



## **Demography of the clonal palm *Prestoea acuminata* in the Colombian Andes: sustainable household extraction of palm hearts**

Authors: Gamba-Triminiño, Catherine, Bernal, Rodrigo, and Bittner, Jens

Source: Tropical Conservation Science, 4(4) : 386-404

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/194008291100400403>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## Research Article

# Demography of the clonal palm *Prestoea acuminata* in the Colombian Andes: sustainable household extraction of palm hearts

Catherine Gamba-Trimiño<sup>1\*</sup>, Rodrigo Bernal<sup>2</sup> and Jens Bittner<sup>3</sup>

<sup>1</sup>Pontificia Universidad Javeriana, Bogotá, Colombia

<sup>2</sup>Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia

<sup>3</sup>Corporación Autónoma Regional de la Frontera Nororiental – Corponor, Cúcuta, Colombia

jcgamba@javeriana.edu.co, rgbernalg@unal.edu.co, jbittner@tiho-hannover.de

\*Corresponding author email: [jcgamba@javeriana.edu.co](mailto:jcgamba@javeriana.edu.co)

### Abstract

*Prestoea acuminata* is a highland clonal palm traditionally used as a source of palm hearts by the Awá Indians of Colombia and Ecuador; its commercial use thrived in the 1980's. Extraction pressure on the resource is particularly strong during Holy Week, as campesinos use it as a substitute for meat. We studied *P. acuminata* demography at La Planada Reserve, southwestern Colombia, and elaborated a ramet-based matrix model to assess the impact of different palm heart harvest regimes. The 1.5 ha study area had 1182 genets, composed of 5389 ramets. Harvestable stems were 23-40 years old and accounted for 0.32% of the stable stage distribution (SSD). Ramet population asymptotic growth rate  $\lambda$  was 1.0485, and was more sensitive to changes in the survival of stemless ramets. Observed stage distribution (OSD) differed from predicted SSD, which suggests the population was exhibiting transient dynamics. As our census was conducted four years after a severe ENSO, we argue that the OSD could be reflecting this environmental disturbance. Thus, harvest simulations must be interpreted with caution. Although *P. acuminata* ramets are abundant at La Planada, the typical genet architecture, with many stemless ramets ( $\approx 20$ ) and only 1-2 stems appropriate for palm heart extraction, accounts for a very low resource yield (127 palm hearts  $\text{ha}^{-1}$  in our survey). This, and its slow growth rate, make *P. acuminata* suitable only for household extraction. As harvest has a strong effect on sexual recruitment, we recommend a maximum annual extraction of 10% of harvestable ramets.

**Key words:** Arecaceae, La Planada, Matrix Projection

### Resumen

*Prestoea acuminata* es una palma clonal de tierras altas utilizada tradicionalmente como fuente de palmito por los indígenas Awá de Colombia y Ecuador, que fue explotada comercialmente en los años 1980's. La presión de extracción sobre el recurso es particularmente fuerte durante la Semana Santa, pues los campesinos lo consumen en reemplazo de la carne. Para evaluar el impacto de diferentes regímenes de cosecha, estudiamos la demografía de *P. acuminata* en la Reserva La Planada, suroccidente de Colombia, y elaboramos un modelo matricial para los rametes. Las 1.5 ha estudiadas tenían 1182 genetes compuestos de 5389 rametes. Los tallos cosechables tenían 23-40 años y representaron el 0.32% de la distribución estable de estados (SSD). La tasa de crecimiento asintótico para los rametes fue de  $\lambda=1.0485$ , siendo más afectada por cambios en la supervivencia de los rametes sin tallo. La distribución observada de estados (OSD) y la SSD estimada fueron significativamente diferentes, lo que sugiere que la población estaba atravesando por dinámicas transitorias. Dado que nuestro censo se llevó a cabo cuatro años después de un severo El Niño, argumentamos que la distribución observada podría estar reflejando esta perturbación ambiental. Por lo tanto, las simulaciones de cosecha deben ser interpretadas con precaución. Aunque los rametes de *P. acuminata* son abundantes en La Planada, la arquitectura típica de un genete, con muchos rametes sin tallo ( $\approx 20$ ) y sólo 1-2 tallos apropiados para extracción, hace que la oferta del recurso sea muy baja (127 palmitos  $\text{ha}^{-1}$  en nuestro estudio). Este hecho y su lento crecimiento hacen que *P. acuminata* sea apropiada solo para extracción a nivel doméstico. Dado que la cosecha tiene un fuerte impacto en la reproducción sexual, recomendamos una extracción máxima anual del 10% de los tallos cosechables.

**Palabras clave:** Arecaceae, La Planada, Proyección matricial

Received: 7 June 2011; Accepted: 4 October 2011; Published: 12 December 2011.

**Copyright:** © Catherine Gamba-Triminiño, Rodrigo Bernal and Jens Bittner. This is an open access paper. We use the Creative Commons Attribution 3.0 license <http://creativecommons.org/licenses/by/3.0/> - The license permits any user to download, print out, extract, archive, and distribute the article, so long as appropriate credit is given to the authors and source of the work. The license ensures that the published article will be as widely available as possible and that the article can be included in any scientific archive. Open Access authors retain the copyrights of their papers. Open access is a property of individual works, not necessarily journals or publishers.

**Cite this paper as:** Gamba-Triminiño, C., Bernal, R. and Bittner, J. 2011. Demography of the clonal palm *Prestoea acuminata* in the Colombian Andes: sustainable household extraction of palm hearts. *Tropical Conservation Science* Vol. 4(4):386-404. Available online: [www.tropicalconservationscience.org](http://www.tropicalconservationscience.org)

## Introduction

Palm heart, a traditional Amerindian food, has emerged in the last decades as an exotic export for international cuisine, and nowadays it is the most important South American palm product entering international trade [1]. Although cultivation of *Bactris gasipaes* for palm heart extraction has increased in the last decade [2, 3], a large proportion of palm heart in commerce is still obtained from wild species, mainly in the genus *Euterpe*: *E. edulis* [4, 5], *E. oleracea* [1, 6, 7], and *E. precatoria* [8].

Palm heart, or palmito, corresponds to the developing leaves of the plant, which are located at the centre of the crown. Thus, palm heart extraction of single-stemmed palms results in the palm's death, whereas clonal palms, composed of many ramets, can be harvested without killing the genetic individual (genet), which may offer a better perspective for sustainable management.

*Prestoea acuminata* is a highland, clonal palm, traditionally used as a source of palm hearts by the Awá Indians of Colombia and Ecuador [9], and it was also the source of a canning industry that thrived for a short period in Ecuador in the 1980's [10]. Although commercial exploitation has now ceased [1], the Awá still consume *Prestoea* palm heart in small quantities throughout the year, whereas campesinos in southwestern Colombia consume it as a substitute for meat during Holy Week. During this period, forest patrolling is required at protected areas to avoid illegal palm heart extraction.

Although palm heart extraction from *P. acuminata* does not cause the death of the individual, as pressure on the resource increases, the growth rate of the basal ramets might not be enough to compensate for the harvested stems, leading to a shortage of stems tall enough to provide palm heart. Also, the depletion of tall stems would cause a reduction in seed production, affecting the population's genetics and spatial distribution. Sustainability analyses are then required to provide harvest guidelines and to avoid overexploitation.

In this paper we describe the demography of an unharvested population of *Prestoea acuminata* at La Planada Nature Reserve, southwestern Colombia, and elaborate a ramet-based matrix model for this species. We report growth and survival rates for the different life stages of the palm, and estimate age for significant biological landmarks. We use matrix model projections to assess the impact of different palm heart harvest regimes on ramet population dynamics, and to determine resource availability over time. We discuss model limitations, research gaps, and ecological constraints and advantages for sustainable palm heart extraction from *Prestoea acuminata*. We provide management recommendations that could contribute to the sustainable use of this species, and formulate a hypothesis regarding the significance of its clonal strategy.

Galeano et al. [11] proposed a six-step research protocol for studying palm management sustainability, including, but not exclusively relying on, the use of matrix models, and emphasizing the need to use research findings to discuss and implement an adaptive management plan. In this paper we cover several points from that protocol, providing information relevant for the production of a participatory management plan for *Prestoea acuminata* in southwestern Colombia.

Matrix population models [12] are commonly used to study population dynamics and modeling sustainable harvest [13]. A basic matrix model consists of a population divided into discrete stages or age classes, and a matrix **A** of transition probabilities from one class to another, across one time interval. Such models make it possible to estimate the asymptotic growth rate ( $\lambda$ ) and age structure of populations over time, to evaluate the relative importance of demographic processes on  $\lambda$  (elasticity analysis), and to determine optimal harvesting regimes based on demographic data. Hence, if  $\lambda > 1$ , the population is expected to grow in the long term; if  $\lambda = 1$ , it will remain stable; and if  $\lambda < 1$ , it will decline.

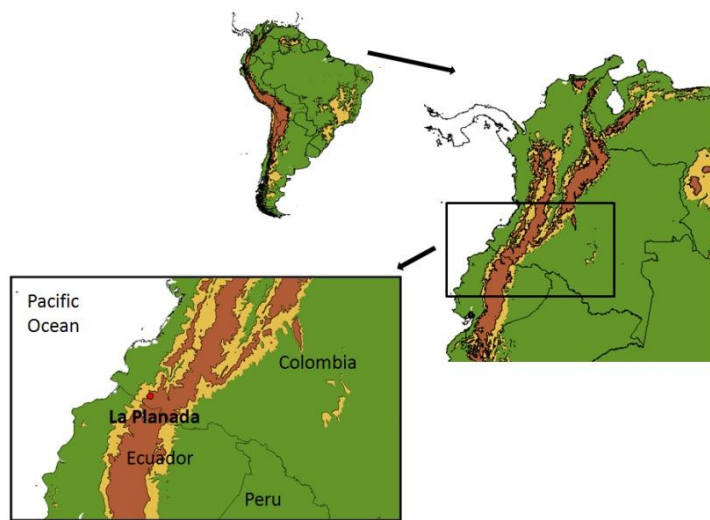
However, these models assume that the populations are in equilibrium, *i.e.*, that model predicted stable stage distribution (SSD) does not significantly differ from observed stage distribution (OSD), which is not always the case [14]. Some recent uses of matrix models in connection with non-timber forest product (NTFP) extraction include the Brazil nut *Bertholletia excelsa* [15]; stems of the climbing palm *Desmoncus orthacanthos* [16]; palm hearts of *Euterpe edulis* [5]; and leaves of the understory palmlet *Lepidocaryum tenue* [17].

In most NTFP studies, stage-based matrix models are built from repeated measures of vital rates (survival, growth, and reproduction) of individual plants. Researchers follow a cohort for a certain period, and from these data, population growth rates ( $\lambda$ ) are calculated. Short sampling periods could introduce error into these estimations though, as noted by Schmidt et al. [13] in reviewing published studies for 46 NTFP species. An alternative to this approach is the time-specific model, where survival is calculated from size class distributions [11, 18-20]. This model assumes that size class distribution at any particular time reflects the population's growth and survival rates during many years, and could therefore be less subject to bias relating to temporal variation [19]. In this study we used a combination of these two approaches.

## Methods

### Study site

Our study was carried out within the 25 ha La Planada Forest Dynamics Plot (01° 10' N, 77° 59' W) at La Planada Nature Reserve (hereafter referred to as the Humboldt plot). La Planada is a private reserve on the Pacific slope of the Andes, in the Department of Nariño, Colombia (Fig. 1) [21]. It covers an area of 1800 ha between 1300 and 2100 m of elevation. Rainfall in the area is 4900 mm per year, with a marked dry period in July-August, and mean daily temperatures ranging from 12°C to 25°C [22]. The area is classified as premontane wet forest in Holdridge's life zone system [23]. The 25 ha plot was established in 1996 by the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt and the Center for Tropical Forest Sciences (CTFS) of the Smithsonian Tropical Research Institute (STRI) at an altitudinal range of 1700-1840 m. All woody species  $\geq 1$ cm diameter at breast height (DBH) have been grid-mapped, identified, tagged and measured on two separate occasions (1997 and 2002-2003). The plot holds primary forest with a canopy 15-25 m tall and some trees with diameters  $> 1$ m DBH. According to the 2002 census, the plot had a total of 204 woody species; see [24, 25; <http://www.ctfs.si.edu/site/La+Planada/census/>] for a detailed description.



**Fig. 1. Location of study area.**

### **Study species**

*Prestoea acuminata* var. *acuminata* (hereafter referred to as *P. acuminata*; Fig. 2 is an understory, clonal, monoecious palm, distributed in scattered patches along the wet highlands of northern South America (Venezuela to Bolivia) and Central America (Nicaragua to Panama). It belongs to the Neotropical tribe Euterpeae, which also comprises the genera *Hyospathe*, *Euterpe*, *Neonicholsonia*, and *Oenocarpus* [26]. Each genet of this species is composed of numerous ramets, forming clumps of well-developed stems and stemless shoots of different sizes. Stems reach 15 m tall and 15 cm in diameter, and have a crown of 7-11 pinnate leaves, ca. 3 m long. Inflorescences are infrafoliar and protandrous, and they produce globose, black fruits, 1-1.2 cm in diameter. Each infructescence may produce 573-2659 mature fruits [9]. Most fruits fall directly to the ground, but at La Planada they are also eaten and dispersed by four species of birds (*Rupicola peruviana*, *Snowormis cryptolophus*, *Andigena laminirostris* and *Chamaepetes goudotii*), and one rodent species (*Orizomys albigularis*) [9]. The seeds germinate within one month when dispersed by animals, and within two months when the fruits fall near the parent tree [9].



**Fig. 2. *Prestoea acuminata* different life stages. A) Seedling at La Planada Reserve, Colombia (Photo C. Gamba-Triminiño) B) Cultivated clonal juvenile at private collection in Colombia (Photo R. Bernal) C) Adult individuals at Ucumari Park, Colombia (Photo R. Bernal) (Photo R. Bernal)**

### Field measurements

Field measurements and data analysis agree with the methodological protocol of Galeano et al. [11]

PHENOLOGY, RAMET PRODUCTION AND MORTALITY. In August 1998 we measured and tagged 20 randomly selected individuals (ramets,  $n = 494$ ) in a ca. 3 ha forest patch 400 m north of the Humboldt plot. We counted all ramets per genet, and for each ramet we recorded stem length (measured with a measuring tape attached to a telescoping pole), number of living leaves, leaf size of stemless shoots (recorded as the number of pinnae on one side of the rachis in the newest leaf) and reproductive status (recorded as flowering buds, flowers, immature or mature fruits or evidence of old reproductive structures). Over a 21-month period, monitored every four months, we followed the production of leaves, ramets, pinnae and reproductive structures, and recorded ramet mortality.

POPULATION STRUCTURE. During April-June 2002 we censused and tagged all *P. acuminata* ramets in fifteen 20 x 50 m (0.1ha) plots randomly located within the Humboldt plot. We recorded the same data as in 1998, but did not monitor these individuals over time. We censused seedlings in two 25 m<sup>2</sup> subplots nested within each of the 0.1ha plots (0.075 ha).

### Age estimates

SEEDLINGS with bifid leaves: We bypassed the seed stage and started our model from the seedling stage. We used Knudsen's [27] data from a population of *P. acuminata* in Ecuador, at 2000 m of elevation.

STEMLESS RAMETS: When ramets have not yet developed an aerial stem, the number of pinnae on each side of the rachis increases from one leaf to the next. We used this increase in number of pinnae, combined with leaf production rate, to estimate age in stemless ramets [11, 18]. To have an estimate of total age, the duration of the seedling class was added to this calculation (but vegetatively-produced ramets bypass the seedling class).

STEMS: In palms, it is very easy to visualize historical leaf production, as every new leaf leaves a scar on the stem [11, 28]. Age estimates for stems of *P. acuminata* were obtained by dividing the number of leaf scars on the stem by the leaf production rate [11, 20]. To have an estimate of total age, both seedling and stemless stage durations were added to this calculation. Counting the number of leaf scars on standing stems of *P. acuminata* at La Planada is difficult, as they are usually covered by numerous epiphytes. Although light and nutrient conditions alter stem growth rates, Lugo & Rivera-Batlle [29] showed that for a population of *P. acuminata* var. *montana* in Puerto Rico, scar estimations from regression analyses were very close to the estimates based on counts of all leaf scars. Hence, we estimated the number of leaf scars per meter by extrapolating from counts made on 20 adult stems that had been felled (see Results for regression analyses).

### Population dynamics

Collected data were pooled to build a ramet-based matrix model. In this model, every ramet of the genet is regarded as a separate individual [17, 30, 31]. During our monitoring period only 30 ramets died; therefore, in order to avoid having very high survival rates that could not reflect the actual dynamics of the population, we used a time-specific model (but used observed survival figures for some classes, see Methods - Matrix parameters).

SIZE CLASSES: One of the constraints of the time-specific model is that life classes must have similar duration [11, 19]. Based on age estimations, we divided the population into eleven size classes of similar duration, seeking also category limits that represented significant biological landmarks (see Appendix 1 for a description of each class).

MATRIX PARAMETERS: Survival probability for ramets in size class  $i$  was estimated from the ratio of number of ramets in size class  $i+1$  over the number of ramets in size class  $i$  ( $P_i^* = N_{i+1}/N_i$ ) [18-20]. As size class 2

comprises both sexually and asexually generated ramets, we estimated the seedling survival probability  $P_1^*$  from the number of solitary individuals in class 2. Having estimated the category-specific survival probability  $P_i^*$ , we derived the annual survival probability as follows:  $\sigma_i = (P_i^*)^{1/T_i}$ , where  $\sigma_i$  is the category-specific annual survival probability, and  $T_i$  is the category duration in years [18, 19]. We used observed annual survival for size classes that had high death rates (size classes 2 and 3); and for the largest class (11) we used  $\sigma_{10}$  (See Appendix 1 for observed and estimated survival rates).

We used a fixed stage duration model to calculate stasis and progression probabilities. In this model, the probability of growing into the next size class,  $i+1$ , for individuals within size class  $i$  is not constant, but depends on age distribution within the class. This model is useful when the “stages” are actually groups of age classes and when only relatively crude estimates of survival are available over broad age ranges [12, 32]. Thus, during the interval  $(t, t + 1)$ , all the oldest individuals will progress to the next class, and all younger individuals will move up within the class. The proportion of ramets surviving and remaining in the class is  $P_i = \sigma_i (1 - \gamma_i)$ , and the proportion of individuals that survive and progress into the next class is  $G_i = \sigma_i \gamma_i$ , where  $\gamma_i$  is an approximately constant annual probability of growing, calculated as  $\gamma_i = [(\sigma_i/\lambda)^{T_i} - (\sigma_i/\lambda)^{T_i-1}] / [(\sigma_i/\lambda)^{T_i} - 1]$ , and  $\lambda$  is an initial estimate of the overall population increase or decline, which we first set as 1. We applied then an iterative procedure, using the dominant eigenvalue obtained from the matrix, until the initial  $\lambda$  and the final  $\lambda$  were equal to the fourth decimal place [12].

In order to calculate sexual reproduction, all ramets with reproductive structures were taken into account, even those carrying old buds. We calculated sexual reproductive output  $F_i$  as the mean seedling production per ramet.  $F_i = (N_{ir}/N_r) * (N_o/N_i)$  [18, 31], where  $N_{ir}$  is the number of reproducing ramets in class  $i$  (i.e. producing mature fruits; calculated from 21 months of phenological observations on 22 adult stems),  $N_r$  is the total number of reproducing ramets in all classes,  $N_o$  is the total number of seedlings entering the population per year, and  $N_i$  is the total number of ramets in class  $i$ .  $N_o$  was derived from the total number of seedlings in category 1,  $N_1$ , using a geometric series  $N_o = N_1 / [1 + \sigma_1 + \sigma_1^2 + \sigma_1^3 + \dots + \sigma_1^{T_1-1}]$  [19].

We calculated vegetative output  $V_i$  as  $V_i = \sigma_i V_i^*$  [33], where  $V_i^*$  is the ramet production rate for a ramet in class  $i$ . For each genet,  $V_i^*$  was derived by dividing the ramet production rate (estimated from our monitoring period), by the number of ramets with appropriate size for asexual reproduction in the genet.

We solved the matrix for the dominant eigenvalue,  $\lambda$ , and for right and left eigenvectors, stable-stage distribution (SSD) and reproductive value ( $v$ ) respectively, using PopTools [34]. We performed a log-linear analysis [35] to test for differences between stable stage distribution and observed stage distribution and estimated confidence intervals for  $\lambda$  using the analytical formulae derived by Alvarez-Buylla & Slatkin [36].

### Modeling harvest

Ramets are not usually harvested until their stems are > 4 m (size class 8) [27]. We simulated different annual intensities by cutting 10, 25, 50, 75 and 100% of the stems > 4 m. We modeled palm heart harvest by reducing stem abundance in the population vector, for size classes 8-11, before that vector was multiplied by the transition matrix [8, 37]. Simulations always started with a harvest, which was then repeated every year up to 100 years. We estimated harvest impact on total population size, on adult individual abundance, and on palm heart availability. We calculated the elasticity of  $\lambda$  to changes in matrix parameters using the right eigenvector ( $w$ ) and the left eigenvector ( $v$ ) [12].

### Sexual vs. vegetative reproduction

In order to estimate the effects of sexual vs vegetative output in  $\lambda$ , we built two additional matrices: 1) taking out entries from sexual output (Fig. 4,  $F_i$ ); 2) taking out entries from vegetative output (Figure 4,  $V_i$ ).

## Results

The 1.5 ha study area contained 1182 genets, which comprised 5389 ramets, not including seedlings (Appendix 1). Density in the plots was on average 788 genets ha<sup>-1</sup> (*SD* = 248.3), and 3593 ramets ha<sup>-1</sup> (*SD* = 1121.9), with an average of only 31 adult ramets ha<sup>-1</sup> (*SD* = 32). Genet size was highly variable, with 2-20 ramets ( $x = 8.86$ ;  $n = 538$ ; *SD* = 7.05), most of them small, stemless shoots. Only 6.4% of the genets had more than three ramets with well-developed stems. Maximum genet size was 70 ramets. The ramet population structure at the study site showed a declining abundance from seedlings to large adult ramets (Appendix 1), with a slightly higher abundance of juveniles 2 (category 3) over juveniles 1 (category 2).

### *Leaf production, growth rate and age*

A sexually generated ramet starts out as a seedling with bifid leaves, and the production of pinnate leaves roughly marks the beginning of another phase. A vegetatively generated ramet starts out with a sword leaf. Stemless ramets had 1-2 active leaves ( $x = 1.51$ ;  $n = 4412$ ; *SD* = 0.79), and produced an average of 1.54 new leaves per year ( $n = 226$ ; *SD* = 0.50). No correlation was found between the number of active leaves and the number of pinnae of the newest leaf. Number of pinnae on each side of the rachis increased from one leaf to the next, adding on average 1.5 pinnae per year ( $n = 190$ ; *SD* = 1.24) until the leaf had at least 35 pinnae per side. However this rate was not a constant, and we could differentiate a minority (27.4%) of fast-growing stemless ramets, with an average increase rate of 3.14 pinnae per year (*SD* = 1.04), and a majority (72.6%) of slow-growing stemless ramets, with an average increase rate of 0.91 pinnae per year (*SD* = 0.58). Starting from a leaf with one pinna, and adding 1.5 pinnae per year, it would take an average-growing ramet 22.67 years to develop a leaf with 35 pinnae per side and a visible stem. Nevertheless, for a fast-growing ramet it would take only 10.8 years. Age and class durations based on average pinna increase rate are shown in Appendix 1. These average estimates were used to build the matrix model. Age estimates for fast-growing ramets vs. average-growing ramets for significant biological landmarks are shown in Table 1.

Both the number of leaves in the crown and the leaf production rate increased as ramets developed an above-ground stem. We performed a regression analysis relating annual leaf production rate ( $y$ ) to stem length ( $x$ ) ( $y = 0.35x + 1.64$ ;  $r = 0.82$ ;  $n = 144$ ;  $P < 0.001$ ), and used this regression to calculate leaf production rate for stems up to 11 m tall, as for taller stems leaf production rate was observed to level off. Regression analyses showed two kinds of relationship between leaf scar numbers ( $y$ ), and stem length ( $x$ ). Because of this, we estimated leaf scar numbers from height data using two different equations: for stems 0 to 4 m,  $y = 7.75x + 4.85$ ;  $r^2 = 0.9976$ ;  $n = 20$ ; and for stems > 4m,  $y = 19.32e^{0.16x}$ ;  $r^2 = 0.9979$ ;  $n = 16$ . Combined, the height-dependent patterns of leaf production rate and the number of leaf scars per meter resulted in the height-dependent stem elongation pattern shown in Fig. 3. For significant biological landmark age estimates see Table 1.

**Table 1.** Age estimates (yrs) for significant biological landmarks of *Prestoea acuminata* life history at La Planada Reserve, Colombia. Age estimates include seedling stage duration for modeling purposes (but vegetatively-produced ramets bypass this stage). Fast and average growing rates refer to the stemless stage and number of pinnae to one side of the rachis in the newest leaf.

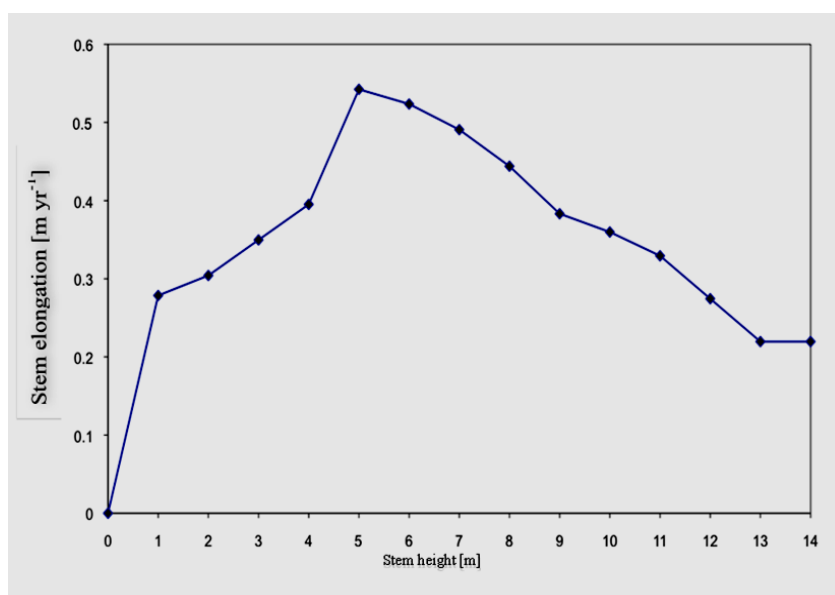
	Fast-growing ramets	Average-growing ramets
Clonal phase beginning (23 pinnae)	12.31	19.97
Visible stem (35 pinnae)	16.15	27.98
Harvestable size (4 m)	28.39	40.22
Sexual maturity beginning (7.5 m)	35.5	47.33
Longevity (14.05 m)	57.54	69.37



### Vegetative and sexual reproduction

Individual palms began producing ramets in the mid-juvenile phase (class 4), when they still lacked an aboveground stem and had on average 23 pinnae on each side of the leaf rachis. Over a 21-month period we recorded an average annual production of 2.6 ramets per genet ( $n = 20$ ;  $SD = 2.5$ ), with no pulses, and no significant differences among clones of different sizes or functional status.

Sexual reproduction began at an average height of 7.5 m (class 9). Out of 1182 genets censused in 2002, 3.3% contained at least one adult-sized ramet, whereas only 0.59% contained more than one. Clones with adult stems had, on average, 19.2 ramets ( $n = 39$ ;  $SD = 10.6$ ) (Appendix 1). Eight of the 22 adult ramets that we monitored produced mature fruits annually. Five of them belonged to category 10 (stem 10.2-12.4 m long). Estimated annual seedling recruitment in the 1.5-ha study area was 17660.



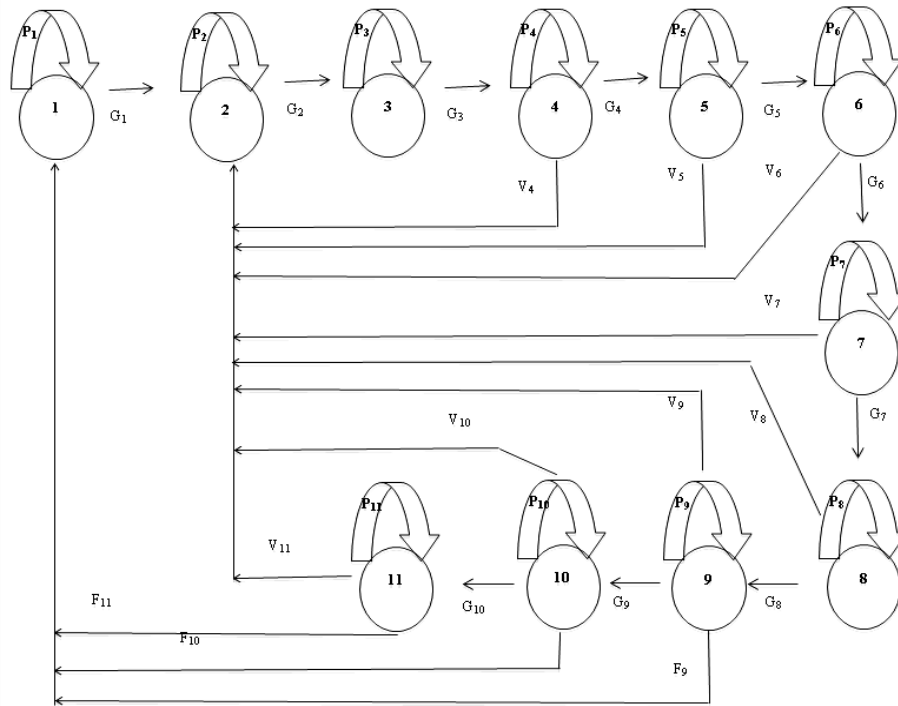
**Fig. 3. Stem elongation pattern [m yr<sup>-1</sup>] of *Prestoea acuminata* at La Planada Reserve, Colombia. Estimated from a regression analysis relating annual leaf production rate ( $y$ ) with stem length ( $x$ ); and a regression analysis relating leaf scar numbers ( $y$ ), and stem length ( $x$ ). See Results**

### The matrix model

The life cycle of *P. acuminata* is shown in Fig. 4 and the annual transition matrix in Appendix 2. Dominant eigenvalue  $\lambda$  (i.e. the asymptotic growth rate for the ramet population) was  $1.0485 \pm 0.0151$  (95% confidence interval). Stable stage distribution (SSD) showed a reverse-J shape (Table 2), and was significantly different from the observed stage distribution ( $G = 32919$ ;  $P < 0.001$ ). Ramets appropriate for palm heart extraction accounted for only 0.32% of the predicted SSD. Reproductive value showed a peak in category 10 (adults with stem 10.24-12.4 m) (Table 2).

The elasticity matrix (Appendix 3) shows that the largest contribution to  $\lambda$  corresponds to stasis probability of stemless shoots. Stasis of all stages accounts for 77.2% of the value of  $\lambda$ , progression for 17.5%, vegetative output for 5.14%, and sexual output for 0.16%. The demographic transitions of harvestable ramets have a minimal impact on  $\lambda$  (2.22% with all transitions added up). Harvest simulations did, however, show a strong effect of harvest on total ramet population size (Table 3), mainly as a consequence of the reduction in the number of adult individuals, and of the associated decrease in sexual recruitment. Even the mildest simulated extraction regime, cutting 10% of the stems every year, caused adult ramet abundance to drop below 50% of the undisturbed density after 40 years. According to the model, palm heart availability (Table 3) and recovery time to obtain initial yield are also severely affected by harvest: starting with a current palm heart availability of 50-310 palm hearts ha<sup>-1</sup> ( $x = 127$ ;  $SD = 70$ ), under a regime of 10% annual palm heart extraction, it would take 41 years before a similar harvest could be achieved. The

asymptotic growth rate for a matrix without sexual entries was  $\lambda = 1.0467$ , whereas for a matrix without vegetative entries was  $\lambda = 0.9700$ .



**Fig. 4.** Life cycle for *Prestoea acuminata* ramet population model at La Planada Reserve, Colombia.  $P_i$ , stasis probability, i.e. annual probability of surviving and remaining in the same size class;  $G_i$ , progression probability, i.e. probability of surviving and growing to the next size class;  $F_i$ , size-specific sexual reproductive output;  $V_i$ , size-specific vegetative output.

## Discussion

### *Natural history of P. acuminata: labor division inside the clone?*

Size-based age estimations in a population assume equal performance of all individuals, although some plants can actually grow faster or slower as a result of both environmental and genetic factors [28, 38]. For clonal palms, these growth rate variations can occur even among ramets [33]. *P. acuminata* stemless ramets displayed two differentiated growth rates, so we prefer to indicate age as a range (see Table 1); but for the matrix model, we used the average growth rate. Lugo & Rivera-Batlle [29] could also differentiate individuals with slow and fast growth rates in a *P. acuminata* var. *montana* population in Puerto Rico, but they followed only stem growth rates.

The sigmoidal stem elongation pattern found for *P. acuminata* (Fig. 3) has been reported for other palms [8, 28, 37], and it could reflect high construction costs for reproductive structures [39] and structural support constraints at the palm base [40]. The latter explanation could be of particular importance at La Planada, as plants are always covered by numerous bromeliads and other epiphytes filled with water, which impose additional pressures to structural stability. Although we did not assess clonal integration inside *P. acuminata* genets [e.g. 41], the species' genet architecture (with many stemless ramets and just one or two well-developed stems) (Appendix 1) and observed differential growth rates for stemless ramets, suggest a high level of physiological integration and ramet specialization.

**Table 2.** Observed stage distribution (OSD), stable stage distribution (SSD) and reproductive value ( $v$ ) for an unharvested *Prestoea acuminata* ramet population at La Planada Reserve, Colombia. From the pooled data of fifteen 0.1 ha plots

	Size class	OSD	SSD	$v$
1	Seedlings	0.85002	0.40486	1.0000
2	Juveniles 1	0.02930	0.27055	126.0835
3	Juveniles 2	0.03738	0.15623	241.8067
4	Clonal juv. 1	0.03635	0.09154	367.8932
5	Clonal juv. 2	0.01986	0.04417	636.3973
6	Subadults 1	0.01565	0.02180	477.2211
7	Subadults 2	0.00649	0.00769	560.1274
8	Subadults 3	0.00368	0.00248	599.0832
9	Adults 1	0.00081	0.00050	2449.7469
10	Adults 2	0.00033	0.00015	4320.1983
11	Adults 3	0.00014	0.00005	251.5034

Data suggest that vegetative growth in *P. acuminata* may be a light and/or nutrient foraging strategy, with 'labor division' inside the clone --many stemless ramets capturing understory sunflecks, and resources in general, to support high sexual reproduction costs [see 39, 42, 43], and only one reproductive stem per clone. Having only one adult ramet per clone would also help to reduce geitonogamy. Data do not seem to support the hypothesis of 'parental care,' where tall ramets capture light to support stemless ramet growth [see 44], as vegetative reproduction started before any stem was developed, and ramet production neither decreased nor stabilized when sexual reproduction started. Further analysis of allometric relationships in *P. acuminata* [e.g. 40], and of growth rate variations among genets of different sizes may help to elucidate these hypotheses.

**Table 3.** Effects of palm heart harvest intensity on *Prestoea acuminata* palm heart availability, sexual recruitment and total population size at La Planada Reserve, Colombia, after 40 years of projection. This table must be interpreted with caution, as predicted SSD substantially differed from OSD (see discussion)

Annual harvest intensity	0%	10%	25%	50%	75%	100%
Total availability of palm heart ha <sup>-1</sup>	183	124	85	56	42	34
Adult ramets ha <sup>-1</sup>	60	27	11	3	1	0
Seedlings ha <sup>-1</sup>	35073	12853	3866	670	87	0
Total ramet-population size ha <sup>-1</sup>	86188	58849	46833	41775	40407	39890

*The matrix model: ENSO related transient dynamics?*

The very poor match found between the observed stage distribution (OSD) and the stable stage distribution (SSD) predicted by the model suggests that the studied population was away from equilibrium. Transient dynamics can be strong when populations are moved away from their SSD following an unusual disturbance [14, 45]. The 1997-98 El Niño Southern Oscillation (ENSO) was one of the strongest ever recorded [46], causing a water shortage and high temperatures at La Planada, and a pause in flowering bud production for *P. acuminata* [9]. Considering that our population census was carried out in 2002, only 4 years after this ENSO, *P. acuminata* observed distribution may be reflecting this severe disturbance.

Martínez-Ramos et al. [47] studied the effects of the 1997-98 ENSO on the vital rates of the understory palm *Chamaedorea elegans* in Mexico, and found a strong increase in mortality and a decrease in fecundity during the dry season, and increases in leaf production and flowering during the rainy season following El Niño. Understanding how *P. acuminata* population dynamics at La Planada might have been affected by this event is not easy with available data, but some speculations can be made. An increase in seedling and juvenile mortality during the ENSO, for example, could explain the discrepancies between the OSD and SSD for juvenile 1 and 2. Similarly, an episodic reproductive outburst after the ENSO, when drought conditions ended, could explain the observed seedling overabundance. Episodic recruitment events have been reported to produce population models where SSD is different from current observations [14, 45, 49]. As ENSO-related droughts are likely to become more frequent and severe due to global warming [48], the consequences of such climatic change on long-lived plant fitness and sustainable management of NTFPs should be urgently assessed.

Several studies have shown that the transient potential of a projection matrix model may be affected by model design [14, 49], in particular by matrix size and complexity [15]. Our choice for a time-specific model required establishing several size classes of similar duration (see Methods – population dynamics). Although some of the published models for palms have similar matrix sizes [8, 50], the small number of individuals in our larger classes might have introduced some error into the model [11, 19]. Separating the effect of the species' life history from that caused by model complexity is challenging [49]. However, we believe that our choice of a time-specific model was instrumental in revealing the influence of environmental stochasticity, an effect that could have been overlooked by a short-term study of mortality and recruitment rates in a 'normal' year. Moreover, in areas where long-term field monitoring studies can be interrupted by social causes, like warfare or heavy logging, time-specific models have the potential to provide information urgently needed to make management decisions.

To what extent, then, can we draw conclusions from our matrix model? Williams et al. [14] in a review of 46 published matrix models, found that 20% of the studied populations were far from their predicted stage distributions; those studies yielded estimates of population metrics that could be quite inaccurate, with important effects on near-term projections of population size and growth rate. Thus, for example, when transient dynamics are in place, the asymptotic population growth rate ( $\lambda$ ) would overestimate near-term population growth rate for populations with individuals concentrated in stages with low reproductive value. Hence, Table 3 should be interpreted with caution, as harvest could have a stronger effect on population size.

The asymptotic growth rate  $\lambda$  of *P. acuminata* was higher than that of most other understory palms studied to date [see 17 for a comparison of demographic parameter among clonal understory palms]. The observed and predicted (SSD) inverted-J population structure, with a dominance of juveniles, as well as the matrix simulation carried out without vegetative reproduction entries, indicate the importance of shoot recruitment for the population dynamics of *P. acuminata*. The role of forest dynamics on this vegetative growth requires further study [e.g. 51].

Some studies of clonal plants have reported an increase in ramet production and growth after harvesting ramets from a clone [52, 53]; however, preliminary results of experimental harvest treatments that we conducted on 100 genets (20 individuals per treatment, 4 treatments, 1 control; monitored over 21 months) suggest that this is not the case for *P. acuminata* [R. Bernal & J. Bittner unpublished data]. We urge caution in interpreting these results, though, as long-term density-dependent responses to harvest at the population level were not evaluated [see 54].

Our results reinforce the view that management decisions for NTFP should not be based on  $\lambda$  values alone [11, 13]. This could be especially true when dealing with clonal plants and ramet-based models, and when the observed population distribution deviates substantially from predicted stable distribution [55]. Ideally, populations with contrasting harvest levels should be evaluated, so that changes in  $\lambda$  and in population size, or in the size of important categories (*i.e.*, adult and harvestable sizes), relative to the undisturbed situation, could be attributed to harvest [8, 13; *e.g.* 5]. Latest advancements in the field of matrix projection models promise to bring demographic models much closer to the real world, in particular in the analysis of effects of spatial and temporal environmental variation on populations [45].

### *Constraints and advantages for sustainable palm heart extraction from P. acuminata*

*Prestoea acuminata* exhibits some advantageous traits for sustainable harvest. (1) It is one of the most common trees in the study area; (2) palm heart extraction does not imply the death of the genetic individual; (3) ramet population is expected to grow in the long term; and (4) stems appropriate for extraction belong to a category with a minimal contribution to observed ramet density and to the ramet population growth.

On the other hand, this species exhibits a number of disadvantageous characteristics. Ramets exploited for palm heart are old ( $\approx$  23-40 yr), which means that their replacement takes many years. *P. acuminata* displays a low-yield genet architecture, with a maximum of 2-3 harvestable stems per mature plant, *i.e.*, an average of 127 palm hearts ha<sup>-1</sup> in our survey. These figures are considerably lower than those of related palms. The single-stemmed *Euterpe edulis* has densities of up to 500-650 harvestable individuals per ha and requires about 5-10 years to reach harvest size [5]; multi-stemmed *Euterpe oleracea*, with 4-8 well developed stems per mature palm, reaches harvest size in 3-6 yr [56]; and cultivated *Bactris gasipaes* can be harvested in 2-5 yr, producing up to 4000- 7200 palm hearts per hectare [57].

Palm heart harvest from *P. acuminata* has also a strong effect on sexual recruitment. Some demographic studies on solitary palms have found that, under natural conditions, relatively few individuals are responsible for a large percentage of the population's reproductive output [19, 58]. *P. acuminata* population structure suggests a strong dependence of a relatively large population (788 genets ha<sup>-1</sup> on average), on a proportionally small number of genetically effective ramets (31 adult ramets ha<sup>-1</sup> on average). These individuals are responsible for genetic diversity and structure, demographic structure, and spatial distribution patterns for the entire population. A genet-based model for *P. acuminata* population, as well as population genetic studies (especially neighborhood size estimates), would improve our results and would help to accurately assess the minimum number of fruiting ramets that should be maintained in the forest [*e.g.*, 58].

### **Implications for conservation**

Our results show that the sustainable harvest potential of *P. acuminata* under natural conditions is too low to be economically viable. However, sustainable household extraction, as for traditional consumption by Indians and campesinos, is possible. In order to achieve a sustainable palm heart yield while providing ecological benefits, we recommend that annual extraction should not exceed 10% of all harvestable stems, *i.e.* 5-31 palm hearts ha<sup>-1</sup> in our current population. This would leave an average of 28 adults ha<sup>-1</sup> (0-108 adults ha<sup>-1</sup>; *SD* =28.96). As a comparison, the management strategy for the Brazilian palm *Euterpe edulis* in the Atlantic forest is to maintain 50-60 seed trees ha<sup>-1</sup> [58]. We would like to emphasize that our management recommendations are not based on the matrix model alone, but on the species' demography

as a whole (*i.e.* growth rates, population structure, age estimates, genet architecture, etc). We also recommend allowing fruiting, rotating individuals or plots, and establishing evaluation procedures to adjust harvest quotes. Extraction should be permitted only outside La Planada, and should be permanently monitored, as it is imperative to be able to compare unharvested population dynamics with those of harvested populations on a long-term basis. Moreover, 'undisturbed' populations inside the Reserve could serve as an old-growth genetic source for harvested populations outside it [see 59].

Some studies have shown how a culturally driven extraction can become an uncontrolled, nontraditional source of income [60, 61]. Since informal stalls selling *P. acuminata* palm hearts were observed during Holy Week at villages near our study site, quantitative data on *P. acuminata* local palm heart demand, consumption motivations and preferences should be obtained [60]. Current and past harvest practices [11, 62], traditional ecological knowledge and traditional resource management of the species should also be studied in detail [63]. In this paper we have provided ecological information necessary to discuss and implement a participatory, adaptive management plan for *Prestoea acuminata*. This management plan should include all stakeholders, and institutions such as the Catholic Church, in order to accommodate cultural use while guaranteeing resource sustainability.

## Acknowledgements

We are grateful to Reserva Natural La Planada staff and forest for their hospitality, and to Instituto de Investigación de Recursos Biológicos Alexander von Humboldt and Banco de la República (Proyecto 877-1998) for their funding. This work would not have been possible without the valuable, and good-humored, field assistance of Carlos Caguasango, Olga Lucía Guzmán and Francisco Guanga. Special thanks to Martha Vallejo, Arturo Gálvez, Natalia Córdoba and Eduardo Zea for their help and encouragement; and to Christopher Dick, Gloria Galeano and Allen Schlossman for valuable suggestions on earlier versions of the manuscript. Pieter Zuidema and two anonymous reviewers provided insightful comments that significantly improved the manuscript.

## References

- [1] Bernal, R., C. Torres, N. García, C. Isaza, J. Navarro, M. I. Vallejo, G. Galeano and H. Balslev. 2011. Palm management in South America. *The Botanical Review* 77. doi:10.1007/s12229-011-9088-6.
- [2] Borchsenius, F. and M. Moraes R. 2006. Diversidad y usos de palmeras andinas (Arecaceae). In: *Botánica económica de los Andes Centrales*. Moraes R, M., Øllgaard, B., Kvist, L.P., Borchsenius, F. and Balslev, H. (eds.), pp.412–433. Universidad Mayor de San Andrés, La Paz.
- [3] Jhonson, D. 2002. Palmitos (*Euterpe* spp.). In: *Explotando el Mercado verde: Certificación y manejo de productos forestales no maderables*. Shanley, P., Pierce, A., Laird, S. and Guillén, A. (eds.), pp.92-101. Nordan Comunidad, Montevideo, Uruguay.
- [4] Galetti, M. and Fernandez, J.C. 1998. Palm heart harvesting in the Brazilian Atlantic forest: changes in industry structure and the illegal trade. *Journal of Applied Ecology* 35: 294-301.
- [5] Quitete Portela, R.d.C., Bruna, E.M. and Maes dos Santos, F.A. 2010. Demography of palm species in Brazil's Atlantic forest: a comparison of harvested and unharvested species using matrix models. *Biodiversity Conservation* 19: 2389-2403.
- [6] Orlande, T., Laarman, J. and Mortimer, J. 1996. Palmito sustainability and economics in Brazil's Atlantic coastal forest. *Forest Ecology and Management* 80: 257-265.
- [7] Vallejo, M. I., Valderrama, N., Bernal, R., Galeano, G., Arteaga, G. and Leal, C. In press. Producción de palmito de *Euterpe oleracea* en la Costa Pacífica colombiana: estado actual y perspectivas. *Colombia Forestal* 14.
- [8] Zuidema, P.A. and Boot, R.G.A. 2000. Demographic constraints to sustainable palm heart extraction from a sub-canopy palm in Bolivia. In: *Demography of exploited tree species in the Bolivian Amazon*. Zuidema, P. (ed.), pp.53-79. PROMAB Scientific Series 2, Riberalta, Bolivia.

- [9] Guzmán, O. 2000. *Propagación natural y artificial de Prestoea acuminata (Arecaceae) en la Reserva Natural La Planada, Nariño, Colombia*. Trabajo de Grado, Universidad de Nariño, Pasto, Colombia.
- [10] Balslev, H. and Henderson, A. 1987. Palm portrait, *Prestoea palmito*. *Principes* 31: 11.
- [11] Galeano, G., Bernal, R., Isaza, C., Navarro, J., García, N., Vallejo, M.I. and Torres, C. 2010. Evaluación de la sostenibilidad del manejo de palmas. *Ecología en Bolivia* 45(3): 85-101.
- [12] Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. 2nd ed. Sinauer Associates, Inc. Sunderland, Massachusetts.
- [13] Schmidt, I.B., Mandle, L., Ticktin, T. and Gaoue, O.G. 2011. What do matrix population models reveal about the sustainability of non-timber forest product harvest? *Journal of Applied Ecology* 48. doi:10.1111/j.1365-2664.2011.01999.x
- [14] Williams, J.L., Ellis, M.M., Bricker, M.C., Brodie, J.F. and Parsons, E.W. 2011. Distance to stable stage distribution in plant populations and implications for near-term population projections. *Journal of Ecology* 99: 1171-1178. doi:10.1111/j.13652745.2011.01845.x
- [15] Zuidema, P.A. and Boot, R.G.A. 2002. Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon. Impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology* 18: 1-31.
- [16] Escalante, S., Montaña, C. and Orellana, R. 2004. Demography and potential extractive use of the liana palm, *Desmoncus orthacanthos* Martius (Arecaceae), in southern Quintana Roo, Mexico. *Forest Ecology and Management* 187: 3-18.
- [17] Navarro, J.A., Galeano, G. and Bernal, R. 2011. Impact of leaf harvest on populations of *Lepidocaryum tenue*, an Amazonian understory palm used for thatching. *Tropical Conservation Science* 4(1): 25-38.
- [18] Bernal, R. 1998. Demography of the vegetable ivory palm *Phytelephas seemanii* in Colombia, and the impact of seed harvesting. *Journal of Applied Ecology* 35: 64-74.
- [19] Pinard, M. 1993. Impacts of stem harvesting on populations of *Iriartea deltoidea* (Palmae) in an extractive reserve in Acre, Brazil. *Biotropica* 25: 2-14.
- [20] Pinard, M.A. and Putz, F.E. 1992. Population matrix models and palm resource management. *Bulletin de l'Institut Français d'Études Andines* 21: 627-649.
- [21] Cabrera Galvis, M., Amorocho Llanos, D., Moreno, P., Jaramillo, M.F. and Cadavid, J. 1997. *Reserva Natural La Planada*. Fundación FES, Cali, Colombia.
- [22] Mendoza-Cifuentes, H. and Ramírez-Padilla, B. 2000. *Plantas con flores de La Planada*. IAvH – FES – WWF, Bogotá, Colombia.
- [23] Instituto Geográfico Agustín Codazzi. 1977. *Zonas de vida o formaciones vegetales de Colombia*. Instituto Geográfico Agustín Codazzi, Bogotá, Colombia.
- [24] Samper K., C. and Vallejo, M.I. 2007. Estructura y dinámica de poblaciones de plantas en un bosque andino. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 31(118): 57-68.
- [25] Vallejo, M. I., Samper, C., Mendoza, H. and Otero, J.T. 2004. La Planada forest dynamics plot, Colombia. In: *Forest diversity and dynamism: Findings from a network of large-scale tropical forest plots*. Losos, E. and Leigh, E.G. (eds.), pp.517-526. University of Chicago Press, Chicago.
- [26] Dransfield, J., Uhl, N.W., Asmussen, C.B., Baker, W.J., Harley, M.M. and Lewis, C.E. 2008. *Genera Palmarum. Evolution and Classification of the Palms*. Royal Botanic Gardens, Kew.
- [27] Knudsen, H. 1995. *Demography, palm-heart extractivism, and reproductive biology of Prestoea acuminata (Arecaceae) in Ecuador*. MSc Thesis, Aarhus University, Denmark.
- [28] Henderson, A. 2002. *Evolution and ecology of palms*. The New York Botanical Garden Press.
- [29] Lugo, A.E. and Rivera Batlle, C.T. 1987. Leaf production, growth rate, and age of the palm *Prestoea montana* in the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology* 3: 151-161.
- [30] Caswell, H. 1985. The evolutionary demography of clonal reproduction. In: *Population biology and evolution of clonal organisms*. Jackson, J.B.C. Buss and R.E. Cook (eds.), pp.187-224. Yale University Press, London.
- [31] Huenneke, L.F. and Marks, P.L. 1987. Stem dynamics of the shrub *Alnus incana* spp. *rugosa*: transition matrix models. *Ecology* 68: 1234-1242.

- [32] Crowder, L.B., Crouse, D.T., Heppell, S.S. and Martin, T.H. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* 4: 437-445.
- [33] Zuidema, P.A. and Werger, M.J.A. 2000. Life history of a clustered understorey palm: an integrated analysis of genet and ramet demography using population matrix models. In: *Demography of exploited tree species in the Bolivian Amazon*. Zuidema, P. (ed.), pp.81-107. PROMAB Scientific Series 2, Riberalta, Bolivia.
- [34] Hood, G.M. 2010. PopTools version 3.2.3. <http://www.poptools.org>
- [35] Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. W.H. Freeman and Company, New York.
- [36] Álvarez-Buylla, E.R. and Slatkin, M. 1991. Finding confidence limits on population growth rates. *Tree* 6: 221-224.
- [37] Olmsted, I. and Álvarez-Buylla, E.R. 1995. Sustainable harvesting of tropical trees: demography and matrix models of two palm species in Mexico. *Ecological Applications* 5: 484-500.
- [38] Lieberman, M., Lieberman, D. and Vandermeer, J.H. 1988. Age-size relationships and growth behavior of the palm *Welfia georgii*. *Biotropica* 20: 270-273.
- [39] Piñero, D., Sarukhán, J. and Alberdi, P. 1982. The costs of reproduction in a tropical palm, *Astrocaryum mexicanum*. *Journal of Ecology* 70: 473-481.
- [40] Avalos, G. and Fernández Otárola M. 2010. Allometry and stilt root structure of the neotropical palm *Euterpe precatoria* (Arecaceae) across sites and successional stages. *American Journal of Botany* 97(3): 388-394.
- [41] Hutchings, M.J. and D.K. Wijesinghe. 1997. Patchy habitats, division of labour and growth dividends in clonal plants. *Trends in Ecology and Evolution* 12: 390-394.
- [42] Chazdon, R.L. 1988. Sunflecks and their importance to forest understory plants. *Advances in Ecological Research* 18: 1-63.
- [43] Stuefer, J.F., De Kroon, H. and During, H.J. 1996. Exploitation of environmental heterogeneity by spatial division of labour in a clonal plant. *Functional Ecology* 10: 328-334.
- [44] Chazdon, R.L. 1992. Patterns of growth and reproduction of *Geonoma congesta*, a clustered understory palm. *Biotropica* 24: 43-51.
- [45] Salguero-Gómez, R. and de Kroon, H. 2010. Matrix projection models meet variation in the real world. *Journal of Ecology* 98: 250-254.
- [46] McPhaden, M.J. et al. 1999. Genesis and evolution of the 1997-98 El Niño. *Science* 293: 950-954.
- [47] Martínez-Ramos M., Anten, N.P.R. and Ackerly, D.D. 2009. Defoliation and ENSO effects on vital rates of an understorey tropical rain forest palm. *Journal of Ecology* 97: 1050-1061.
- [48] Timmerman, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. and E. Roeckner. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398: 694-696.
- [49] Stott, I., Franco, M., Carslake, D., Townley, S. and Hodgson, D. 2010. Boom or burst? A comparative analysis of transient population dynamics in plants. *Journal of Ecology* 98: 302-311.
- [50] Rodríguez-Buriticá, S., Orjuela, M.A. and Galeano, G. 2005. Demography and life history of *Geonoma orbygniana*: An understorey palm used as foliage in Colombia. *Forest Ecology and Management* 21: 329-340.
- [51] Fantini, A.C. and Guries, R.P. 2007. Forest structure and productivity of palmitero (*Euterpe edulis* Martius) in the Brazilian Mata Atlântica. *Forest Ecology and Management* 242: 185-194.
- [52] Damman, H. and Cain, M.L. 1998. Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*. *Journal of Ecology* 86: 13-26.
- [53] Eriksson, O. 1993. Dynamics of genets in clonal plants. *Trends in Ecology and Evolution* 8: 313-316.
- [54] Freckleton, R.P., Silva Matos, D.M., Bovi, M.L.A. and 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. *Journal of Applied Ecology* 40: 846-858.
- [55] Zuidema, P.A. and Zagt, R.J. 2000. Using population matrices for long-lived species: a review of published models for 35 woody plants. In: *Demography of exploited tree species in the Bolivian Amazon*. Zuidema, P (ed.), pp.81-107. PROMAB Scientific Series 2, Riberalta, Bolivia.



- [56] González Pérez, H. and Arango Moreno D.A. 2002. Efectos del clima y la densidad sobre la dinámica poblacional de *Euterpe oleracea* Mart. (Arecaceae) en un bosque neotropical. *Crónica Forestal y del Medio Ambiente* 17: 5-22.
- [57] Mora-Urpí, J. 2002. Presente y futuro del palmito en Costa Rica. *Agronomía Costaricense* 26: 95-100.
- [58] Reis, M.J., Fantini, A.C., Nodari, R.O., Reis, A., Guerra, M.P. and Mantovani, A. 2000. Management and conservation of natural populations in Atlantic rain forest: the case study of palm heart (*Euterpe edulis* Martius). *Biotropica* 32: 894-902.
- [59] Sezen, U.U., Chazdon, R.L. and Holsinger, K.E. 2007. Multigenerational genetic analysis of tropical secondary regeneration in a canopy palm. *Ecology* 88: 3065-3075.
- [60] Sylvester, O. and Avalos, G. 2009. Illegal palm heart (*Geonoma edulis*) harvest in Costa Rican national parks: Patterns of consumption and extraction. *Economic Botany* 63: 179-189.
- [61] Vergara, L.K. and Bernal, R. 2004. Demografía de *Ceroxylon alpinum*, una palma de cera amenazada: impacto de la extracción de ramo para Semana Santa. In: *Libro de Resúmenes Octavo Congreso Latinoamericano y Segundo Colombiano de Botánica*. Rangel-Ch., J.O., Aguirre-C., J. and Andrade-C., M.G. (eds.), pp. 207. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá.
- [62] Ticktin, T. 2004. The ecological implications of harvesting non-timber forest products. *Journal of Applied Ecology* 41: 11-21.
- [63] Ticktin, T. and Johns, T. 2002. Chinanteco management of *Aechmea magdalenae*: implications for the use of TEK and TRM in management plans. *Economic Botany* 56: 177-191.

**Appendix 1.** Size classes of *Prestoea acuminata* ramet population at La Planada Reserve, Colombia. Age estimates are based on average pinna increase rate, and include seedling stage duration for modeling purposes (but vegetatively-produced ramets bypass this stage). Genet size class corresponds to the largest alive ramet in the genet. Number of pinnae refers to one side of the rachis in the newest leaf.

Size class	Number of ramets & genets (1.5 ha)	Average number of ramets per genet	Class duration estimate (years)	Annual survival (estimated)	Annual survival (observed)	Age estimate (years)
1 Seedlings	30520 30520	1	5.3	0.4209	NA	0 - 5.3
2 Juveniles1, stemless ramets with 2-9 pinnae	1052 311	1	5.4	NA	0.9293	5.31 - 10.71
3 Juveniles2, stemless ramets with 10-17 pinnae	1342 177	1.02	5.5	0.9949	0.9714	10.72 - 16.22
4 Clonal juveniles1, 18-26 pinnae Clonal reproduction begins	1305 136	1.51	5.8	0.9010	1.0000	16.23 - 22.03
5 Clonal juveniles2, 27-35 pinnae	713 112	3.06	5.93	0.9607	1.0000	22.04 - 27.97
6 Subadults1, stems 0.01-1.79m	562 173	6.42	6.2	0.8676	0.9924	27.98 - 34.18
7 Subadults2, stems 1.8-4.19m	233 131	9.22	6.4	0.9150	1.0000	34.19 - 40.59
8 Subadults3, stems 4.2-7.49m Minimum harvestable size	132 103	12.43	6.72	0.7981	0.9121	40.6 - 47.32
9 Adults1, stems 7.5-10.23m Sexual reproduction begins	29 23	19.78	7.02	0.8819	1.0000	47.33 - 54.35
10 Adults2, stems 10.24-12.4m	12	18.42	7.4	0.8884	1.0000	54.36 - 61.76
11 Adults3, stems 12.41-14.05m	5 4	17.75	7.6	NA	1.0000	61.77 - 69.37

**Appendix 2.** Annual transition matrix A describing the flux of *Prestoea acuminata* ramets from one year to the next at La Planada Reserve, Colombia. From the pooled data of fifteen 0.1 ha plots

	1	2	3	4	5	6	7	8	9	10	11
1	0.4159								228.3580	919.7754	0.0000
2	0.0050	0.7996		0.2072	0.6063	0.6313	0.5630	0.4902	0.3820	0.3352	0.4459
3		0.1298	0.8237								
4			0.1477	0.7963							
5				0.1047	0.8315						
6					0.1292	0.7867					
7						0.0810	0.8190				
8							0.0960	0.7505			
9								0.0476	0.8115		
10									0.0703	0.8219	
11										0.0665	0.8249

**Appendix 3.** Elasticity matrix for a *Prestoea acuminata* ramet population at La Planada Reserve, Colombia

	1	2	3	4	5	6	7	8	9	10	11
1	0.0011								0.0007	0.0009	0.0000
2	0.0016	0.1710		0.0150	0.0212	0.0109	0.0034	0.0010	0.0002	0.0000	0.0000
3		0.0532	0.1950								
4			0.0532	0.1681							
5				0.0382	0.1465						
6					0.0171	0.0513					
7						0.0062	0.0221				
8							0.0028	0.0070			
9								0.0018	0.0062		
10									0.0009	0.0034	
11											0.0001