Phenology and Germination of the Chonta Palm, *Astrocaryum gratum*, in a Sub-montane Forest

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Chonta palm (*Astrocaryum gratum*) is found in sub-montane neotropical forests, and its basic biology has been little studied. The phenology of *Astrocaryum gratum* was observed during 25 months in Madidi National Park and Pilón Lajas Biosphere Reserve and Indigenous Territory (Bolivia). The effect of light availability on seed germination of Chonta was also evaluated. The percentage of emerging seeds regardless of whether they were in the shade or sun was not significant; however, buried seeds germinate in higher proportion than ones left uncovered. *Astrocaryum gratum* plays an important role as a food resource for wildlife, affecting its distribution and movement, and therefore must be considered when designing wildlife management plans.

The palm *Astrocaryum gratum* Kahn & Millan (locally called Chonta palm) is distributed along the eastern Andean piedmont and adjacent areas of the southwest Amazon basin and its periphery in Bolivia and Peru (Kahn 2008). It is scattered throughout the forest, but high density aggregations per hectare can also be found (Beck & Terborgh 2002), all growing in sandy soils, and areas temporarily flooded as well as sub-mountane forest (Kahn 2008).

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Astrocaryum gratum and the other species of *Astrocaryum* subg. *Monogynanthus* section *Huicungo* were joined together in a large species complex called *Astrocaryum murumuru* by Henderson (1995); this position was not followed by Govaerts and Dransfield (2005) and Kahn (2008). Section *Huicungo* includes 15 species. *Astrocaryum gratum* belongs to subsection *Sachacungo* (with *A. macrocalyx*, *A. urostachys*, *A. perangustatum* and *A. cuatrecasanum*), which differs from subsection *Murumuru* (this includes *A. murumuru*, *A. chonta* and *A. ulei*) in the calyx of the pistillate flower that is longer than the corolla. Moreover, *Astrocaryum gratum* is a solitary trunked palm, while *A. murumuru* is a multistemmed (caespitose) palm

Astrocaryum gratum (Fig. 1) is shade-tolerant and can grow up to 15 m tall. *Astrocaryum gratum* has 6–25 pinnate leaves, which are flat and very large, and spread horizontally. They have 90–105 pinnae on each side, regularly distributed and arranged in the same plane. Flat black spines are present along the stem and leaf midrib (especially at early ages). The calyx of the pistillate flower is glabrous or glabrate with bristles (Kahn & Millan 1992, Kahn 2008). The interfoliar inflorescences, branched to one order, are 1–1.5 m long (Kahn 2008). The orange-yellowish fruits are ovoid, covered with tiny spinules, and the fresh succulent pulp is very aromatic and covers a single endocarp (herein called the seed).

As with other species of the genus, *A. gratum* is pollinated by bees and other insects (Listabarth 1992). Seed dispersal patterns normally occur both with a natural seed rain or seed rain caused by birds or arboreal mammals, particularly monkeys, which consume the mesocarp and drop the seeds to the ground. On the ground, the seeds often attract a large number of terrestrial animals capable of secondary dispersal, such as the agouti (*Dasyprocta punctata*), which hoards the seeds at distances up to 200 m. Seed predators, such as the white-lipped peccary (*Tayassu pecary*), also consume seeds that have fallen to the ground (Henderson 1995, Beck & Terborgh 2002, Aliaga-Rossel et al. 2008, Aliaga-Rossel & Painter 2010). This palm is considered a keystone species, because it supports many animal species with its fruits, seeds and seedlings during periods of food scarcity (Terborgh 1986, Cintra & Horna 1997).

Despite the importance and abundance of Chonta palm, there are few studies related to its phenology, fruit cycle and germination. This information is relevant not only to understand plant dynamics but also to provide insight into wildlife movements and distribution. This work describes the phenology and germination of the Chonta palm in two regions of a sub-montane forest in Bolivia.

Material and Methods

This study was conducted in Madidi National Park and Natural Area of Integrated Management; MNP (13°20’–14°00’ S, 68° 10’–69°10’ W), and Pilón Lajas Biosphere Reserve and Indigenous Territory; RBIT (14°25’–15°27’ S, 66°55’–67°40’ W). The study sites are similar in elevation gradient and present similar habitats, ecosystems and landscapes, and thus similar biodiversity composition. Soil and other abiotic characteristics are similar for both areas.

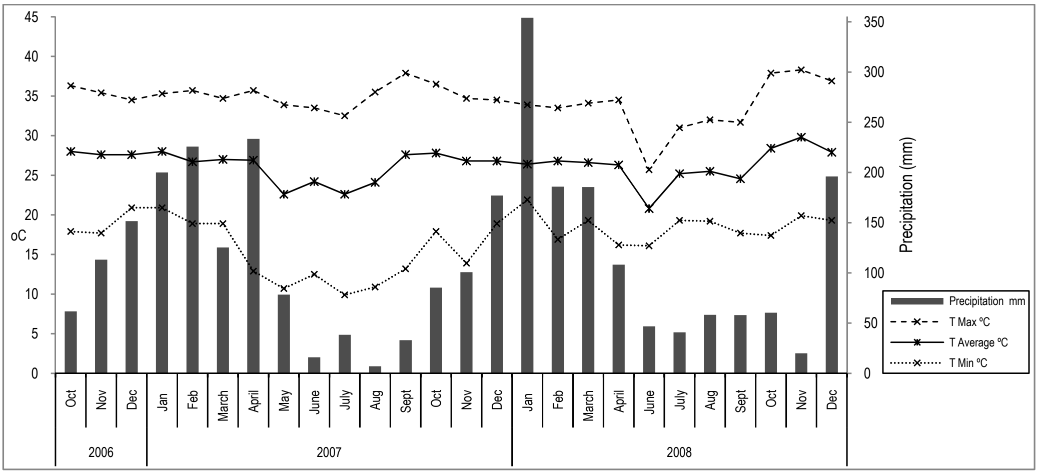
The mean precipitation in this region is estimated at over 2000 mm annually with northeastern slopes receiving the majority of the rainfall; there is a marked rain shadow to the southwest. The mean annual temperature is 26°C (Navarro & Maldonado 2004), the area is tropical, with well defined, seasonal dry (June to September) and rainy periods (October to May) (Fig. 2). The vegetation in the region is a piedmont sub-montane evergreen forest (Navarro & Maldonado 2004) with transitions into moist lowland forest with Amazonian affinities; similar forest types are found on abandoned river terraces of piedmont areas. The floristic diversity of the lowland forest is considerable, with 204 species of 2.5 cm or more diameter at breast height (dbh) per 0.1 ha, a large number of plant families, and high densities of other palm species (Foster & Gentry 1991, Navarro & Maldonado 2004).

This study was done during “El Niño” (2007) and “La Niña” (2008) events, but carried out from November 2006 to December 2008, with no data collected in November 2008. Different patches of Chonta palms (*Astrocaryum gratum)* in each of the study sites were randomly selected, each at least 1.5 km apart from one another, and one transect (250 × 25 m) was established in each patch, within which all adults of *A. gratum* (capable of producing flowers and fruits) were identified and their DBH measured. Each individual was tagged. In order to understand fruiting patterns of the palms, I observed the reproductive status of the palms once a month and categorized them

1. *Astrocaryum gratum*. Photograph by H. Montecinos.

into one of two groups: a) Flowers (includes flower buds and open flowers) and b) Infructescences (including immature and mature fruits). Different stages of the inflorescence (buds, open flowers, etc.) were not distinguished due to the difficulty of observing the inflorescences among the leaves. If an individual had two bunches in different stages (e.g., flowers and immature fruits), the two bunches were analyzed independently. I observed the approximate distance that mature fruits drop naturally and noted the general abundance of fruits and seeds found on the forest. Finally, I randomly collected 13 fruit bunches from different trees and counted the number of fruits on each.

To determine the influence of light availability on seed germination and to test the importance of the presence a known palm secondary seed disperser (Agouti, *Dasyprocta punctata*) on germination, I collected 300 fruits from different fruit bunches on different individuals. The fruits were washed and the fresh the pulp was removed to reduce attracting other predators and remove pulp previously infected by fungus or insects. The seeds were inspected for any sign of damage or insect predation. Only intact, undamaged seeds were used for the experiment. An area where adult palms were not present was selected to avoid direct seed predation by animals attracted to these sites. There, in five



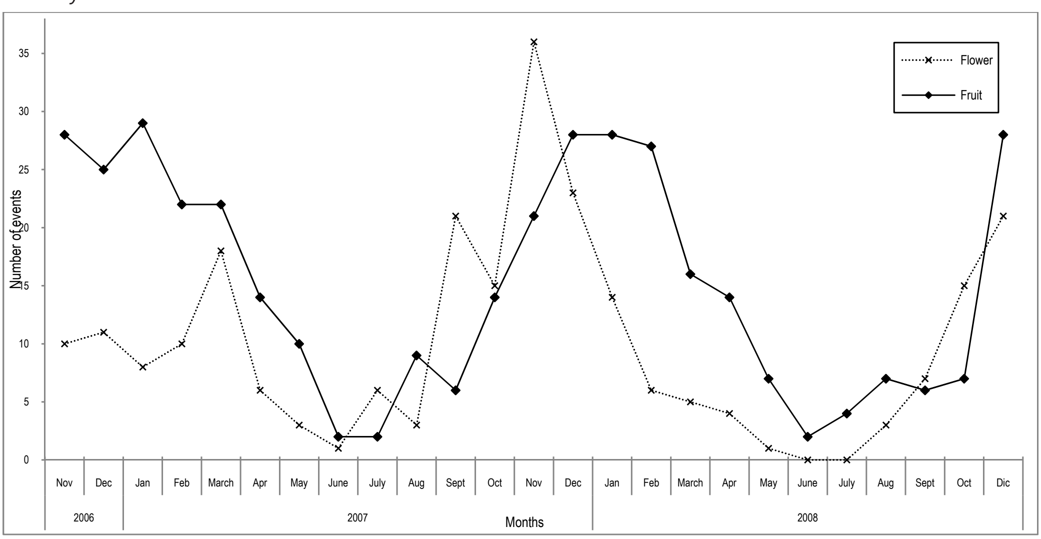
2. Precipitation (mm) and temperature (°C; maximum, minimum, average). From October 2006 to December 2008. Data obtained by the National Service of Hydrography and Meteorology (SENAHMI), Bolivia.

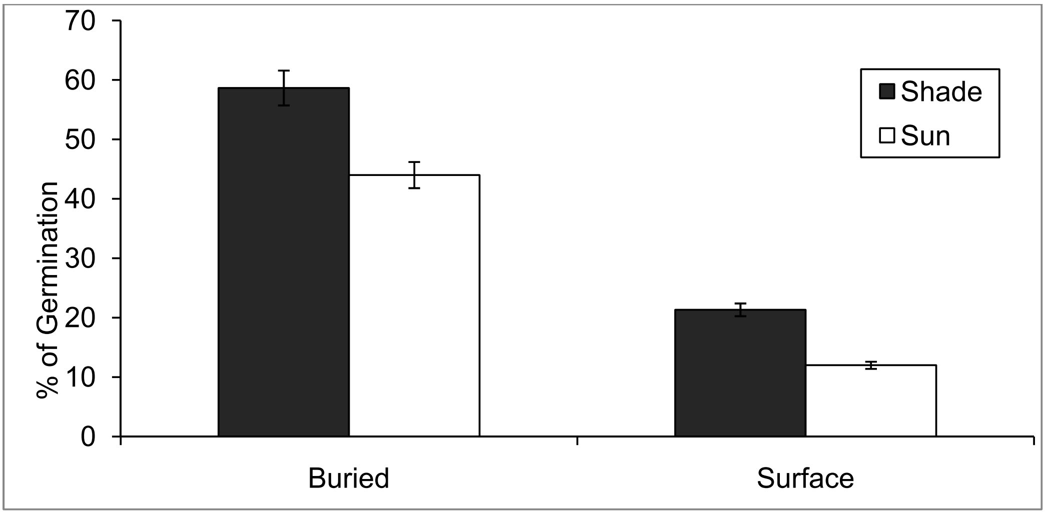
replicates, 15 seeds per treatment were buried 3–5 cm below the surface, imitating the hoarding burial activity of an agouti. There were four treatments: a) Seeds left at the soil surface just covered with a thin layer of dead leafs (placed in the shade), b) Seeds left at the soil surface covered with a thin layer of dead leaves (directly exposed in a sunny area), c) Seeds buried in the shade, d) Seeds buried in soils exposed to the sun. The seeds were set in rows of 5 seeds, 10 cm apart. Sun and shade treatments were approximately 70 m apart. To observe the growth of the radicle and the plumule (i.e., germination), it is necessary to dig up and disturb the seed; to avoid this and any possible damage to the radicle, germination was considered successful when seedling leaves reached the surface. The fate of the non-emerged seeds was not followed; therefore I cannot indicate if they were predated, attacked by fungus or were naturally non-viable seeds. The different germination treatmens were analyzed using a one-way Anova.

Results

During the 25-month period, 62 healthy adults of *A. gratum* were identified. Reproductive individuals are approximately 10–25 m tall, with a DBH of 14.3–28.65 cm (average 20.1

3. Flower and fruit production of Chonta palm (*Astrocaryum gratum*) during "El Niño" (2007) and "La Niña" (2008) events in a sub-montane forest. Several mature fruits are found on the floor from December to mid-February.





4. Percentage of *Astrocaryum gratum* seeds germinated (percentage of emergence) under two treatments (dark blocks are located in shade areas; light blocks buried in sunny area) under different light availability. Error bars 5% value.

cm SD=3.21) and 8–19 (n=72, mode 9; median 10) leaves. Precipitation and temperature in the region are presented in Figure 2.

Phenology

Each flowering period was relatively short, starting with the peduncular bract opening. Pistillate flowers were immediately receptive and soon pollinated. When the pistillate flowers were no longer receptive the staminate flowers open. After fertilization the gynoecium and the accrescent perianth grew into a young fruit, which developed slowly. The majority of adult trees was observed with flower buds and open flowers during almost all months (83%), with no apparent synchronization (Fig. 3). In 2008, no flowers were observed in July. Some trees were observed to produce two inflorescences at the same time.

Fruiting started in August with a peak between December and March. Individual palms of *A. gratum* produced one to three (average two) infructescenses every year, each containing from a few hundred to thousands 6–10 cm long fruits (average 700.3, SD 237. 3; n=13), although several adult individuals (10%) did not produce any fruits in a year.

Fruiting for *Astrocaryum gratum* was not synchronized; however, a higher number of infructescences was observed during the rainy season (from November to end of February), with the highest peak from December to February.

Mature fruits fell one at a time, and ripe fruits were found generally 5 m away from the parental tree, where many terrestrial animals (vertebrates and invertebrates) feed on them. The highest number of fruits was observed on the forest floor during December to February, decreasing in the dry season. No ripe fruits were observed on the floor in June–July during the "La Niña" event in 2008.

Seeds and germination

Seeds in all treatments germinated (i.e. had emerged) after 8–11 months (34%). The first plumule appeared at the eighth month, but the majority of seeds emerged after 11 months. Of the seeds left on the soil surface, 21% of the seeds in the shade germinated, but only 12% seeds in the sun germinated (12%) (Fig. 4). There was a significant difference in germination between all seeds buried and seeds left uncovered (d.f. 1; F=52.22; p>0.000) in shade and sunny areas. There was no significant difference between seeds buried in the shade or the sun (df. 1; F=1.76; p>0.2). These results suggest that natural germination is highly dependent on seed burial, as a result of scatter-hoarding activity from rodents such as the agouti (*D. punctata*).

Discussion

This may be the first study on the phenology of *Astrocaryum gratum* anywhere in its distribution. Cabrera and Wallace (2007) studied the phenology of palms for a period of 11 months, including an *Astrocaryum* species (n=10), identified as *A. murumuru* by the authors; this was probably *A. gratum*, since it is the only *Astrocaryum* species of section *Huicungo* growing in the region (Kahn 2008).

During the study period three *A. gratum* trees died when a big tree fell due to strong winds. These gaps caused by the collapse of big trees play an important role in the community structure (Denslow 1987, Hubbell et al. 1999) by permitting seedlings to growth faster and possibly replace the parental tree. One of the adult trees died after 17 months of recording without producing flowers or fruit, but it was a reproductive individual, as indicated by the one-year old seedlings and old endocarps observed around it.

The inflorescence is characterized by the presence of several white to yellowish flowers, which attract several insect species. The flowering period is relatively short, and flowers rapidly transform into immature fruits. However, flowering is preceded by a period of inflorescence enlargement, which is longer for a larger species with massive inflorescences; these emerging inflorescences appear one or two months before anthesis begins (Henderson 2002). Like other palm species, *Astrocaryum* produces many young inflorescences, but some of these abort early in development, due to factors such as abnormal development, strong winds or heavy tropical storms. For example, from May to August (lowest production of flowers and fruits), several cold fronts characterized by temperatures as low as 10ºC, heavy rains and wind (Fig. 2), arrived in the region and destroyed many flowers.

Phenological patterns in palms are not always synchronized, even within a single population of of a species, and are highly related to environmental characteristics such as seasonality, weather and insolation levels. For example, Foster (1996) found that if the preceding dry season was too wet, many tree species flowered but failed to produce fruit. Although different *A. gratum* trees flower regardless of the season, the population showed a flowering peak between June to August, months which coincide with less intense precipitation (end of the dry season and the beginning of rainy season). In contrast, Cintra and Horna (1997) found that for a species of section *Huicungo* identified as *A. murumuru*, flowering was abundant in the rainy season, from October to January. Other species of *Astrocaryum* also appear to be synchronous and seasonal in their flowering and fruiting. *Astrocaryum aculeatum* has flowers from July to January and fruit production from February to August, and *A. vulgare* flowering and fruit production are from January to July. The two species are clearly asynchronous in their flowering with respect to each other (Moussa & Kahn 1997). Foster (1996) and Leigh and Windsor (1996) indicated that flower production might be triggered by water stress caused by the dry season.

The relatively low number of fruit bunches per year produced by each palm is similar to those found in other species of *Astrocaryum*. This genus varies greatly in the number of fruits produced. *Astrocaryum gratum* produced 700 (± 237.2) per bunch compared with the species identified as *A. murumuru* in Peru, which produced 349.2 (± 184.7) fruits per bunch (Cintra & Horna 1997), or *A. standleyanum* in Central America, which produced 300–800 fruits per bunch (Smythe 1989).

Fruit production is dependent on the numbers of flowers produced during the flowering period. Inflorescences may have up to 3000 individual flowers; however, only 19% become fruit. Sist (1989) indicated 36% fruit-set for *Astrocaryum sciophilum*. These low numbers are explained by several factors that affect the number of fruits produced by a palm, including early abortion and predation of immature fruits (Henderson 2002).

I also observed the highest concentration of ripe fruits on the forest floor during the rainy season from December to February. In contrast, Cintra and Horna (1997) found a concentration of ripe fruit from March to April for *A. murumuru*, while Peres (1994) in Brazil reported fruiting during rainy season (January to May) for the same species. This fruit and seed rain in different seasons has an important implication for wildlife. *Astrocaryum gratum* is used by wildlife for a long period of time (ca. 10 months of fruit availability). The seed then may be picked by secondary dispersers, such as rats and agoutis (Aliaga-Rossel et al. 2008, E. Aliaga-Rossel unpubl. data) or by seed predators, such as peccaries (Janzen 1971, Beck & Terborgh 2002). In this study, a snail (Mollusca: Gastropoda) was observed eating a ripe fruit.

Between May and June, when there is a low number of fruits available, many of the *Astrocaryum* seeds found on the floor of this study are infected with Coleoptera (family Bruchidae) (Delobel et al. 1995), which may attract different mammals to eat them (Silvius 2002). Also, the high concentration of fruit on the floor can be inversely related to fauna. For example, in areas with high concentration of white-lipped peccaries, they arrived at a fruiting tree and immediately destroyed all the seeds or young seedlings by turning over all the soil around the area. In contrast, in a defaunated forest, large numbers of fruits can be found below the parental tree (E. Aliaga-Rossel unpubl. data).

The seed experiment was started at the beginning of the rainy season when most of the seeds and ripe fruits are normally found on the forest floor. The experiments were set in an area with no chance of inundation, in order to minimize the potential effects that the events of the "La Niña" might have on the experiments on seed germination and emergence. *Astrocaryum* seeds are resistant and hard, resulting in slow germination. In this study the plumule of *A. gratum* appeared from 8 to 11 months; this period is within the range of rates of germination of other palm species (Cintra & Horna 1997, Rauch 1998, Meerow 2004); however, the emergence of the plumules is not always uniform, and variation could be related to the different degrees of maturation of the seed, humidity and angle. This rate of germination and the percent of total germination will vary among years, region or even from plant to plant collected in different seasons (Rauch 1998, Meerow 2004). For example, *Astrocaryum aculeatum* seeds germinated in artificial conditions took approximately 253 days for the complete expansion of the first bifid leaf, but in natural conditions germination could take up to 1044 days (Rauch 1998, Gentil & Ferreira 2005, Meerow 2004).

As was anticipated, buried seeds germinated in higher proportion than the ones left at the surface, reinforcing the relevant effect of secondary dispersers (agoutis, squirrels) that scatter hoard seeds and reducing the probability of seed predation from insects or other mammals (Cintra & Horna 1997, E. Aliaga-Rossel pers. obs.). Burial of the seeds by secondary dispersers also provides protection from exposure to drying and the necessary conditions to germinate. The results of this study indicate that when seeds are buried in the soil, they are more likely to germinate and emerge. Therefore, the hoarding of seeds is an important event for the survivorship of new individuals, the removal of these dispersers can affect the recruitment of this palm.

Heavy rains during the period of this study might have had a profound effect on the process of germination, by reducing direct sun exposure, by increasing sedimentation and leaf fall or by softening the soil and facilitating the growth of the radicle. Seeds left at the surface in this experiment were covered with a single layer of dead leaves, but after some months these were naturally covered with a fine layer of soil and another layer of dead leaves fallen from adjacent trees. This cover protects and increases moisture for the seed.

The experiments were set in an area without adult *Astrocaryum* palms in order to avoid seed predators, because a positive correlation exists between predation and seed density (Janzen 1971). In areas outside the zone of the experiment, at the end of May, seeds showed signs of fungus or insect infestation. In the experiments only two seeds, both in the unburied, shade area, showed signs of bruchid predation. This very low percentage of infestation can be the result of the removal of the fruit pulp (reducing the fruits' chances of being found) and the long distance from parental trees. In general, high aggregations of seeds are heavily predated by white-lipped peccaries, bruchids and other granivorous creatures and have a low likelihood of establishing into seedlings (Beck & Terborgh 2002, Silvius 2002).

The relatively low percentage of germinated seeds is common among palms. At a site in Peru, only five seeds of *Astrocaryum* (identified as *A. murumuru*) germinated with 5% survivorship (Cintra & Horna 1997). Despite the low germination rate and the high seed predation, prolific seed production maintains the population dynamics.

In contrast to other *Astrocaryum* species, such as *A. aculeatum* or *A. vulgare* which are used for ice cream or wine (juice) in Brazil (Moussa & Kahn 1997), *A. gratum* is not extensively used in the area. The indigenous people use the trunks for arrows, the hard endocarp for handicrafts such as rings and the leaves and stems are occasionally used as fences. The utilization of this common species has the potential to be expanded to satisfy the market for handicrafts for people living close to the touristic town of Rurrenabaque, Bolivia, so a knowledge of the phenology of this species is important to develop management plans for this use.

This study was done during "El Niño" (2007) and "La Niña (2008) events. Two of the areas where I plotted the palms flooded twice due to the river overflow (abnormal rainy season for both years, Fig. 2), but this did not affect the survivorship of adult trees, because *A.*

gratum has a preference for wet areas (Svenning 1999, Henderson 2002). The results presented here on flowering or fruiting are still representative.

The regular precipitation cycles (dry or rainy season) are part of the natural cycle in the Amazon basin (Sioli 1984). However, the global current effects known as the "La Niña" or "El Niño" are becoming more frequent and intense. Both phenomena signify continuous and long lasting droughts or flooding much higher than in a normal year. Therefore it is important to continue long term studies related to climate change and the response of the tree and of the community to a "normal year."

Although *A. gratum* flowers and fruit can be observed most of the months, there is a peak season for both. Flowering might be stimulated by environmental conditions such as water stress. Fruiting peaks correspond to the rainy season, when the palm is an important food resources for wildlife affecting distribution and movement. Therefore the palm must be considered when designing wildlife management plans. Future studies should examine pollinator populations, presence of pollinators in different seasons and factors influencing reproductive patterns of *A. gratum*. Also studies are needed of the role of water in seed germination, the fate of seeds in the wild, and relationship between seed predators and dispersers.

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