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Propagation of the Palm Flora in a Lowland Tropical Rainforest in Costa Rica: Fruit Collection and Germination Patterns

Juan Manuel Ley-López[1] and Gerardo Avalos[2,3]

Abstract

Palms are important structural components of tropical rain forests. Nonetheless, information on their propagation potential under nursery conditions to facilitate their use in forest restoration is scarce. This article studies the propagation potential of a tropical palm assemblage focusing on seed collection and germination patterns in the rainforest of Tirimbina, Costa Rica. From October 2013 to January 2016, we evaluated palm fruit availability and analyzed the germination potential of 5,172 seeds from 21 species monitored weekly for 57 weeks. Palm fruits were available all year; the percentage germination was 65.6%, and 90% of seeds germinated in 7 to 25 weeks. Contrary to the prevalent view that palms have low germination, germination was completed relatively fast. Palm propagation is limited by low species abundance rather than by fruit availability or germination potential. To propagate palms for restoration projects, we suggest to determine the species abundance and diversity at the study site, identify propagation priorities according to the species conservation status, and collect fruits throughout the year in a systematic way to include the greatest species and habitat diversity and infer the phenological patterns that will guide future seed collection. Our results are relevant to foster palm propagation with the purpose of including palms in forest restoration and increase our understanding of palm ecology, conservation, and regeneration strategies.

Keywords

Arecaceae, nursery, palm management, palm seeds, restoration, Tirimbina, understory

Introduction

Restoration is becoming more common in tropical forests. There is an urgent need to recover species diversity and ecosystem function especially in heavily deforested areas (Holl, 2017). However, the lack of sufficient information on the propagation of native species represents one of the main barriers to improve restoration initiatives. The low abundance of some species, overextraction, and seed scarcity (because of supra-annual flowering, short fruiting periods, and high seed predation) combine to prevent native plants from being widely used in forest restoration. Research on the propagation of tropical species for restoration purposes has focused on trees, but information for other groups is still lacking (Blakesley et al., 2002; Lu et al., 2016; Sautu, Baskin, Baskin, & Condit, 2006).

Although still understudied, palms represent an important and potentially useful group for forest restoration. They are dominant elements in many rainforests and play important structural and functional roles (Ter Steege et al., 2013), influencing forest dynamics, biomass accumulation, and providing critical food resources for animals (Beck, 2006; Genini, Galetti, & Morellato, 2009). They are one of the groups of angiosperms with the greatest number of cultural and economic uses (Campos & Ehringhaus, 2003; Dransfield et al., 2008), especially for human groups immersed in the tropical rainforest (Macía et al., 2011; Smith, 2014). However, despite their abundance and ecological and cultural

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importance, palms are rarely used in restoration projects because of lack of knowledge on the propagation requirements of native species.

Phenological studies have shown that palms produce high fruit biomass, as many species remain reproductive throughout the year (Genini et al., 2009). However, phenological information has rarely been used to guide seed collection (Buisson, Alvarado, Stradic, & Morellato, 2017; Kuaraksa, Elliot, & Hossaert-Mckey, 2012; Luna-Nieves, Meave, Morellato, & Ibarra-Manríquez, 2017). The general opinion is that palms are difficult to propagate because of low germination percentages and extended germination times (Tomlinson, 1990). Around 25% of palm species require more than 100 days to germinate, showing germination percentages of less than 20% (Tomlinson, 1990). In a review of palm germination for 457 species, Orozco-Segovia, Batis, Rojas-Aréchiga, and Mendoza (2003) concluded that most palms begin germination within 120 days. However, the information for species with late and sporadic germination remains incomplete because of different criteria used to quantify germination (Orozco-Segovia et al., 2003). Responses of long germination trajectories are rarely evaluated. Covering the whole germination spectrum is relevant as long and gradual trajectories represent adaptive strategies that improve species success during seedling establishment (Donohue, Rubio de Casas, Burghardt, Kovach, & Willis, 2010). In addition, knowledge on germination behavior is crucial in restoration projects where maintaining genetic diversity is a priority (Mijnsbrugge, Bischoff, & Smith, 2010).

Although palm germination has been revised by A. Henderson (2002) and Orozco-Segovia et al. (2003), most studies concentrate on one species, or a small group of species and genera, especially those with economic value, often including ornamental, edible, and in some cases, endangered species. There is a dearth of information looking at palm propagation for restoration purposes, whereas germination patterns among genera and species of the same community have rarely been analyzed (Manokaran, 1978). Finally, germination studies are generally carried out in growth chambers, conditions that do not resemble the rustic nurseries in which plants are commonly propagated in restoration programs (i.e., Ferretti & Britez, 2006; Holl, Zahawi, Cole, Ostertag, & Cordell, 2011; Leopold, Andrus, Finkeldey, & Knowles, 2001).

In this study, we evaluated the propagation potential of tropical palms under standard nursery conditions in Tirimbina Biological Reserve (TBR), one of the richest areas for palm diversity in Costa Rica (Kohlmann et al., 2010). We estimated palm species abundance, described the temporal patterns of fruit availability, determined the efficiency of obtaining seeds by walking through the Reserve every week, and compared the trajectories of temporal germination during 57 weeks to characterize the germination of this palm flora and to make recommendations to facilitate their propagation. Given the high diversity of palms at the site (27 species distributed in 11 genera), we expected to find variability in propagation potential because of species differences in abundance, availability of mature fruits, and germination responses. Generating basic information on the propagation of tropical palms is the first step toward their conservation, management, and sustainable use and is essential to establish successful restoration programs.

Methods

Study Site

The study was conducted at TBR, Sarapiquí, Heredia, Costa Rica (10°25′N; 84°47′W). The mean annual temperature and rainfall are respectively 24.3°C and 3,777 mm. The area encompasses two life zones: tropical wet forest and tropical wet premontane forest basal transition, following Holdridge, Grenke, Hatheway, Liang, and Tosi (1971). TBR protects 345 ha of mature lowland rainforests with most of the reserve covered by primary forest. Most of the area surrounding TBR has been deforested. The Sarapiquí River borders the west limit of the reserve for an approximate distance of 2.5 km, while the Tirimbina River crosses the reserve across 3 km, entering the southeast corner and leaving TBR through their northwest-most portion. The area is relatively flat (180–220 m) and several small creeks and hillsides crisscross the reserve (Figure 1). A trail network of 10 km provides ample access to the reserve. Selective logging was done occasionally between 1962 and 1990. More than 1,200 plant species have been identified at TBR, of which 27 are native palms belonging to 14 different genera (Ley-López & Morales, 2015). Although palms represent only 2.25% of the species, they contribute significantly to forest structure (Aguilar-Barquero & Jiménez-Hernández, 2009; Lieberman & Lieberman, 1987). According to Kohlmann et al. (2010), TBR includes one of the most diverse areas for palms in Costa Rica.

Palm Abundance, Fruit Collection, and Seed Germination

Palm abundance was estimated from 15 linear transects of 100 × 4 m following the layout of the trails (Figure 1). Transects were stratified covering all the main forest environments found in TBR, including gallery forests, flat areas, hillsides, forest edges, and forest interior (Figure 1). In each transect, we recorded and identified all adult palms located within 2 m on each side of the trail. We considered adult palms as those that reached the minimum size for which we have seen reproductive individuals in each species. Locating palms close to the

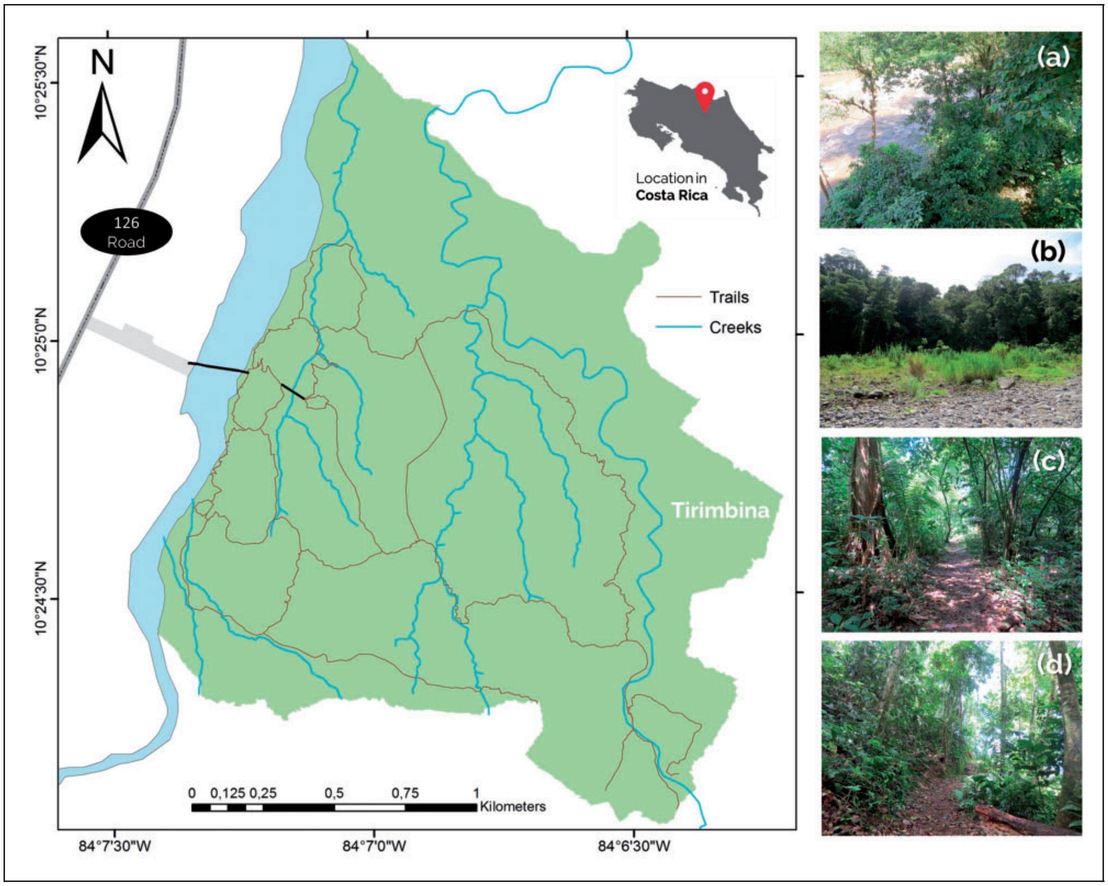

Figure 1. Map of Tirimbina Biological Reserve, Heredia, Costa Rica, and some of its main environments. (a) Gallery forest, (b) Forest edge, (c) Flat area, and (d) Hillside.

trails is the simplest way to collect seeds for propagation studies. Palm abundance (Table 1) was defined according to these categories: (a) rare (R), species with less than 4 individuals; (b) uncommon (UC), species with 5 to 10 individuals; (c) common (CO), species with 11 to 20 individuals; (d) very common (VC), species with 21 to 50 individuals; and (e) abundant (AB), species with more than 50 individuals. Here, our main objective was to estimate the feasibility of finding reproductive individuals according to their abundance along the trails.

From October 2013 to November 2014, we walked the TBR trails in random order twice a week looking for ripe fruits (Figure 2). During each survey, we recorded the species with mature fruits. Our ultimate goal was not to measure the phenological patterns of fruit production per se but to determine the availability of seeds for planting purposes in the nursery. Seeds were collected from the first individual of each species that presented mature fruits in good condition. Attempts were made to collect seeds from at least 10 different individuals per species. For rare species, with few individuals and with highly localized distribution, we carried out specific monthly walks, which were maintained until January 2015.

Seed collection, viability, cleaning, sowing, and germination conditions were implemented following the methods of Meerow (1991). For understory palms, seeds were extracted by hand from fully ripe fruits, whereas for subcanopy species, we used an extension pole to reach the fruits. We also collected seeds from recently fallen, fully ripe, and undamaged fruits. Fruit maturity was evident because of changes in fruit size and color. Seeds were taken to the greenhouse, separated completely from the mesocarp and other fruit parts, and cleaned by hand with a damp cloth to eliminate germination inhibitors that could have been present in the endocarp. Because our main goal was to document germination under standard, simple nursery conditions, we did not use chemical or physical scarification. We submerged seeds in water and discarded seeds that floated or showed evident physical or herbivory damage. A seed subsample was cut open to check for the presence of viable endosperm; if the endocarp was firm and the embryo filled the chamber, we assumed that the seeds were viable (Meerow, 1991).

Seeds were sown within 48 hr after field collection and were placed in germination trays filled with peat moss soil.

Table 1. Study Species, Distribution, Forest Strata, Palm Abundance, Number of Parent Individuals per Species (*N*), Total Number of Seeds Sown, Month of Collection of Ripe Fruits, Germination Percentage (%*G*), Mean Length of Germination in Weeks (MLG), First and Last Week in Which a Seed Germinated, and Germination Time in Weeks in Which 50% of the Seeds Germinated (GT_{50}).

Species	Distribution	Forest strata	Palm abundance	Parent individuals	Seeds sown	Month	%*G*	MLG	First	Last	GT_{50}
Asterogyne martiana (H. Wendl.) H. Wendl. ex Hemsl.	Guat–Ecu	U	AB (73)	15(0)	384	9-10-11	88.0 (±12)	10.2	7	29	9
Astrocaryum alatum H. F. Loomis	Hond–Pan	U	R (0)	0	–	–	–	–	–	–	–
A. confertum H. Wendl. & Burret	CR–Pan	SC	R (0)	0	–	–	–	–	–	–	–
Bactris caudata H. Wendl. ex Burret	Nic–Pan	U	UC (7)	15(3)	317	4-6-7-9-10-11	65.6 (±30.2)	21.4	10	23	21
B. coloradonis L. H. Bailey	Nic–Ecu	U	R (1)	0	–	–	–	–	–	–	
B. gracilior Burret	Nic–Pan	U	C (12)	18(2)	388	1-2-3-4-5-6-7-10	58.3 (±27.4)	22.9	10	41	22.5
B. hondurensis Standl.	Hond–Ecu	U	UC (5)	17(1)	241	1-5-6-8-10-11-12	72.2 (±27.4)	23.0	10	45	23
B. longiseta H. Wendl. ex Burret	CR	U	R (4)	1(0)	36	8	36.1	15.5	10	31	12.5
Chamaedorea deckeriana (Klotzsch) Hemsl.	Nic–Pan	U	R (0)	8(0)	231	1-10-11	83.5 (±13.8)	13.5	9	24	12.5
C. lucidifrons L. H. Bailey	Nic–Col	U	R (0)	4(0)	123	9-10-11	83.7 (±17.7)	13.6	7	19	14
C. pinnatifrons (Jacq.) Oerst.	Mex–Bol	U	R (3)	10(0)	225	8-9-10-11-12-1	89.8 (±19.1)	12.9	8	22	11.5
C. tepejilote Liebm.	Mex–Col	U	VC (45)	10(0)	207	8-9-10	89.4 (6.4)	10	7	16	9
Desmoncus moorei A. J. Hend.	CR–Nic	Cl	R (1)	2(0)	157	4	65	12.3	8	19	11.5
Euterpe precatoria Mart.	Guat–Bol	SC	VC (21)	6(0)	125	2-4-5	66.4 (±23.5)	8.8	4	20	7
Geonoma congesta H. Wendl. ex Spruce	Hond–Col	U	AB (101)	12(0)	270	5-6-7-9-10-12	64.1 (±22.2)	22.2	9	57	19
G. cuneata H. Wendl. ex Spruce	Nic–Ecu	U	AB (82)	30(1)	738	3-5-10-11-12	64.1 (±26.6)	16.8	8	41	15.5
G. deversa (Poit.) Kunth	Guat–Bol	U	AB (66)	16(2)	500	1-2-4-5-8-9-10-11	59.2 (±28.4)	25	10	57	22
G. interrupta (Ruiz & Pav.) Mart.	Mex–Bol	U	UC (5)	9(3)	317	4-6-7-8-9-10-11	34.7 (±20.5)	10.7	6	25	10
G. longevaginata H. Wendl. ex Spruce	Nic–Pan	U	C (13)	12(1)	330	5-6-7-8-10-11	55 (±29.4)	18.2	7	53	14
Iriartea deltoidea Ruiz & Pav.	Nic–Bol	C*	VC (22)	5(2)	113	4-5-6-7-12	52.6 (±43.1)	12.5	7	47	10
Pholidostachys pulchra H. Wendl. ex Burret	Nic–Ecu	U	R (0)	0	–	–	–	–	–	–	
Prestoea decurrens (H. Wendl. ex Burret) H.E. Moore	Nic–Ecu	U	C (13)	1(0)	26	9-10-11-12	96	6	5	7	6
Reinhardtia gracilis (H. Wendl.) Drude ex Dammer	Mex–Col	U	R (3)	0	–	–	–	–	–	–	
R. simplex (H. Wendl.) Drude ex Dammer	Mex–Col	U	R (0)	0	–	–	–	–	–	–	
Socratea exhorriza (Mart.) H. Wendl.	Nic–Bol	C*	UC (8)	8(1)	90	1-5-11-12	66.7 (±26.6)	13	8	27	11.5
Synechanthus warscewiczianus H. Wendl.	Nic–Ecu	U	C (13)	15(2)	238	1-2-4-5-6-10-11-12	61.8 (±34.7)	13.6	6	38	12.5
Welfia regia Mast.	Hond–Ecu	SC	VC (21)	6(1)	116	2-3-5-6-8-9	57.7 (±30.3)	13.9	7	32	12.5
Total/Mean			519	220(19)	5,172	–	65.6 (±28.5)	16.4	7.7	32	14

Note. Data were collected at Tirimbina Biological Reserve. The total number of individuals found in transects and number of individuals with less than 15% of germination is given within parentheses. See main text. AB = abundant; C = common; C* = canopy; CL = climber; R = rare; SC = subcanopy; U = understory; UC = uncommon; VC = very common.

We spaced seeds at 1 cm intervals and planted them at a depth of 1 cm. The trays were maintained in the greenhouse under a plastic, transparent roof, which permitted exposure to natural light. The greenhouse had an ambient temperature of 26°C and 30% full sunlight. Trays were watered manually twice a week to keep the soil sufficiently humid but not saturated or waterlogged.

In each seed cohort, germination was checked once a week for 57 weeks. Germination was defined as the emergence of the first cataphyll from the soil surface. Defining germination as the emergence of the shoot apex from the soil surface could overestimate the actual time of germination in palms with remote germination, for which the shoot develops slowly belowground

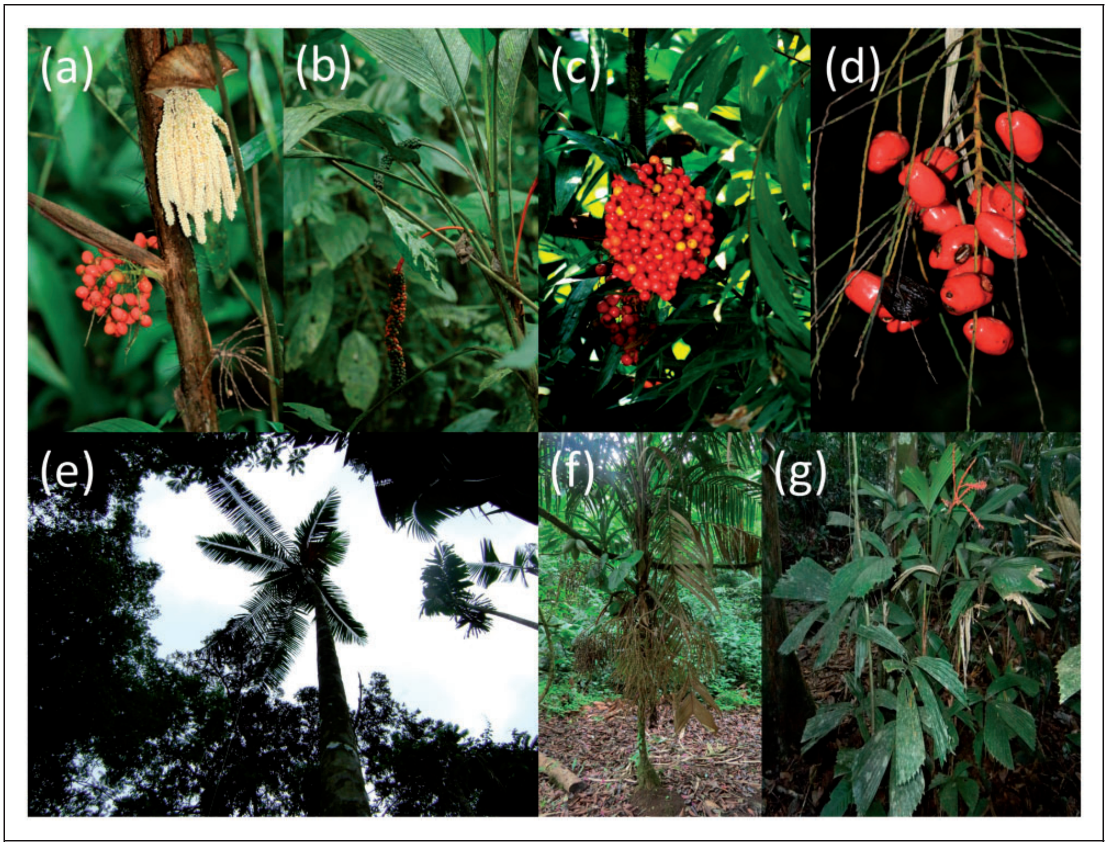

Figure 2. Examples of palm species found at Tirimbina Biological Reserve, Heredia, Costa Rica. *Bactris gracilior* (a), *Chamaedorea deckeriana* (b), *Desmoncus moorei* (c), *Synechanthus warscewiczianus* (d), *Euterpe precatoria* (e), *Geonoma interrupta* (f), and *Reinhardtia gracilis* (g). *Source*: Emmanuel Rojas and JML.

(F. M. Henderson, 2006). However, this condition did not affect our estimation of the germination time as all of our study species present adjacent germination (F. M. Henderson, 2006). At the end of 57 weeks, we inspected nongerminating seeds for viability by submerging them in water or cutting them in half and checking for the presence and consistency of the endosperm. Nonviable seeds were clearly empty or rotten. For all palm species, we recorded the month of seed collection, the final percentage of germination ($\%G =$ number of germinated seeds/number of seeds sown), the mean length of germination in weeks (MLG), which corresponded to the time difference between the first and the last germination week, and the number of weeks required to attain 50% of $\%G$ (GT_{50}). GT_{50} was measured using a linear interpolation of the two germination values closest to the median germination time.

Statistical Analyses

Temporal germination patterns were evaluated using survival analysis, which is a more robust technique than other traditional analysis protocols (i.e., germination indexes or regression analysis) according to McNair, Sunkara, and Frobish (2012). Survival analysis takes into account several properties of the germination process, such as the delay in germination initiation, germination percentage, germination rate, and germination time change. In germination studies, the presence of right-censored observations violates the assumptions of classical statistical methods; alternatively, survival analysis concentrates on the distribution of the germination times of individual seeds instead of the cumulative germination, comparing the homogeneity in the temporary patterns of germination between the groups (McNair et al., 2012).

We estimated the survival functions using the nonparametric product limit method (Kaplan–Meier) for census groups. To test for the homogeneity of survival functions across genera and species, we used the nonparametric log-rank test statistic (χ^2) following the recommendations of McNair et al. (2012). Multiple comparisons were corrected with a sequential Bonferroni protocol (Holm–Bonferroni method). All statistical analyses were carried out using R Statistical software (http://www.r-project.org) and the functions survfit and survdiff from the package survival (Therneau, 2014).

Results

Palm Abundance

We recorded 519 individuals belonging to 21 out of the 27 species recorded at TBR (Table 1). Four species were considered abundant (*Asterogyne martiana, Geonoma congesta, Geonoma cuneata*, and *Geonoma deversa*), comprising more than 60% of the individuals (Table 1). The high abundance of these species is reflected in their presence in almost all of TBR as well as their high density in some transects. Twelve species were considered uncommon to very common. These species were found in most of the sites but in low abundance (i.e., *Bactris hondurensis* and *Synechanthus warscewiczianus*) or were habitat specific. *Chamaedorea tepejilote* was very common but found only in riparian habitats, while *Geonoma interrupta* and *Prestoea decurrens* were found only close to creeks (Table 1). Eleven species were considered rare, six of which were not found on transects. All of these are very rare and only a few individuals have been located at specific places in TBR. *Chamaedorea deckeriana* has only been observed in an area of less than 1 ha in the northwest boundary of the reserve, whereas *Astrocaryum alatum* has been previously reported in the reserve but was not observed in this study. Rare species found along transects grow in very low densities with no apparent relationship to habitat type (i.e., *Astrocaryum confertum, Chamaedorea lucidifrons*, and *Desmoncus moorei*) or in a few specific places (i.e., *Reinhardtia gracilis*). Most palms (446) belong to understory species, whereas only 72 were canopy or subcanopy species. We found only one individual of the climbing species *D. moorei* (Table 1).

Fruit Availability and Seed Collection

We found fruits in 21 of the 27 native palms of TBR. As expected, species abundance and fruit phenology determined seed collection. All species in which no fruits were found were classified as rare. Some rare species, like *C. deckeriana*, had short and synchronous fruiting periods and grew in patches, but the rest of rare species had very few individuals so that characterizing the pattern of fruiting phenology was difficult. For rare species, our approach was to collect seeds in an opportunistic and punctual manner. It is likely that more intensive sampling covering difficult access sites in TBR would have increased the probability of finding more individuals and therefore, obtaining seeds of more rare species.

Continuous fruit availability throughout the year facilitated seed collection in the majority of the species cataloged as uncommon to abundant. Seed collection was limited by low fruit production (*B. hondurensis*), asynchronous fruit ripening (*Chamaedorea* spp.), rapid fruit consumption by the local fauna (*S. warsecwiczianus* and *C. tepejilote*), and in a few instances, seed predation (we observed larvae of curculionid beetles inside the seeds of *G. deversa, G. interrupta, Geonoma longevaginata*, and *Iriartea deltoidea*). At TBR, ripe fruits were available year-round with an average of 8 fruiting species per month. October and November had the highest number of fruiting species (15 and 13 species, respectively), while February and March had the lowest number of fruiting palms (5 and 3, respectively). The rest of the year was relatively constant with 6 to 11 palm species bearing ripe fruits (Table 1). In most species, high fruit yield facilitated seed collection, which is particularly important for the nursery propagation of uncommon and rare species.

However, these data should be analyzed with caution as the absence of fruits in a species may imply irregular or complex fruiting patterns associated with low population densities rather than the total absence of fruits. In rare species, the low abundance of individuals does not allow to infer clear phenological patterns of fruit production, whereas the fruiting period is likely to be longer than our results suggest in common to abundant species. For example, the 10 species in which we found fruits for more than six months showed irregular fruiting patterns. In these species, it is possible that fruit production is continuous for most of the year, but with a low number of individuals producing fruits in each period. Most species showing fruits for more than six months belong to *Bactris* and *Geonoma* (Table 1).

Germination Patterns

Our results indicate that germination was not the main obstacle to propagate native palm species. Average percentage germination was 65.6%, with only two species (*B. longiseta* and *G. interrupta*) showing germination values lower than 50% (Table 1). In most species, there was high intraspecific variation in %*G* meaning that seed quality could affect seedling production. For instance, while most species had individuals reaching germination percentages close to 100%, a few individuals of *Bactris* spp., *Geonoma* spp., and *S. warsecwiczianus* showed low germination (0%–15%).

In addition, seed dormancy and germination speed posed no major obstacles to propagate this palm flora. In all species, germination started before 10 weeks, and 90% of all seeds germinated between weeks 7 and 25 (Figures 3 and 4). MLG and GT50 were 16.4 and 14 weeks, respectively, meaning that obtaining a high number of seedlings relatively fast is possible (Table 1). The period needed to complete the whole germination response was 40 weeks, at which time 99% of all seeds completed germination. The exception was *Bactris* and *Geonoma* palms, in which only a small percentage (0.5%) of the nongerminating seeds was still viable after week 57 (Figures 3 and 4).

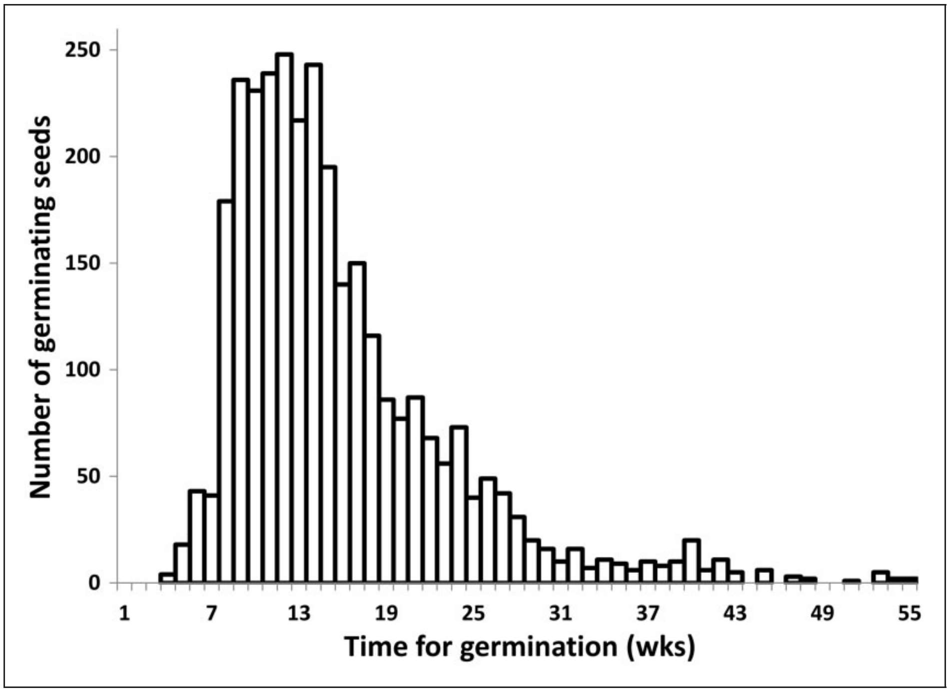

Figure 3. Frequency distribution of germination over 57 weeks for the 21 palm species studied at Tirimbina Biological Reserve, Heredia, Costa Rica, from October 2013 until January 2016.

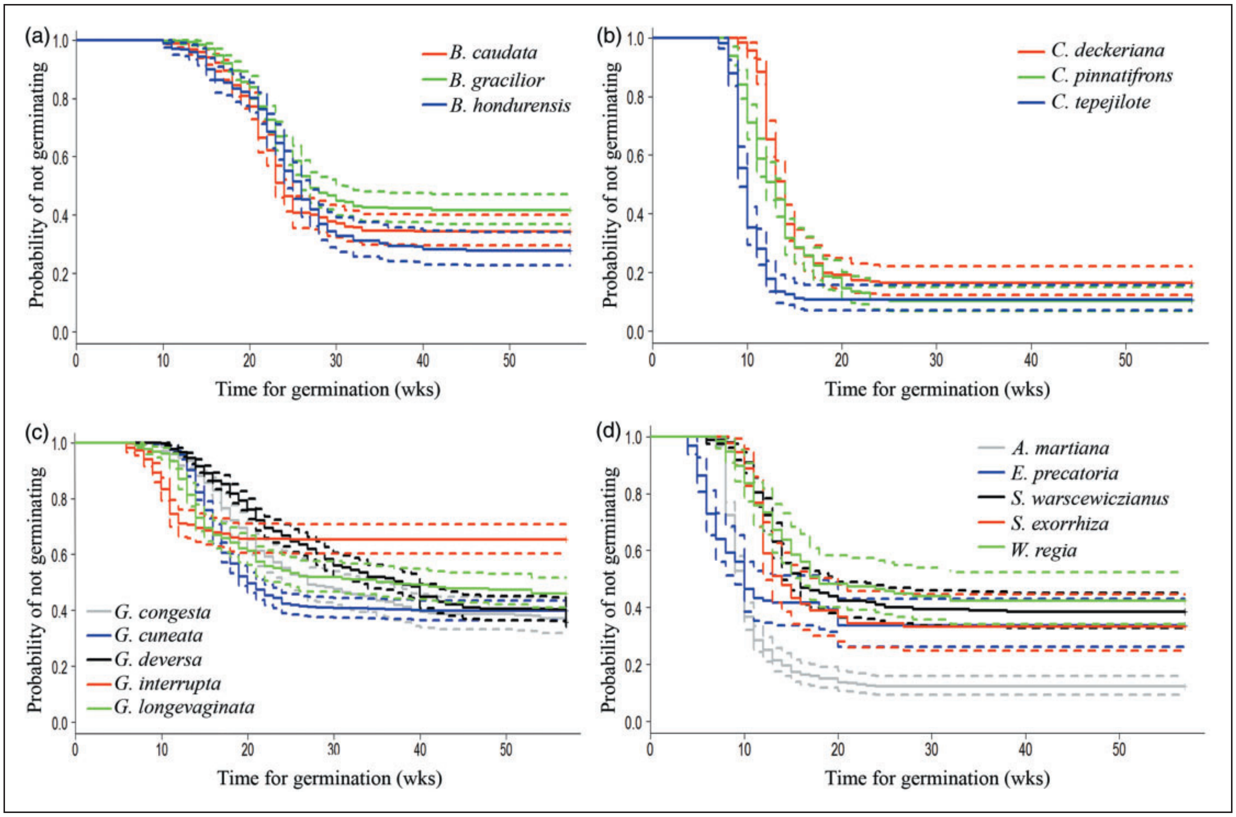

Figure 4. Kaplan–Meier estimates of survivor functions for 16 palm species over 57 weeks at Tirimbina Biological Reserve, Heredia, Costa Rica. Upper and lower lines from the same color represent pointwise 95% confidence intervals. *Bactris* spp. (a), *Chamaedorea* spp. (b), *Geonoma* spp. (c), and all other species: *Asterogyne martiana, Euterpe precatoria, Synechanthus warscewiczianus, Socratea exorrhiza*, and *Welfia regia* (d).

There were differences in germination trajectories across genera and species (Figure 4; *Bactris* spp. $\chi^2 = 11.9$, $df = 2$, p-Holm = .0076; *Chamaedorea* spp. $\chi^2 = 82.8$, $df = 2$, p-Holm = .001; *Geonoma* $\chi^2 = 41.2$, $df = 4$, p-Holm = .001). *Bactris* and *Geonoma* were characterized by long and gradual trajectories whereas other species showed shorter trajectories that leveled off around 20 weeks (Figure 4). Congruent with differences in germination trajectories, species diverged in synchrony and average germination time. Species with higher germination percentages (*A. martiana, Chamaedorea* spp., *Euterpe precatoria*, and *P. decurrens*) consistently showed shorter fruiting periods and lower MLG and GT_{50}. *Euterpe precatoria* showed the fastest germination rate ($GT_{50} = 7$ weeks) with one individual starting and ending germination in weeks 5 and 7, respectively. The longest germination time was recorded in the genus *Geonoma* (Table 1, Figure 4). Here, one individual of *G. congesta* and another of *G. deversa* took 24 and 27 weeks, respectively, to begin germination, and did not complete it until after 57 weeks. Species in the genus *Bactris* also had a high value of GT_{50}. In summary, it takes 20 weeks to germinate most of species in this palm flora and obtain a high number of seedlings, but in the genera *Bactris* and *Geonoma*, it will take 40 weeks if the goal is to cover the entire germination response.

Discussion

Palm Abundance, Fruit Collection, and Seed Germination

The use of native species in rainforest restoration is limited by a multiplicity of factors, including the lack of appropriate seed collection methods considering the reproductive phenology, as well as the abundance, dispersion patterns, and habitat preferences of adult plants (Hoffmann, Blum, Velazco, Gill, & Borgo, 2015). Securing access to seeds of native species is critical to initiate successful restoration processes, especially when the goal is to restore the functionality of complex and diverse systems such as tropical rainforests. This could pose significant challenges for landowners and restoration managers who have limited resources and decide to use the most abundant and better known species.

As many other tropical areas, TBR is characterized by a high palm diversity and abundance with continuous fruit production. To our knowledge, our work is the first effort to link these two factors with palm propagation for restoration purposes, even though information on tropical palm composition and palm phenology is already available (De Steven, Windsor, Putz, & León, 1987; A. Henderson, Fischer, Scariot, Whitaker-Pacheco, & Pardini, 2000; Peres, 1994). Palm propagation at TBR is more limited by the low abundance of rare species than by germination capacity or by ecological constraints such as supra-annual flowering, fruit predation, or seed predation.

Obtaining seeds from several species is crucial for restoration projects (Rodrigues, Lima, Gandolfi, & Nave, 2009), although most tropical species grow at very low densities, which clearly represents an obstacle for successful propagation. At TBR, more than half of the palm species are rare, uncommon, or habitat specific, and usually known from a few specific places in the reserve. Constraints on the propagation of low abundance tropical species have been discussed mainly for highly threatened species (Hoffmann et al., 2015), including potential negative effects on genetic diversity and plant performance caused by using seeds from small populations (Mijnsbrugge et al., 2010). For this reason, extensive monitoring and focal searches need to be in place to secure finding sufficient viable seeds (Wang et al., 2016). In the case of TBR, more intensive searches would allow finding more individuals of rare species, but this would make sampling more difficult for collection purposes in general. Therefore, initial efforts should focus on species with an additional conservation value (i.e., endemic or threatened) and in which it is subsequently possible to find sufficient individuals for their propagation. In the case of the rare palms at TBR, abundant fruiting could be advantageous as it allows the production of a large numbers of seedlings even when only a handful of mature individuals are found.

In addition to low population density, fruiting seasonality represents a second challenge to obtain sufficient seeds from different species (Blakesley et al., 2002). Phenological behavior is a fundamental aspect to consider when planning seed collection protocols, both at the species and community level (Morellato et al., 2016). In our case, we did not mark individuals, and several species were very scarce, making it difficult to draw complete conclusions regarding the overall pattern of fruiting phenology of palms at TBR. The characterization of the phenological behavior is affected by sampling size (Morellato et al., 2010). However, our data facilitated the characterization of the basic behavior of most species and its implications for seed collection. For example, data show that species of *Bactris* present fruits most of the year, whereas those of *Chamaedorea* are mainly seasonal.

According to Newstrom, Frankie, and Baker (1994), the phenological behaviors of tropical plants could be categorized as continual, subannual, annual, and supra-annual.

At TBR, almost half of the species showed continual to subannual patterns producing fruits all year round in large quantities (or at least for more than 6 months a year), which clearly represents an advantage for seed collection purposes. Nonetheless, for these, fruit production could be the result of the reproduction of low proportion of fertile individuals so that at a specific time, it is still difficult to obtain large seed quantities. To secure greater genetic diversity, several collections should be done throughout the year. On the other hand, a second group of species showed annual flowering (i.e., *A. martiana, Chamaedorea* spp.), which limits the seed collection period. For the TBR palms, fruit production coincided with the peak and end of the rainy season, which was the best time to collect seeds to increase species diversity. Finally, supra-annual flowering has been considered as another significant obstacle for obtaining sufficient seeds in tropical trees (Holl, 2002), but this does not seem to represent a significant problem in tropical palms in which very few show supra-annual fruiting (e.g., some canopy species, A. Henderson, 2002). The only species with this type of fruiting behavior at TBR is *R. gracilis* (J. M. L., personal observation).

Following fruiting seasonality, germination potential is the third key aspect for palm propagation. Few studies have addressed the germination behavior of palm floras. Our results show that germination percentages were similar or higher than those reported for tropical rainforest tree species (Garwood, 1983; Sautu et al., 2006).

Methodological, anatomical, and ecological factors explain our germination results. First, fruit collection was done weekly for a whole year, and seeds were sown immediately, which reduced the probability of observing lower germination percentages as many species have short viability and cannot resist prolonged storage (A. Henderson, 2002). Several studies reporting low palm germination concentrated on species from seasonal habitats. Hard seed coats, fibrous mesocarps and endocarps, and remote germination are characteristic of palms adapted to xeric conditions. Nonetheless, all palms in our study show adjacent germination, and most of them (with the exception of *Bactris* spp. and *D. moorei*) have thin endocarps, both traits being associated with fast germination (A. Henderson, 2002). These conditions provide an advantage in the humid climatic conditions of tropical rainforests which facilitate high and fast germination (Vázquez-Yanes & Orozco-Segovia, 1993), helping seeds and seedlings to escape predators and pathogens (Daws, Garwood, & Pritchard, 2005).

In tropical rainforests, germination has been considered slow when it takes more than 4 (Garwood, 1983) or 12 weeks (Blakesley et al., 2002). According to our data, most seeds germinated in 25 weeks, but 10% of them required more than 40 weeks. In addition, germination curves were long in some species, and there was significant variation in the percentage and timing of germination within and among species. This poses challenges for nursery management in which the goal is to obtain a rapid and homogenous germination. A common practice is to select plants with specific characteristics or harvest seedlings from seeds with faster germination. However, this should be avoided if possible for restoration purposes where the aim should be to represent the genetic and ecological base of the species under consideration (Thomas et al., 2014), and is particularly important in palms with ample germination responses (Ataroff & Schwarzkopf, 1992; Harms & Dalling, 1995). A simple strategy to cover a higher germination spectrum would be to increase the number of individual palms as well as to explore pregermination treatments that accelerate germination (Potvin, Cansari, Hutton, Caisamo, & Pacheco, 2003).

Implications for Conservation

Identifying viable propagation techniques is the first step toward successful forest restoration, conservation, and sustainable use. Here, we demonstrated the feasibility of obtaining large seedling numbers from several native palm species using basic nursery conditions. The main goal of tropical forest restoration is to recover species diversity and maintain functional ecosystems through the use of threatened species (Volis, 2016b). Nonetheless, several aspects should be considered to propagate tropical palms for restoration. We suggest the following steps:

1. Field sites should be sampled systematically to cover the most relevant environments to obtain a representative sample of the diversity, abundance, and location of the target species.
2. Define species propagation priorities taking into account their conservation status, use, and cultural and economic values.
3. Design a seed collection schedule and protocol considering the conservation priorities, abundance, species distribution, logistic limitations, and available phenological information.

Following these steps, in TBR, there would be seven palm species of high priority for propagation according to their level of endemism. Of these, *Bactris caudata, B. gracilior*, and *G. longevaginata* would be easily located because of their abundance, whereas for *C. deckeriana*, it would be necessary to implement focal collections considering that its location in the reserve has been previously identified. In the case of *B. longiseta* and *D. moorei*, given their very low densities, more specific seed collection programs would have to be developed (see Volis, 2016a; Wang et al., 2016) depending on the economic possibilities of the manager. Finally, for the rest of the palm species, which are abundant (i.e., *A. martiana, B. hondurensis, G. cuneata*, and *S. warsewiczianus*), seed collection could be done opportunistically, trying to obtain a large number of seeds from different individuals.

A second fundamental aspect is the collection periods. Our data indicate that obtaining fruits is possible for most of the year, which is a reasonable assumption if there is no previous information. However, while the periodicity of collection is determined by the logistic capacity of the project developer, the specific phenology of the species will determine the most favorable times of the year for fruit collection. We suggest that the data should be collected systematically to determine first the general trends of the species behavior and then develop a schedule fine tuning future seed collection (Luna-Nieves et al., 2017). Thus, for TBR, one collection every 3 months (1-4-7-10) would allow fruits to be obtained in 18 of the species, whereas an intensive collection in October would yield fruits in 15 species.

Despite their ecological role and cultural importance in tropical rainforests, palms have been rarely used in restoration projects. Blakesley et al. (2002) recommend the inclusion of plant species with germination rates higher than 60% in habitat restoration, which was the case for most of our study species. Further studies will need to evaluate the growth responses of palm species in the field and their potential for restoration. Although some palm species have good potential to improve growth and survival under sun conditions (Avalos, 2016), the shady environment of regenerating forest could provide good growing conditions for shade-adapted, understory species (Alvarez-Aquino, Williams-Linera, & Newton, 2004). The inclusion of local palms in forest restoration will not only facilitate forest recovery in degraded areas but the maintenance of functional food webs, contributing with the ex-situ conservation of endangered palm species while promoting their sustainable management (Potvin et al., 2003).

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