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Research article

Impact of leaf harvest on populations of *Lepidocaryum tenue*, an Amazonian understory palm used for thatching

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Abstract

Leaves of the palm *Lepidocaryum tenue* are one of the most prized thatching materials in northwestern Amazonia. We studied the population dynamics of this stoloniferous palm in Colombian Amazonia, using ramet-based Lefkovitch matrices, and assessed the impact of leaf harvest on population structure and dynamics, through experimental defoliation. Leaf production rate of unharvested palms ranged between 0.93 leaves per year in seedlings and 1.71 in adults. Vegetative shoots produced through stolons are more important than seedlings for maintaining the population; stolons act also as a reserve to overcome damage in the population. The potential population growth rate was 8.3 % per year ($\lambda = 1.083$). Juveniles had the highest contribution to population growth, and permanence was the most important life parameter. Thus, harvest of leaves for thatching can jeopardize the population if juveniles are also harvested. An initial harvest intensity of more than 50% of the leaves in a crown, or leaving the palm with fewer than four leaves, would have a negative impact on leaf production. Although matrix modeling suggests that all adult ramets can be harvested, this must be taken with caution, as clonal integration may play an important role in population dynamics. Long-term harvest of *Lepidocaryum* leaves is possible, if plots are harvested in turns of four years, thus allowing palms to recover from the previous harvest. A better control on the quality of the braided tiles sold in the market would also ensure their longer duration, thus reducing the pressure on the resource.

Key words: Arecaceae; demography; NTFP; palm thatch; sustainable harvest

Resumen

Las hojas de *Lepidocaryum tenue* son uno de los materiales de techado más apreciados en el noroccidente de Amazonia. Estudiamos la dinámica poblacional de ramets de esta palma estolonífera en la Amazonia colombiana, usando matrices de Lefkovitch, y evaluamos el impacto de cosecha de hojas sobre la estructura y dinámica poblacional usando experimentos de defoliación. La producción anual de hojas en ramets no cosechados fluctuó entre 0.93 hojas en plántulas y 1.71 en adultos. Los brotes producidos por estolones son más importantes que las plántulas para el mantenimiento de la población; los estolones funcionan también como reserva para recuperarse de daños. La poblacional tiene un crecimiento potencial del 8.3% anual ($\lambda = 1.083$). Los juveniles tuvieron la contribución más alta al crecimiento poblacional, y la permanencia fue el parámetro de vida más importante. La cosecha de hojas puede poner en peligro la población si se cosechan juveniles. Se encontró que una intensidad de cosecha de más de 50% de hojas, o dejar menos de 4 hojas por tallo, podría tener impacto negativo en la producción de hojas. Aunque el modelo matricial sugiere que todos los ramets adultos se pueden cosechar, esto debe tomarse con precaución, pues la integración clonal puede ser importante en la dinámica poblacional. La cosecha de hojas a largo plazo es posible, si las palmas se cosechan cada cuatro años, permitiendo así su recuperación. Se recomienda también un mejor control de calidad de los techos vendidos en el mercado, para asegurar mayor duración y menor presión sobre el recurso.

Palabras clave: Arecaceae; cosecha sostenible; demografía; PFNM; techos de palma.

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Introduction

Thatch is a common sheltering cover in many areas of the world, and in some places it is the only available economic option [1]; in many parts of the world, however, traditional thatch is being progressively replaced by other roofing materials, such as tin [1, 2, 3]. In tropical areas, leaves of palms (Arecaceae) are probably the most important thatching material [4], due to their large size and resistance [5]. Although leaves of many species are used for this purpose, people in any particular area prefer one or a few species, which are deemed more durable.

Palm leaf harvest can lead to overexploitation as a result of malpractice or due to an overestimation of the resource [6]. Such overexploitation can negatively impact the survival, growth and reproduction of individuals, and the population's structure and dynamics, thus jeopardizing its permanence. Several studies have assessed the impact of leaf harvest on population parameters [7, 8, 9, 10]. These studies have shown that leaf harvest can have a minor effect on leaf production and reproduction; in some cases, mild defoliation can even stimulate leaf production, although leaf quality can decrease [10]. However, Flores and Ashton [6] found that leaf harvest can have a negative impact on reproduction and on the production of new leaves and new ramets.

Short-term studies, however, do not reveal the real effect of leaf harvest, as palms have reserves that allow them to tolerate a reduction in foliar area [9]. Endress *et al.* [11], for example, found that after six years of leaf harvest, plants of *Chamaedorea radicalis* had an increase in mortality and a decrease in reproductive activity, growth, and population growth rate (λ). Other studies have assessed the effect of leaf harvest using population matrix models, taking λ as an indicator of sustainable harvest. In some cases, prospective analyses have been used to predict a population's response to different leaf harvest regimes [12, 13]; in other cases, population matrix models have been combined with defoliation experiments [e. g., 12].

Prospective analyses, however, do not take into account the fact that some vital parameters have a wider variation than others and thus can have different impacts on λ [14]. As a way out of this inconvenience, some authors have used life table response experiments (LTRE), which reveal changes in λ as a result of changes in any of the vital parameters [15]. These kinds of studies are fundamental for the management of species used for their leaves, as they provide vital information for planning harvest intensity, thus leading to a sustainable management.

Along the Caquetá, Putumayo, and Amazon rivers, in Colombian Amazonia, the preferred palm for thatching is the *puy* or *caraná* palm (*Lepidocaryum tenue*), a stoloniferous understory palmlet with palmately divided leaves. This species has been traditionally used by the Andoke, Bora, Miraña, Muinane, Nonuya, Ticuna, Witoto, and Yucuna Indians to thatch their houses and their large communal *malokas* [16, 17, 18, 19]. However, near the Colombian town of

Leticia and the adjacent Brazilian town of Tabatinga, on the Amazon River, population growth, immigration, and tourism have generated in recent years an increasing demand for leaves of this palm. They are sold as large tiles called *paños* or *criznejas*, 3 m long and 1 m wide (with an effective roof coverage of ca. 0.6 m²), made of about 115 *Lepidocaryum* leaves braided on a split palm stem; these tiles are now a common trade item. This trade has caused an overharvest near the Indian villages, leading to the local exhaustion of the resource, and forcing local people to look for leaves in more distant places.

This study seeks to provide tools for the appropriate management of *Lepidocaryum*. In particular, we investigated population structure and dynamics, the impact of intensive leaf harvest on population growth and individuals' survival, and the optimal harvest level that would guarantee a sustainable production of leaves.

Methods

Species description

Lepidocaryum tenue is a small, dioecious, clonal palm that spreads by means of stolons up to 2 m long [17, 20]. Each individual has many stems up to 6 m tall and 4 cm in diameter. The crown has usually 5-12 leaves (9.5 on average), with a petiole up to 1 m long, and a lamina divided into 2-16 segments, 29-84 cm long, 5-8 cm wide. The inflorescence is interfoliar, erect, with a peduncle up to 1 m long, and 2-18 rachillae up to 15 cm long, arranged along a 10-20 cm long rachis. The fruits are elliptical to globose, up to 3 cm long and 2 cm diameter, and are covered by imbricate scales that turn orange-red at maturity; each fruit has usually one seed. The palm forms large stands in the forest understory, mainly on deep, well-drained *terra firme* soils [21], but it grows also in poorly drained soils that are temporarily flooded [20, 21].

Study site

The study was carried out at El Zafire Biological Station, 24 km NNE of Leticia, Amazonas, Colombia, at 4°00'20" S, 69°53'55" W (Fig. 1); elevation is 80 m. The Biological Station includes three forest types (on white sands, temporarily flooded, and *terra firme*), on which four permanent research plots have been established [22]. The population of *L. tenue* we studied was located in *terra firme* forest.

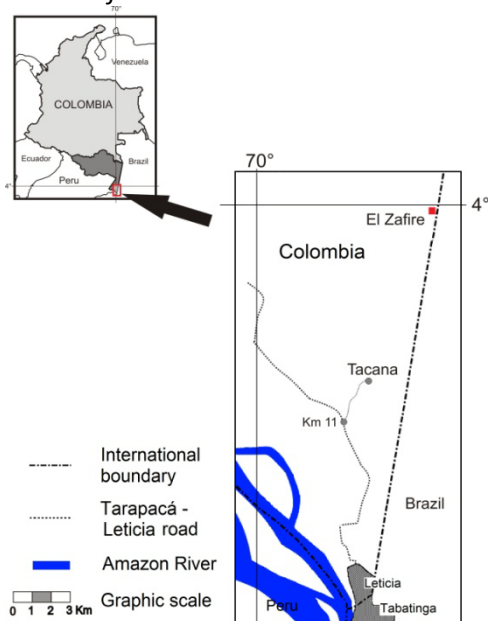


Fig. 1. Location of El Zafire Biological Station.

Measurements

In June 2007 we established three sampling units of 0.04 ha each (20 x 20 m), one unit nested within a one hectare permanent plot and the remaining two nested in a 20 ha permanent megaplot; all sampling units were separated more than 100 m from each other. We tagged and recorded all individuals of all stage classes in the three 0.04 sampling units. Additionally, 25 quadrants of 0.01 ha each (10 x 10 m) were added later to increase the number of individuals of seedlings and juveniles, for a total sampling area of 0.37 ha, where 1653 ramets were measured and marked (Table 1). Because the long stolons of different individuals usually cross over each other, assigning ramets to one individual genet would have required digging the stolons, which is a destructive operation. In order to avoid damage, we constructed a ramet-based model.

In all ramets that still did not have an aerial stem, we counted the number of leaves and the number of veins of the youngest leaf. In all ramets with a recognizable stem we measured stem height and counted the number of leaf scars along the stem, the number of leaves, and the number of inflorescences and infructescences. In all ramets we marked with flagging tape the petiole of the youngest expanded leaf, in order to determine the leaf production rate, which was later combined with the number of leaf scars to determine stem age.

We measured leaf and inflorescence production after 7 and 14 months; in plants without an aerial stem, we counted the number of veins of the most recently expanded leaf. In the same periods we recorded also any new seedlings or vegetative shoots, and death of ramets.

We defined size classes based on leaf structure, number of primary veins, stem development, and presence of reproductive structures (Table 1). We included as seedlings and vegetative shoots all small plants with bifid leaves; we counted as juveniles all individuals with no aerial stem and at least four segments in the newest leaf, and we measured their growth as a function of the increase in the number of primary veins from one leaf to the next one. For ramets with an aerial stem, we divided size classes on account of their number of leaf scars and stem height at the time of the first flowering; we calculated their growth as a function of their leaf production rate and internode length. Leaf production rates found between the first, second, and third data collection events were averaged per size classes and adjusted to one year.

For each fruiting ramet, we counted the number of rachillae per infructescence, and the number of fruits per rachilla. With this data we calculated the average number of fruiting ramets and of fruits per size class; additionally, 100 seeds collected from six palms growing near the plots were sowed in a 1.5 m² grid located adjacent to a permanent *Lepidocaryum* plot; the seeds were covered with a thin soil layer, and germination was checked after 7 and 14 months. We combined fruit production and percentage of germination to estimate the value of fecundity that was used in the matrix. Fecundity of each class was calculated using the equation proposed by Caswell [23].

As both male and female ramets produce new shoots, adults of both genders were used to build the transition matrix. Sexual seedlings and vegetative shoots were differentiated, in order to evaluate the contribution of each reproductive strategy to population growth rate; to differentiate between individuals originated through sexual and asexual reproduction, the area near the root was dug to check for any clonal connection.

Because stolons contribute new ramets to the population, we treated stolon production as a form of fecundity, and calculated the contribution of each stolon-producing size class, employing the same equation used to calculate fecundity. In order to assign values of stolon

production to each size class, we dug out five ramets with no aerial stem, and 20 ramets having an aerial stem, and made a regression between ramet size and number of stolons per ramet. We used the equation of this regression to estimate the proportion of stolons contributed by each size class. Thus, the number of new shoots that entered the population was distributed among size classes according to this proportion.

Although the Lefkovitch matrices we used are based on size classes rather than age classes, we calculated the age of ramets in order to have a better understanding of the dynamics of palm colonies in relation to leaf harvest. For stemless ramets, we calculated size class duration based on the range in vein number; for ramets with an aerial stem, we used the range in internode number [24]. Thus, duration of class i was calculated as $d_i = (m_{i+1} - m_i) / t_i$, where m_i is the lower limit of the class (in number of veins or nodes), m_{i+1} is the lower limit of the next class, and t_i is the annual growth rate (annual vein or leaf production rate). Age of ramets was calculated by adding the duration of size classes. Thus, the maximal age estimated for ramets was that of the tallest ramet found. Age was not used in the matrix model.

We calculated finite growth rate (λ) and its confidence interval, stable stage distribution (SSD), reproductive value, and sensitivity and elasticity of λ , following Caswell [23]. We used a chi-square test to explore differences between the SSD and the observed stage distribution (OSD). We made matrix simulations by modeling two harvest scenarios: harvesting only adults, or harvesting adults and larger juveniles; we selected these two scenarios because both juveniles and adults are exploited by local harvesters, and also because the juvenile classes presented a greater harvest pressure and higher values of elasticity. Simulations were made by multiplying the corresponding life parameters (permanence, growth, retrogression) by a constant $1-i$ (i ranges between 0.00 and 1, and represents the decrease in survival as a result of harvest) [13]. Fourteen-month data were adjusted to 12 months to build annual matrices. All matrices and harvest simulations were made in Microsoft Excel® applying the equations proposed by Caswell (2001).

Experimental leaf harvest

We evaluated the effect of leaf harvest on leaf production rate by experimentally harvesting 240 ramets. These ramets were selected with a local leaf harvester, and harvest was made in the traditional way—an area is selected where palms have petiole and leaf segments longer than 50 cm each, and harvest proceeds from one ramet to the neighboring ones, along the selected path. Harvested ramets were adults (61%) and large juveniles (Juveniles 2 of our model) (39%), the ones usually harvested by local people. We used a randomized design, applying four harvest intensities (100%, 75%, 50%, and 25% of all live leaves on the palm), three repeats for each intensity, and one repeat for each sampling unit— each repeat with sixty ramets. Sixty palms of the demography plots were chosen as control.

The youngest expanded leaf of each harvested ramet was tagged, and leaf production rate was observed after 14 months. We used a Kruskal-Wallis test to check the effect of leaf harvest on the leaf production rate. Difference in leaf production rate among treatments was analyzed by a graphic comparison of their means, considering their confidence intervals.

Results

Density and population structure

We found 1,653 ramets in 0.37 ha, with a range of 55-147 ramets per 100 m² plot. This gives a density of 5,500-14,700 ramets/ha. Genet density is much lower, as a genet has many ramets. Most ramets (49.8%) belonged to the juvenile classes, whereas the density of seedlings was low (6.3%).

Clonal growth and fecundity

Lepidocaryum produces stolons by means of buds located in the lowest nodes (Fig. 2). Stolons are produced at an angle of 120° from each other (i.e., the same phyllotactic pattern of leaves); they are subterranean (ca. 20 cm underground), ringed, and extend up to 2 m long (Fig. 3). Thus, a genet of *Lepidocaryum* is a loose colony of many ramets interconnected underground, and covers a considerable area. The regression equation of stolon number against internode number was $y = 0.0738303 + 0.437218*\sqrt{x}$ ($R^2 = 0.83$; $r = 0.91$; $F_{0.05} = 85.3$; $P < 0.05$). Production of stolons starts at size class Juveniles 2, and their number increases up to an average of 4.17 in Adults 4 (Table 1).

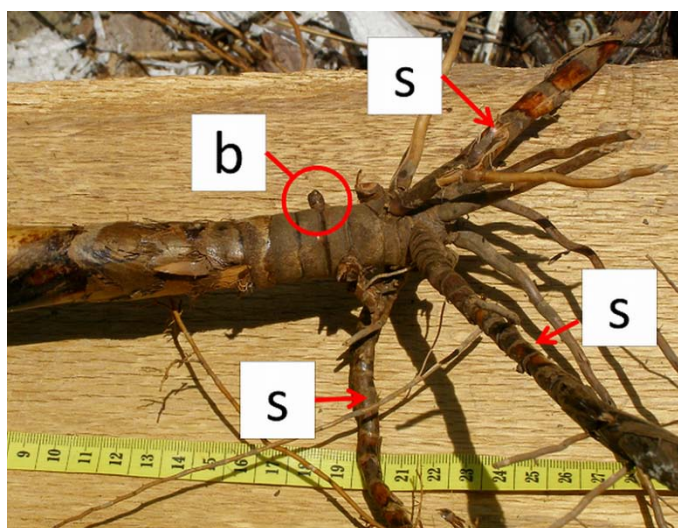


Fig. 2. Production of stolons in *Lepidocaryum tenue*. s, developed stolons; b, bud



Fig. 3. Stems of *Lepidocaryum tenue* dug out to show their connecting stolons.

We were able to assign gender to 65 of the 337 adult ramets studied, which were found with reproductive structures –48 of them were female and 17 were male, i.e., 2.8 males per one female ($\chi^2_{0.05(1)}=3.84$; $\chi^2_c=20.09$). The average number of fruits per ramet was 15 ± 0.98 , with a maximum of 58 fruits in one ramet. The lowest stem height of a fruiting ramet was 21 cm (7 nodes); sexual reproduction usually began at about 60-68 years of age (Table 1). Only four out of the 100 seeds sown had germinated after 18 months, so we used a germination rate figure of 4%.

Ramet growth

Average leaf production rate for all size classes was 1.18 leaves/year (± 0.028 ; $n = 1597$). The leaf production rate increased steadily from 0.93 (± 0.08 ; $n = 194$) leaves per year in sexual seedlings to 1.71 (± 0.2 ; $n = 31$) leaves/year in Adults 4, but had a slightly higher value in vegetative shoots than in juveniles 1 (Table 1).

The annual vein increase rate from one leaf to the next was 0.5 veins on average (± 0.06 veins; $n=1285$); the lowest increase was in Juveniles 2, and the highest increase was in vegetative shoots (Table 1). There was a strong correlation between growth and increase in vein number ($y = 0.933 * x + 1.404$; $R^2 = 0.938$; $F_{0.05} = 9799.4$; $P < 0.001$; $n = 644$), thus showing that vein number is an appropriate variable to estimate growth, as found by Rodríguez-Buriticá *et al.* [24] for *Geonoma*. Average stem elongation per new leaf was 2.78 ± 0.08 cm (range: 0.3-7.1 cm). Vegetative shoots spent less time in their size class (≈ 8 years) than sexual seedlings (≈ 17 years) (Table 1). Maximum estimated longevity was 130 years.

Table 1. Life parameters for the size class of *Lepidocaryum tenue* near Leticia, Colombia.

| Class | Selection criterion | Total ramets | Annual rate of vein increase per leaf | Annual rate of leaf production | Number of fruits per class (fecundity) | Number of stolons per class | Age (with stolon) |
|--------------|---|--------------|---------------------------------------|--------------------------------|--|-----------------------------|-------------------|
| Seedling | Bifid leaf from seeds | 208 | 0.48 ± 0.13 | 0.93 ± 0.083 | | | 16.8 |
| Rhizome | Bifid leaf from rhizome | 366 | 0.91 ± 0.08 | 1.08 ± 0.061 | | | 8.8 |
| Juvenile 1 | Ramets without stem and leaves with up to 18 veins | 362 | 0.58 ± 0.1 | 1.04 ± 0.062 | | | 32.4 (24.4) |
| Juvenile 2 | Ramets without stem, and leaves with ≥ 19 veins and ramets with stems of ≤ 10 rings | 380 | 0.06 ± 0.09 | 1.29 ± 0.060 | | 26 | 53.7 (45.7) |
| Adult 1 | Stem with 11-30 rings; females ramets begin flowering | 148 | | 1.43 ± 0.104 | 11 (0.0025) | 63 | 67.7 (59.7) |
| Adult 2 | Stem with 31-50 rings | 95 | | 1.47 ± 0.120 | 6 (0.0232) | 85 | 81.3 (73.4) |
| Adult 3 | Stem with 51-70 rings | 56 | | 1.56 ± 0.157 | 69 (0.0556) | 93 | 94.2 (86.2) |
| Adult 4 | Stem with ≥ 70 rings | 38 | | 1.71 ± 0.209 | 70 (0.0348) | 99 | 105.8 (97.9) |
| Total | | 1653 | | | 156 | | |

Mortality

Thirty-seven ramets died in 14 months of observation, 40.5% of which were seedlings; the next highest mortalities were those of Adults 4 (18.9%) and Juveniles 1 (16.2%). Most deaths were caused by the fall of tree branches or large leaves of arborescent palms.

Population dynamics

Figure 4 shows the life cycle of *Lepidocaryum tenue*. The finite rate of population increase, λ , was 1.083 (CI=1.04-1.13). This shows that during the study period the population was growing fast. No significant differences were found between SSD and OSD ($\chi^2_{0.05 (7)} = 14.07$; $\chi^2_c = 1.311$).

The highest value of elasticity was that of Juveniles 2 (0.26), especially their permanence (0.21), which means that changes in this parameter or size class will have a large impact on λ . Elasticity decreased towards the upper size classes (Fig. 5). Permanence was the parameter with the highest elasticity value, which means that it is the most important parameter for this population.

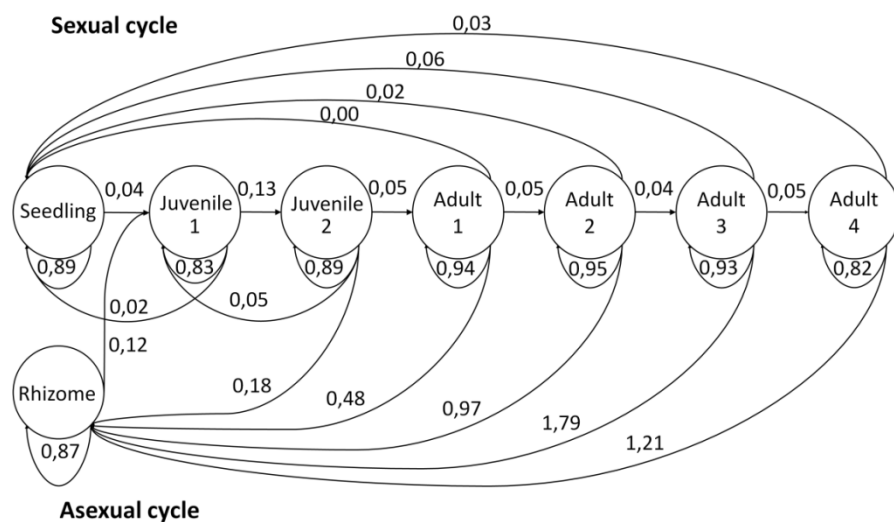


Fig. 4. Life cycle of *Lepidocaryum tenue* near Leticia, Colombia.

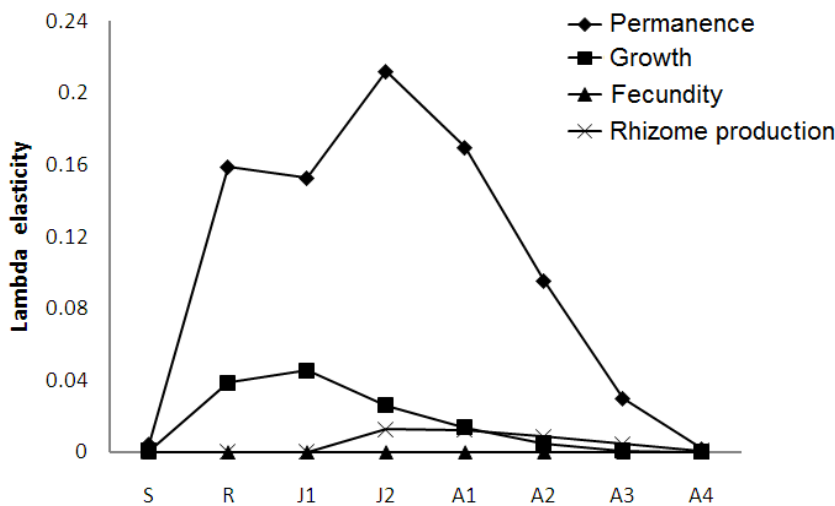


Fig. 5. Elasticity of life parameters in a population of *Lepidocaryum tenue* near Leticia, Colombia. Lambda values are in a logarithmic scale. S, seedling; R, rhizome; J1, juvenile 1; J2, juvenile 2; A1, adult 1; A2, adult 2; A3, adult 3; A4, adult 4.

Harvest experiments

Leaf harvest significantly reduces the annual leaf production rate (KV=25.64; $P < 0.001$). The strongest impact was caused by harvest levels of 75% and 100% of all leaves (Fig. 6).

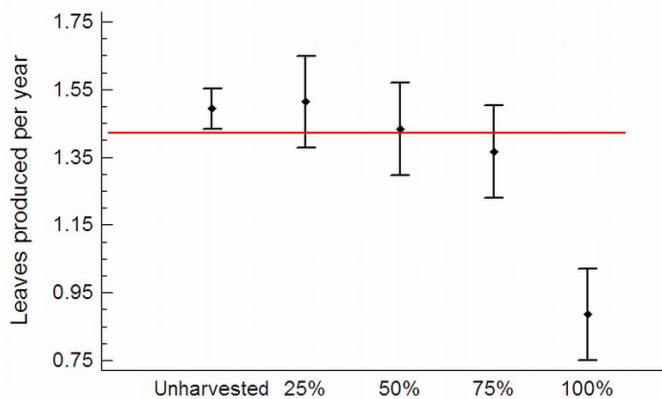


Fig. 6. Average leaf production of *Lepidocaryum tenue* in one year, after harvesting 25%, 50%, 75%, and 100% of all leaves in a ramet. Values include confidence interval. The horizontal line separates treatments that differed significantly from the unharvested palms.

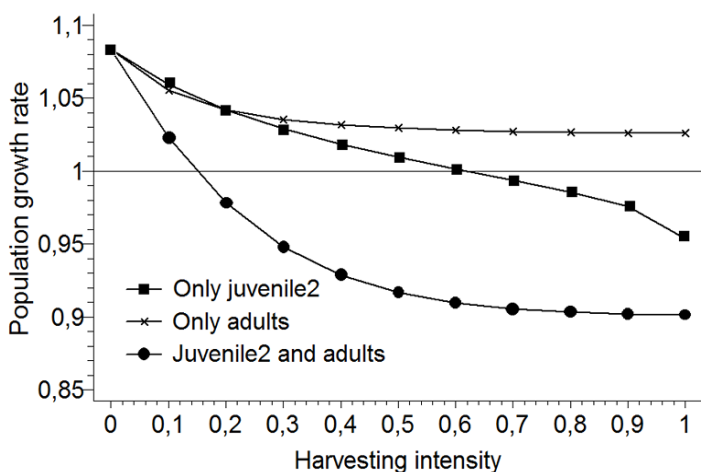


Fig. 7. Change in the finite rate of population growth (λ) of *Lepidocaryum tenue* under various harvest intensities.

Simulation analysis

Leaf harvest simulations showed that leaves from all adult ramets in the population could be harvested, without bringing λ to a value lesser than 1 (Fig. 7). However, when Juveniles 2 were also harvested, there was a drastic drop in λ , thus risking population's survival. Even if only Juveniles 2 were harvested there would be a decrease in λ ; also a harvest intensity of more than 60% of all ramets would jeopardize the population (Fig. 7). Juveniles 2 include ramets without an aerial stem and ramets with a stem up to 50 cm tall (ca. 10 nodes); ramets in this class are usually harvested, as they have leaves appropriate for thatching, and their low size facilitates access.

Table 2. Comparison of ramet density, annual leaf production rate, and population growth rate between *Lepidocaryum tenue* and other understory clonal palms. * Corresponds to mean values.

| Species | Growth | Estimated ramets/ha | Annual leaf production rate | Population growth rate | Reference |
|----------------------------|--------|---------------------|-----------------------------|------------------------|---------------|
| <i>Lepidocaryum tenue</i> | Clonal | 5500 - 14700 | 0.93 - 1.71 (*1.18) | 1.083 | present study |
| <i>Geonoma brevispatha</i> | Clonal | 3228 - 4044 | - | *1.037 | [25] |
| <i>Geonoma congesta</i> | Clonal | 1455 | 2.9 – 3.7 | - | [26] |
| <i>Geonoma deversa</i> | Clonal | 4156 - 9787 | 3 | - | [6] |
| <i>Geonoma deversa</i> | Clonal | - | - | 1.003 – 1.037 | [12] |
| <i>Podococcus barteri</i> | Clonal | - | 1.7-7.5 | 1.0125 | [27] |

Discussion

Lepidocaryum tenue is an abundant palm in *terra firme* forests, where sometimes it completely dominates the understory, reaching higher densities than other understory clonal palms studied so far (Table 2).

The growth habit of *Lepidocaryum tenue*, with its large, loose colonies made up of many stems connected by long stolons, appears to represent a successful demographic strategy. This is evidenced by the fact that vegetative shoots are more vigorous than seedlings from sexual reproduction, and produce leaves at a faster rate. Thus, they go faster through the stage that has the highest mortality, and therefore have a larger chance to survive into juveniles [28]. This is perhaps the reason why the plant invests few resources in sexual reproduction, as indicated by the low fecundity values and the scarcity of sexual seedlings.

An advantage of the clonal growth habit is the possibility of ramets producing stolons when they are still juveniles [28, 25], in this case, 14 years before reaching the adult stage. Additionally, for the dioecious *Lepidocaryum*, vegetative growth has the bonus that male genets can make an important contribution to ramet population. Although we were able to assign gender only to a small sample of the studied palms (65 out of 337 adult ramets), our finding of 2.8 times as many male ramets as females, suggests a stronger contribution of male ramets to the population, rather than a bias in the sex ratio of genets. Sex ratio in several dioecious palms is 1:1 [29, 30, 31, 32]. Thus, male genets in *Lepidocaryum* are probably larger in size than females.

On the other hand, the guerrilla strategy of the genets, with their ramets spread out through long stolons, gives the plant the possibility to explore new areas in the forest, probably forming a shoot bank that can take advantage of favorable microenvironmental changes. Additionally, many different genets, including male and female plants, can intermix spatially, so that any given area in the palm stand is an array of ramets belonging to different genets. This arrangement of stems divides into several individuals any damage caused by tree or branch falls, instead of having large damage in a single genet, as would happen to a cespitose palm with phalanx growth habit.

The investment of energy in vegetative growth could be one of the causes of the low leaf production rate, one of the lowest known among palms (Table 2) (see figures in Henderson [33]). Another cause is probably the low light availability in the forest understory, a factor known to affect leaf production in other palms [e. g. 26]. The low leaf production rate and associated long pre-reproductive period do not limit population growth, though, as the finite population increase rate (1.083) is among the largest known in palms (Table 2).

But a low rate of leaf production is critical indeed for a species used for its leaves. In *Lepidocaryum*, leaves for thatching are collected from Juveniles 2 and ADULT, i.e., including palms that have not yet developed an aerial stem. Harvested palms produce 1.3-1.7 leaves per year, and this figure decreases 4% after a harvest of 50% of all leaves in the crown, and 9% after a harvest intensity of 75% (Fig. 6). However, at a harvest level of 50%, the leaf production rate was still not significantly different from that of unharvested palms, so this is probably the highest recommendable level. With this harvest intensity it would take an average adult palm with 9-10 leaves up to 3.5 years to recover to its original condition. However, as there is perhaps some effect of clonal integration that is not accounted for in our model, the actual time for recovery of the whole genet may be somewhat longer. Therefore, we suggest that individual plots should be collected in turns of no less than four years. This figure is in disagreement with recommendations made by Mendoza [34], which suggest that a second extraction can be made one year after 66% of the leaves are harvested. Our data indicate that after one year leaf production would be too small; thus, harvesters might feel tempted to remove more leaves than the allowed maximum, in order to make the harvesting expedition profitable. Additionally, keeping all ramets with too few leaves will probably slow down genet spreading.

Lepidocaryum plants with well-developed leaves and stem up to 50 cm (Juveniles 2) had the highest elasticity value, and permanence of plants in this class was the most critical demographic parameter at our study site. On the other hand, our simulation showed that harvesting Juveniles 2 would eventually bring lambda to values below 1 (Fig. 7), thus reducing the population at length. This suggests that only adults, i.e., plants with a stem higher than 50 cm, should be collected. With a density of 2,800-5,400 adult palms per hectare, an average of 9.5 leaves per crown, and a harvest intensity of 50%, expected production would be 13,300-25,650 leaves per hectare every 3.5 years (19,475 on average). According to our own observations, this average figure is roughly similar to the number of leaves required to thatch a typical 54 m² house.

One way to reduce pressure on the resource is to improve the quality of the braided tiles sold in the market. A properly braided tile, made with appropriate leaves, will last longer, and will therefore reduce the need for replacement. Any control by authorities on *Lepidocaryum* management must include a careful quality control of marketed tiles.

Implications for Conservation

Undoubtedly, the use of *Lepidocaryum tenue* is an important issue both for the economy of local people and for the conservation of the Amazon forest (the mosaic in Fig. 8 shows different aspects of the palm in its habitat and also of its use). Results presented here indicate that uncontrolled harvest of *Lepidocaryum* leaves might cause a decline of its populations, as a result of the palm's slow growth and of the effect that harvesting one stem may have on other stems in the same clone. Our study offers enough data for proposing management strategies contributing to a sustainable harvest. Cautious management recommendations may be summarized as follows:

1. Only plants with a stem higher than 50 cm may be harvested.
2. Only one half of leaves in the crown may be cut, but in no case should a stem be left with less than four leaves.
3. Plots must be harvested in turns of four years.
4. Strong quality control of *Lepidocaryum* tiles must be implemented.

Introduction of these management practices will certainly improve the quality of the palm stands and will guarantee their sustained leaf production. However, as suggested by Rioja [35], management practices must include zoning of producing areas, a characterization of human groups involved, and detailed information on demand and market chains. In any case, a close monitoring must be introduced also, to make any necessary adjustments. In particular, we recommend carrying out further harvest experiments, in order to use life table response experiments (LTRE) [23]. These LTRE will refine our understanding of harvest effect on clonal growth, especially considering that our model does not take into account the possibility that clonal integration may play an important role in population dynamics.



Fig. 8. Different aspects of *Lepidocaryum tenue* use. (A) Understory of the forest dominated by *Lepidocaryum*. (B) *Lepidocaryum* ramets with all leaves cut. (C) Leaves with four segments preferred for thatching. (D) Juan Carlos, an Andoke Indian braiding a *Lepidocaryum* tile. (E) *Lepidocaryum* braided tiles finished, (F) House thatch made of *Lepidocaryum* leaves.

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