *et al.* 1971).

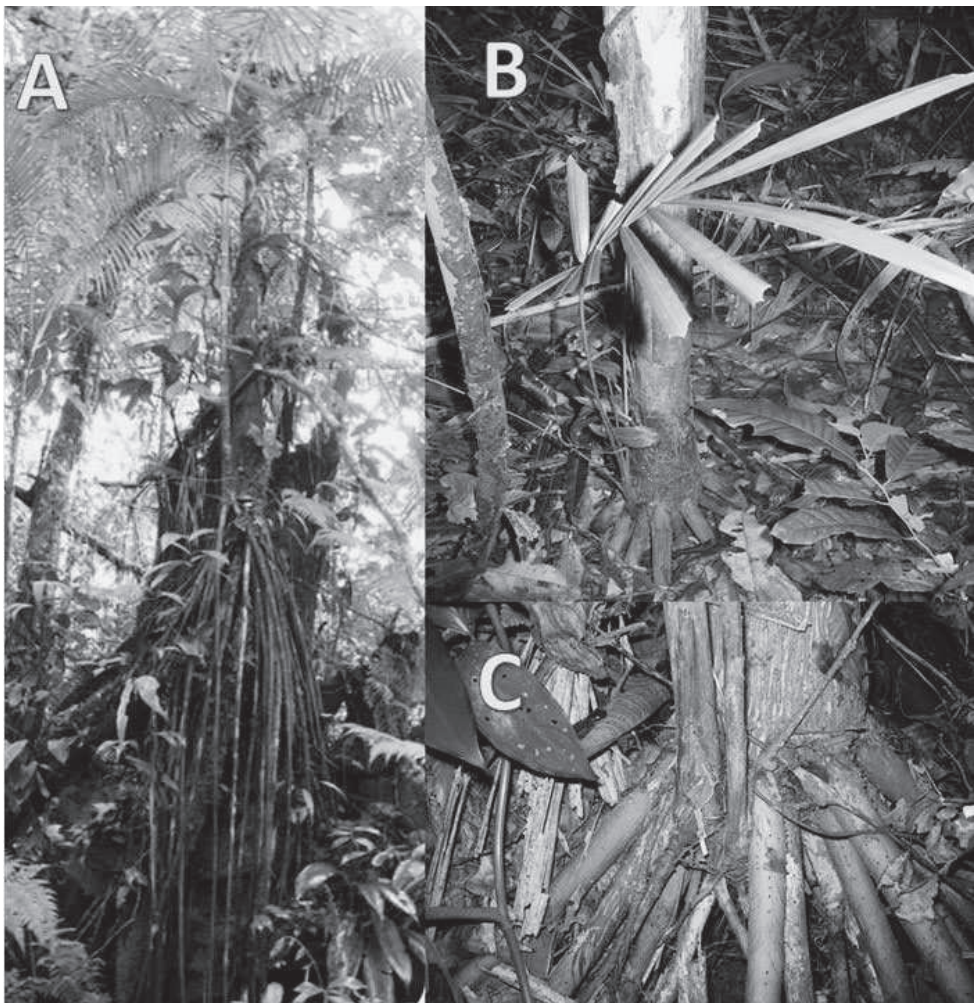

FIG. 1. (A) A 2-m tall *E. precatoria* growing on top of the buttresses of a snapped-off tree in Braulio Carrillo National Park, Costa Rica. The stilt roots are as long as the stem. (B) and (C) Emerging ramets at the base of the trunk of *E. precatoria*.

Our study species, *Euterpe precatoria* Mart. var *longevaginata* (Arecaceae), is distributed from Belize to Bolivia, and in Costa Rica occurs from sea level to 1150 m a.s.l. (Grayum 2003). At our study site, *Euterpe precatoria* is an early forest colonizer, in which seedlings germinate and juveniles thrive under increased light conditions after a disturbance, and individuals remain after the canopy has closed. The slender trunk of *E. precatoria* is solitary, and relatively soft compared with other arborescent palms, a characteristic that facilitates extraction. In contrast to this, in many parts of Amazonia the stems of *E. precatoria* are very hard and used as wall and floor materials by indigenous people (Mejía 1988). Growth of *E. precatoria* is limited by understory light conditions (Poorter 1999, Zuidema 2000). The palm grows best at intermediate light levels (close to 50% of full sun; Richards & Williamson 1975, Poorter 1999), but mechanical constraints restrain palm growth up to 1 m in stem height, after which the growth in height relative to stem diameter follows a linear relationship with a steeper slope (Avalos & Fernández Otárola 2010). Individuals under one meter constitute 80% of the *E. precatoria* population in BCNP. Extraction is concentrated on the tallest reproductive adults (19-22 m), which represent 2% of the population (Avalos 2007). We used morphological data from 192 palms from 30 permanent plots of 15 x 15 m established in BCNP in a primary forest without extraction (Las Palmas trail, 10 plots), in a primary forest where illegal extraction took place in 2000 (La Botella trail, 10 plots), and in a secondary forest without extraction (El Ceibo trail, 10 plots). Plots were separated by at least 50 m. All measured individuals had at least one leaf with a minimum lamina length (from the sheath base to the sheath apex) of 50 cm. The stem height of palms above 8 m was measured using basic trigonometric rules, whereas palms below 8 m were measured directly using either an extension pole or a measuring tape. In each palm we inspected the base of the stilt roots for the presence of ramets. When found, each ramet was examined for physical connection to the mother palm; seedlings emerging between the stilt

roots but unconnected to the mother plant were not considered. Ramets found to have a physical connection to the mother palm were recorded, and those that were at least 10 cm in stem length were tagged and measured. To describe the relationship between number of ramets and the height of the mother palm we applied a logarithmic regression after transforming the number of ramets using the Box-Cox procedure (Quinn & Keough 2002) to correct for normality and equality of variances before running the regression model.

RESULTS

Of the 192 palms examined in this study, 44 (22.8%) had attached ramets. Palms with ramets had an average of two ramets per individual. Out of a total of 92 ramets, only 16 were large enough to be measured and of these, three had other ramets attached. Palms with attached ramets ranged in height from 24 cm to 7.26 m. The majority of the mother palms were 40-90 cm tall, with the incidence of ramets decreasing with increasing mother palm height (Fig. 2).

The heights of the measurable ramets ranged from 34 cm to 1.22 m (N = 16). The majority of these ramets were 40-70 cm tall (Fig. 3) with an average height of 55 cm. The relationship between mother palm height and the number of attached ramets decreased logarithmically with increasing mother palm height (Fig. 4; $r^2 = 0.30$, $P = 0.009$). This relationship showed a higher incidence of ramets among shorter mother palms. We could not find a single ramet over 1.5 m in height attached to a large palm.

DISCUSSION

Plants are modular organisms, composed of repetitive physiological units with different levels of integration, spread over a mosaic of resource distribution that changes in space and time (Sachs *et al.* 1993, Dekroon & Hutchins 1995). In their foraging for resources, clonality allows plants to allocate more energy to sustain modules in areas of high resource availability, while at the same time these modules subsidize (at least temporarily) modules positioned in resource-poor environments (e.g. Avalos & Mulkey 1999). Clonality increases adult persistence through the spread of mortality risks among ramets (Bullock 1980, De Steven 1989). It facilitates the

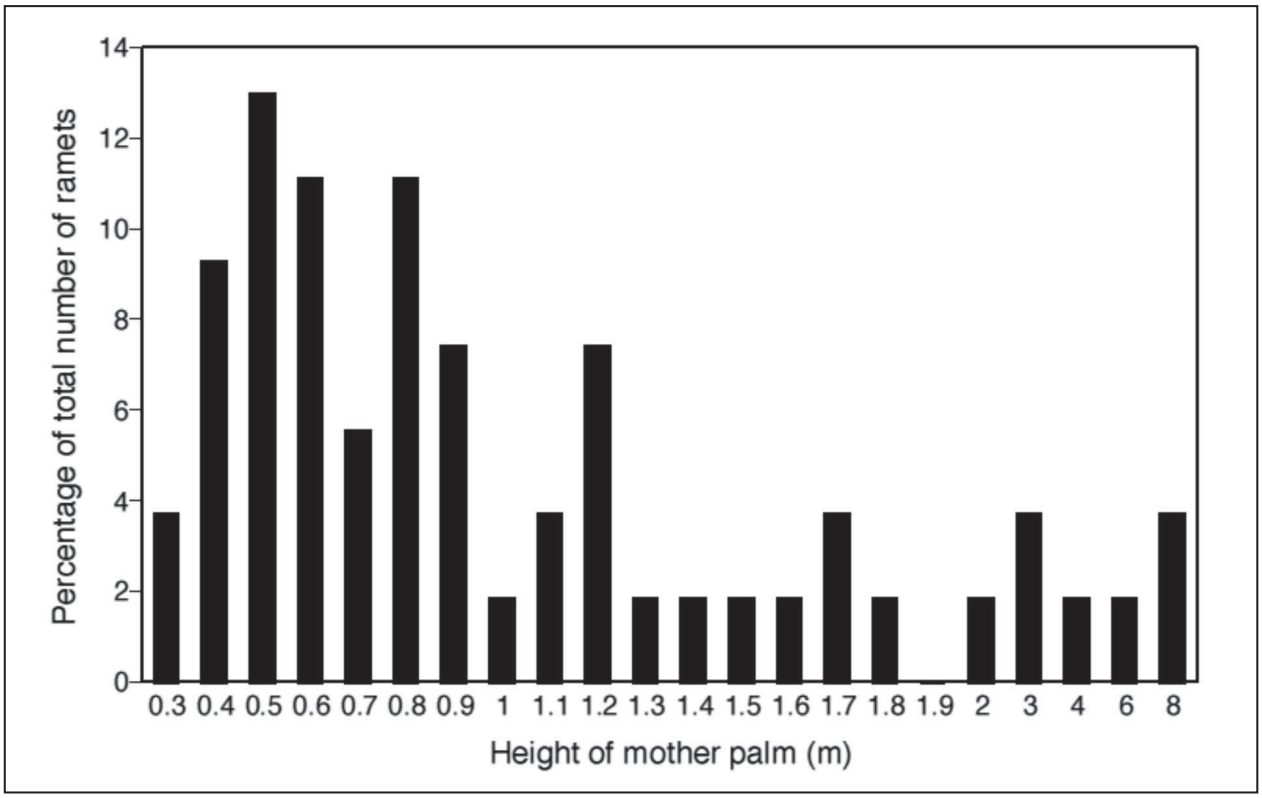

FIG. 2. Height distribution of *E. precatoria* mother palms with attached ramets (44 out of a sample of 192 palms) in BCNP, Costa Rica.

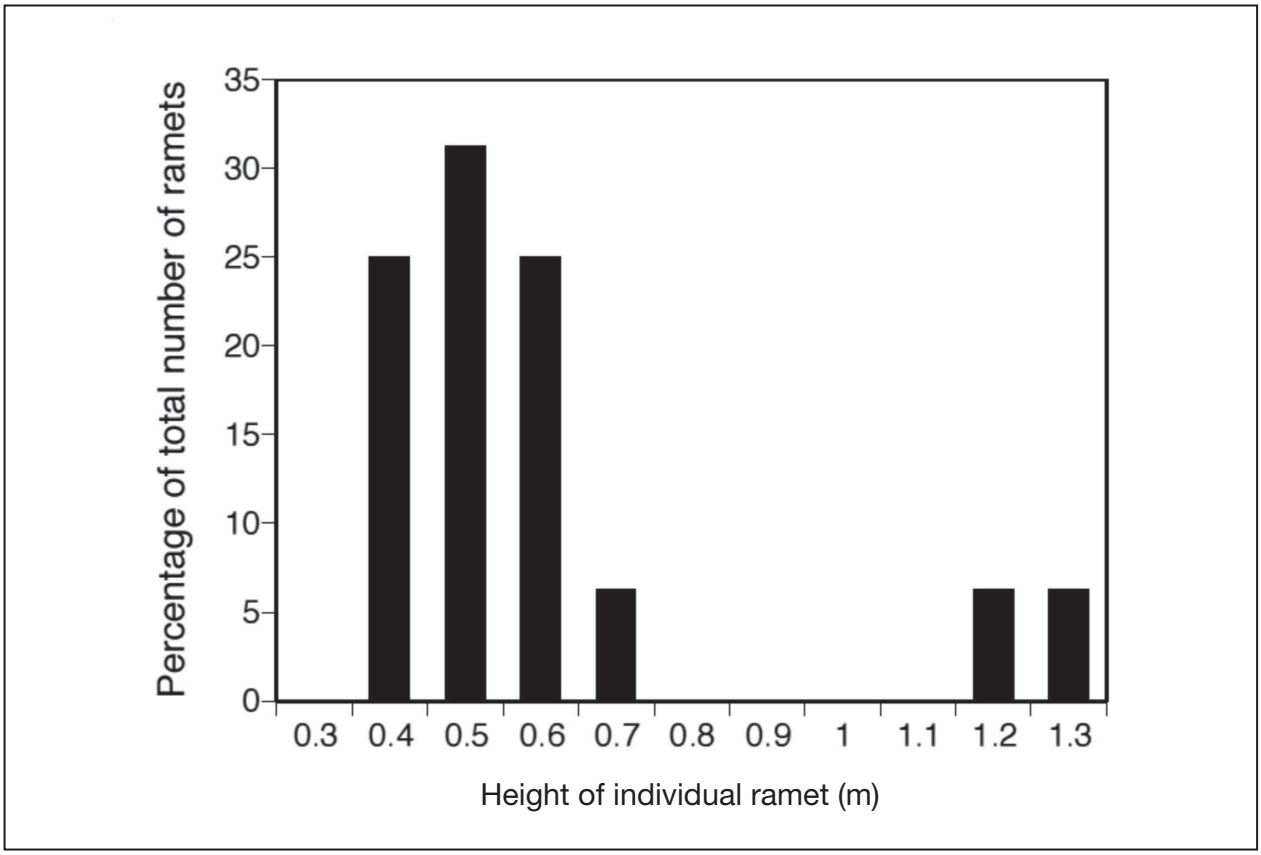

FIG. 3. Height distribution of ramets (N = 16) of *E. precatoria* in BCNP, Costa Rica.

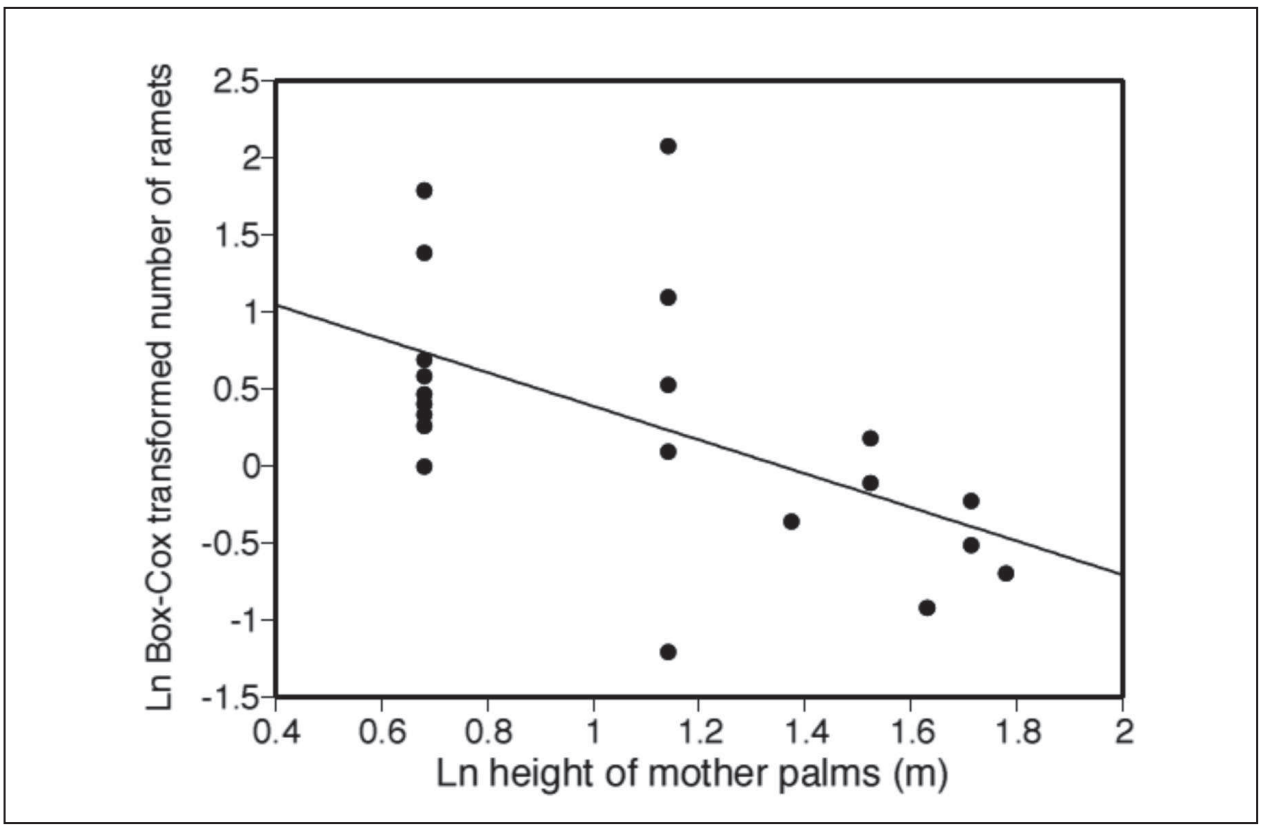

FIG. 4. Relationship between the natural log of mother palm height and the natural log of the number of attached ramets per palm in *E. precatoria* (r^2 = 0.30, P = 0.009).

escape from size-dependent constraints that limit resource acquisition, and thus sexual reproduction (Mendoza & Franco 1998, Souza *et al.* 2003), allowing increased ramet production as an alternative to sexual reproduction when spatial and temporal resources are limited (Villegas 2001). The expression and intensity of clonality is subject to natural selection. Clonality is mediated by the regime of environmental variation characteristic of the habitat where the species has evolved, as reflected in the plant's life-history strategy (Stearns 1976, 1977). This process has been critical as a step towards the expression of different levels of phenotypic plasticity by favoring the selection of the most successful genotypes (Sultan 1987, Stearns 1989, Bell & Lechowicz 1994).

The data presented here demonstrate that *E. precatoria* var *longevaginata* has a significant capacity for ramet production, although this ability was limited to small, most likely young palms. Similar to *E. precatoria*, the palm *Oenocarpus mapora* produces ramets that at the same time generate more daughter ramets in the juveniles stage while being still attached to the mother plant, immediately before the rapid growth phase that takes place after building the basal stem and root support necessary to sustain future increases in height (De Steven 1989). Having numerous ramets limited to younger and smaller mother palms was also prevalent in *Astrocaryum urostachys* and *Phytelephas tenuicaulis*, the two most woody palms out of the 10 species studied by Svenning (2000) in Yasuní, Ecuador. In this study, Svenning (2000) shows an inverse relationship between ramet number and stem diameter across species, indicating that taller and thicker palms had less ramets, without evidence of a trade-off between sexual and clonal reproduction. Clonal growth in understory palms is for the most part a strategy to maximize genet fitness by increasing the size of the genet, rather than a means of propagation (De Steven 1989, Svenning 2000). Souza *et al.* (2003) report the reverse patterns for the understory palm *Geonoma brevispatha*, in which clonal reproduction precedes sexual reproduction, and sexual fecundity and clonal investment scale with genet size. We do not think that the two patterns are contradictory, but rather that they reflect the diversity of growth strategies employed by various palm species to deal with heterogeneous resource distribution (e.g. Kimura & Simbolon 2002), reflecting the need for additional *in situ* studies of clonal growth in both canopy and understory palms.

In *E. precatoria* it is possible that during the earlier stages of seedling establishment, when biomechanical limitations for increasing height are more intense (Avalos & Fernández Otárola 2010), there is investment in ramet production to spread out mortality risks (*bet-hedging strategy*; De Steven 1989), or to acquire more leaf area to cope with the light-deprived conditions of the understory. After overcoming mechanical and energy limitations, the height of the palm increases linearly after 1 m in stem height, leveling off around 10.5 m (see Avalos & Fernández Otárola 2010), when resources are most likely allocated to reproduction (Homeier *et al.* 2002). The lack of ramets in large palms, and the absence of clumps of ramets joined to a large genet (similar to related species in the *Euterpe* clade, *E. oleracea*, *Prestoea decurrens, P. acuminata,* and *Oenocarpus mapora*) shows that ramets in *E. precatoria* var *longevaginata* do not develop into mature plants. It is not clear what factors trigger the production of ramets, or why they do not continue their development.

In BCNP, sexual reproduction of *E. precatoria* starts when individuals reach a height of 6-8.5 m. These observations suggest a negative relationship between ramet production and sexual reproduction. Once palms start sexual reproduction, the incidence of ramets changes from few to none. Our evidence indicates that the production of ramets in *E. precatoria* could be a relict of its past phylogenetic history, where clonal reproduction is common and precedes sexual reproduction (e.g. *E. oleracea, O. mapora* and *P. decurrens*, among other species within the *Euterpe* clade). In addition, in small palms, associated ramets contribute to increasing leaf area, but this effect loses importance as the palm escapes the light-limited understory and transitions into the reproductive stage. Since ramets are small and do not develop into tall individuals that attract the interest of poachers (Avalos 2007), the possibility of enhancing this capacity in *E. precatoria* by genetic manipulation has limited prospects. Because of this limitation, conservation policies must consider programs to promote outlets for controlled extractive activities, such as the implementation of incentives and certification plans to stimulate the cultivation of this species outside protected areas.

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