Factors Affecting the Distribution of a Threatened Madagascar Palm Species Dypsis decaryi

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ABSTRACT

The complex interactions of human disturbance, environmental requirements, seed dispersal agents, seed predators, and herbivores appear to have an important role in the limited distribution of a threatened palm, *Dypsis decaryi*, in southeast Madagascar. Human activities limit the growth and the recruitment of new individuals throughout much of its range. Seed dispersal agents tend to deposit seeds near the parent plant where seed predation is heavier than elsewhere. The success of dispersed seeds depends on the conditions where seeds are deposited. In nature, dispersed seeds deposited in sites with intermediate light and moderate moisture levels have a better chance of escaping predators, germinating, and becoming established.

Dypsis decaryi (Jum.) Beentje & J. Dransf. (Neodypsis decaryi Jum.) (Family Arecaceae, Subfamily Arecoideae, Tribe Areceae),[2] a rare, threatened palm species, is restricted in southeastern Madagascar to a narrow zone (about 20 km wide) between the humid rain forest of the southeast and the dry spiny forest of the southwest (see Fig. 1) (Du Puy et al. 1992, Ratsirarson 1993*b*, Eboroke 1994). *D. decaryi* appears to function ecologically as a "keystone species" (Ratsirarson and Silander 1996; see also Gilbert 1980, Terborgh 1986). It is locally dominant and shows asynchronous, continuous flower production throughout the year, providing crucial food resources for pollinators during certain periods of the year. *Dypsis decaryi* can also be considered a keystone species anthropologically. Local people rely on it for many resources (Ratsirarson 1993*a*). Leaves are harvested for thatching (Fig. 2); inflorescence bracts are collected for making baskets, hats, mats, etc., and the

fruit mesocarp is eaten. Seeds are heavily collected and exported for tropical horticulture use.

The main purpose of this study was to determine the effects of variation in microenvironmental conditions, biotic interactions, and human disturbances on the distribution and performance of *Dypsis decaryi*. Specifically, this study examined: (1) the importance of variation in light and water availability on germination, (2) the role of seed dispersers, seed predators, and herbivores on species distribution patterns, and (3) the effect of human activities on germination and seedling establishment. We focus on the early stages of the life cycle (seed, seedlings) because these represent critical phases in the life history of plants and may provide a key to understanding observed distribution patterns.

Methods

Field Sites. The field site was located in the Andohahela Nature Reserve in southeastern Madagascar, in the third of the three noncontiguous parcels (25°01′S, 46°09′E). This 500-ha reserve was established in 1939 to protect one of the few flourishing populations of *Dypsis decaryi* (Fig. 3). Today, this is the only substantial population throughout the range of the species where significant regeneration is occurring and a complete range of age and size classes can be found (Ratsirarson 1993b). Several small, isolated populations of *Dypsis* can also be found along ephemeral watercourses in the second parcel of the reserve, where some successful recruitment also occurs. In existing populations elsewhere, seedling and juvenile stages are rare or absent.

Granitic bedrock is the most abundant parent material at the study site and the soils are shallow oxisols with a low pH (Jenkins 1987, Nicoll and Langrand 1989). The emergent, discontinuous

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1. Distribution of *Dypsis decaryi* in Madagascar. Patterned area indicates the current natural distribution of the palm.

canopy is dominated by *Dypsis decaryi* (Fig. 4). The shrub layer subcanopy is dominated by species adapted to the seasonally dry local conditions and include members of the Apocynaceae, Euphorbiaceae, Didieraceae, and Rubiaceae (Nicoll and Langrand 1989, Eboroke 1994; Ratsirarson, unpublished data).

Light and Water Availability. Critical threshold light levels and water conditions may determine whether seeds germinate, and seedlings or juveniles survive (Uhl and Dransfield 1987). A germination experiment was initiated in June 1992, using a nursery plantation near the field site. The effects of three different treatments (seed presoaking, shading, and watering regime) on seed germination were examined. This information can be used not only to understand the optimal condition for seed germination and the subsequent effects on the distribution of the palm, but also to enhance ex situ conservation of the species (Chazdon 1988). Mature fruits were collected randomly from the natural range of the species and air dried

for approximately 10 weeks. Seeds were sown in test beds of locally available, loamy soils (approximately equal mixtures of silt, clay, and sand). Germination (emerging leaves) was recorded weekly and followed over five months with results tallied at 30, 60, 90, 120, and 150 days after sowing. The percentage of seeds germinating three months after sowing and the time required (in days) for 50% of seeds to germinate in each treatment were recorded.

Three levels of seed pretreatment were chosen: a control (no soaking) (G1), seeds soaked in water for 24 hours (G2), for 72 hours (G3), or soaked in boiling water for five minutes (G4). We selected these pretreatments because they stimulated germination in other palms (Nagao and Sakai 1979, Doughty et al. 1986, Broschat and Donselman 1988). Three different levels of shading were provided: no shading (S1), shading at 20 cm (heavy shading) (S2), and shading at 40 cm (moderate shading) (S3) above the ground. Grass culms were cut and arranged horizontally (approximately 8 cm thick) on a wooden framework to provide the shading, which is a standard, local plantation practice. Equipment to measure light levels in these treatments was not available. Three different levels of watering were chosen: no supplemental watering (W1), watering once a day (W2), and watering twice a day (W3). Watering was continued throughout the experiment. In total, this constituted a $4 \times 3 \times 3$ factorial design (36 treatments). Forty seeds were used in each treatment. Each treatment was replicated twice. A three-way analysis of variance statistical design was used to analyze the data.

Fruit and Seed Dispersal. The predicted seedling recruitment (i.e., dispersal) profile of the palm was determined using a seedling recruitment model, in order to understand the effective dispersal patterns in *Dypsis* (Ribbens et al. 1994). Two transects of 100 m each were established through the palm population inside the reserve. The number of the palm seedling recruits in each successive 2×2 m quadrat along the transects was counted. Seedling recruitment was predicted as a function of adult size (height) and distance from potential parents, using a maximum likelihood statistical analysis. This approach determines the best match between the observed and the predicted seedling distributions (see Ribbens et al. 1994 for details). The height of the adult individuals, which is the best predictor of reproductive output (Ratsirarson 1993b), within 20 m

Table 1. Effect of seed pretreatment on germination of Dypsis decaryi.

Seed treatments		Percentage of seeds germinating after 90 days (N = 18)		Number of days to 50% seeds germination (N = 18)	
No. presoaking (G1)	Average	29.3	a*	110.22	a
	SD	22.3		24.62	
	Range	0–72.5		60–170	
Presoaking in water for 24 hours (G2)	Average	21.27	a	128.33	a
	SD	21.8		36.86	
	Range	0–62.5		60–200	
Presoaking in water for 72 hours (G3)	Average	38.9	b	99.55	b
	SD	23.3		27.3	
	Range	7.5–82.5		55–160	
Presoaking in boiling water for 5 minutes (G4)	Average	0.00		0.00	
	SD	0.00		0.00	
	Range	0.0–0.0		0.0–0.0	

* Statistically significant differences among values are indicated with different letters using Duncan's multiple range test at the 5% level.

from the transect was recorded, and the distance between the center of the quadrat and the adult individuals was taken. The mapping of adult palms relative to the seedling transect quadrats was accomplished by triangulation from compass bearings and observed distances along the transect.

Seed Predation and Herbivory. Some of the *Dypsis* seeds on the ground were consumed by either scolytid beetles (*Lanurgus* sp.) or nocturnal mouse lemurs (*Microcebus murinus*, Miller). The beetles bore through the bony endocarp and lay their eggs inside the seeds (Fig. 5). The larvae develop inside while feeding on the endosperm and the seed embryo. The emerging females leave after mating within the seeds and search for new seeds on which to oviposit (see Ratsirarson 1993b). The percentage of seeds infested by these beetles was counted in July 1992 inside successive 1 × 1 m plots, laid out along a transect through a stand of 30 parent plants.

Mouse lemurs crack open the dry seeds, and eat the endosperm (Fig. 6). An experimental study on seed predation was initiated to determine whether the escape of the seeds from lemur predation was habitat-dependent. Seed removal was studied in a two factorial design with the treatments being beneath or away (i.e., adult individuals at least 10 m away) from parent plants, and in an opening (gap) or covered (non-gap) site. A gap is defined as a cleared area at least 5 m in diameter. All non-gap sites were more than 20 m away from a gap area. The resulting combination of factors are referred to as: open with *Dypsis*

decaryi, open without *Dypsis decaryi*, covered with *Dypsis decaryi*, and covered without *Dypsis decaryi*. A pile of 50 seeds was set on the ground at each site in June 1992. Each treatment was replicated 10 times. Seeds were censused after 7, 14, 27, 32, and 50 days. Based on our earlier studies, any removed seeds were most likely eaten by nocturnal mouse lemurs (see also below).

Results

Light and Water Availability. The time needed for 50% of seeds to germinate varied from 55 to 200 days (Tables 1–3). The percentage of germinating seeds after 90 days was greater (40%) for seeds presoaked in water for 72 hours than for the other treatments (Table 1). Soaking in boiling water was lethal. The percentage of germinating seeds after 90 days and the time required for 50% of the seeds to germinate were greater in treatments without shading (Table 2). Watering twice a day increased the percentage of germinating seeds after 90 days, and decreased the time required for 50% of the seeds to germinate (Table 3). Open sunlight and supplemental watering are thus important factors promoting seed germination. Presoaking, shading, or watering treatments alone had a highly significant effect on the time needed for germination as well as the percentage seed germination (Table 4). The interaction between shading and watering showed significant effects on seed germination after 90 days, but no effect on the time needed for germination (Table 4). For seeds that were not pretreated (G1 treat-

Table 2. Effect of shading on germination of Dypsis decaryi.

Seed treatments		Percentage of seeds germinating after 90 days (N = 18)		Number of days to 50% seed germinations (N = 18)	
No shading (S1)	Average	55.0	a*	89.4	a
	SD	15.9		31.34	
	Range	22.5–82.5		55–170	
Light shading (40 cm from the ground) (S3)	Average	21.1	b	120.06	b
	SD	17.0		26.46	
	Range	0.0–57.5		80–200	
Heavy shading (20 cm from the ground) (S2)	Average	13.8	b	128.67	b
	SD	10.5		23.92	
	Range	0–35		97–180	

* Statistically significant differences among values are indicated with different letters using Duncan's multiple range test at the 5% level.

ment), germination was accelerated when planted in full sunlight with supplemental watering (Table 5).

Fruit and Seed Dispersal. The local distribution of *Dypsis decaryi* adults was significantly aggregated (Ratsirarson 1993b). The predicted seedling recruits tend to be concentrated beneath the parent plants (Fig. 7). A significant correlation was seen between the observed and the expected recruitment in each quadrat along the transect ($r = 0.577$; $p < 0.01$, see Ratsirarson 1993b for details). Mean dispersal distance was calculated by distributing expected recruits around a standardized parent plant and determining the average distance from parent to recruit (see Ribbens et al. 1994 for methods). The mean dispersal distance calculated was quite small, 2.78 m. Fruits are small in size (mean diameter = 1.41 ± 0.12 cm, $N = 150$) and can secondarily be moved by gravity, water, and/or by a variety of vertebrates including ring-tailed lemurs (*Lemur catta*), mouse lemurs (*Microcebus murinus*), black parrots (*Coracopsis vasa*), and wild pigs (*Potamocherus larvatus*) (Ratsirarson, unpublished data), but in any case the viable seeds are apparently not moved far from the parent plant.

The behavior of animal dispersal agents was observed during the peak fruit production. During the fruiting season, ring-tailed lemurs (*Lemur catta*) and mouse lemurs (*Microcebus murinus*) consume the edible parts of the fruit (mesocarp), and drop the unharmed seeds near the parent plant. Lemurs are territorial with restricted home ranges. The territory of ring-tailed lemurs (*Lemur catta*) in the Beza Mahafaly reserve, for example, was reported to be limited between 400 and 900 m² (approximately a radius of 10–16 m) (Ratsirarson 1987). The limited territories in this important dispersal agent may severely restrict the effective dispersal of the seeds. Black parrots (*Coracopsis*

Table 3. Effect of watering on germination of Dypsis decaryi.

Seed treatments		Percentage of germinating seeds after 90 days (N = 18)		Number of days 50% of seeds germinate (N = 18)	
No watering (W1)	Average	22.5	a*	128.28	a
	SD	22.4		36.13	
	Range	0–82.5		55–200	
Watering once a day (W2)	Average	29.9	a	105.33	b
	SD	24.6		22.91	
	Range	0–72.5		55–145	
Watering twice a day (W3)	Average	37.5	a	104.5	b
	SD	21.2		30.71	
	Range	7.5–72.5		60–80	

* Statistically significant differences among values are indicated with different letters using Duncan's multiple range test at the 5% level.

Table 4. *ANOVA: effect of presoaking, shading, and watering on* Dypsis decaryi *germination after 90 days, and on the time required (in days) for 50% of seeds to germinate.*

		P values	
Treatment	df	Germin-ation after 90 days	Germin-ation time
Presoaking	2	0.000	0.006
Shading	2	0.000	0.000
Watering	2	0.001	0.013
Presoaking × Shading	4	0.832	0.827
Presoaking × Watering	4	0.319	0.523
Shading × Watering	4	0.021	0.603
Presoaking × Shading × Watering	8	0.106	0.723

Table 5. *Effect of shading and watering on the germination of* Dypsis decaryi *seeds (non-pretreated).*

Treatment	Percentage of seeds germinating after 90 days ($N = 6$) [Mean ± SD (Range)]	
No shading (S1)	55.00 ± 17.53 (30–72.5)	a*
Moderate shading (S2)	15.41 ± 9.00 (5–25)	b
Heavy shading (S3)	17.50 ± 10.72 (0–30)	b
No watering (W1)	23.33 ± 26.25 (0–72.5)	a
Watering once a day (W2)	29.59 ± 21.81 (5–65)	a
Watering twice a day (W3)	35.00 ± 21.15 (12.5–72.5)	b

* Statistically significant differences among values are indicated with different letters using Duncan's multiple range test at the 5% level.

vasa) consume the edible parts of the fruits, and also tend to drop the undamaged seeds around the parent plant. Wild pigs (*Potamocherus larvatus*) ingest *Dypsis* fruits and deposit the seeds in their feces, often more than 30 m from the closest parent plant. However, the seeds passing through the pig's digestive system fail to germinate (0% of the seeds planted from wild pig's feces germinated after 10 months; Ratsirarson, unpublished data).

Seed Predation and Herbivory. The average percentage of seeds infested by *Lanurgus* sp. (Scolytidae) beetles inside the 1-m² plots was 92% at 1 m from focal plants. Infestation declined with

distance from the parent (Fig. 8). No other insects were observed to feed on *Dypsis decaryi* seeds.

Seeds are also preyed upon by the nocturnal mouse lemurs (*Microcebus murinus*). Their tracks and feces were obvious on remaining seeds. Live traps were used to capture these lemurs using seeds as bait. Three mouse lemurs were caught in 46 traps that were set out beginning in June 1992 and followed for 2.5 months.

Seed disappearance from the seed removal trials was followed over 50 days. Seed removal by mouse lemurs differed among treatments. A chi-
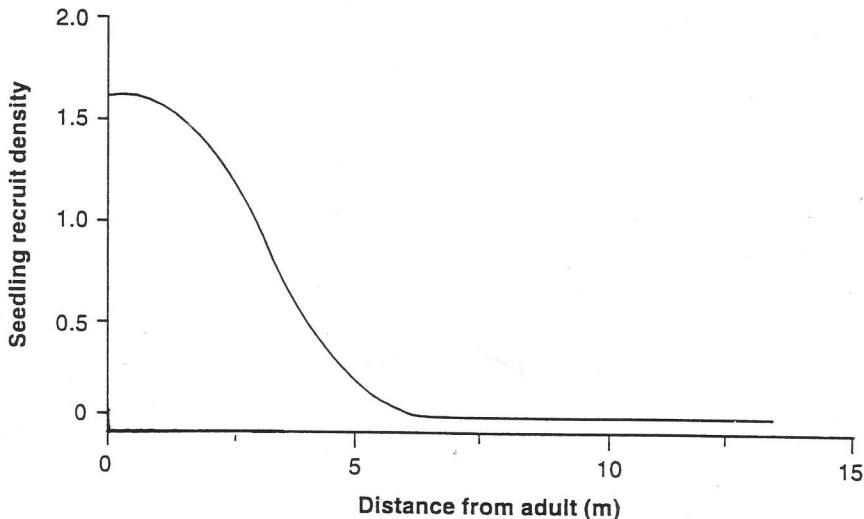
7. Predicted recruitment profile. The predicted density of recruits per m² is shown as distributed around a standardized parent plant of 3 m height.
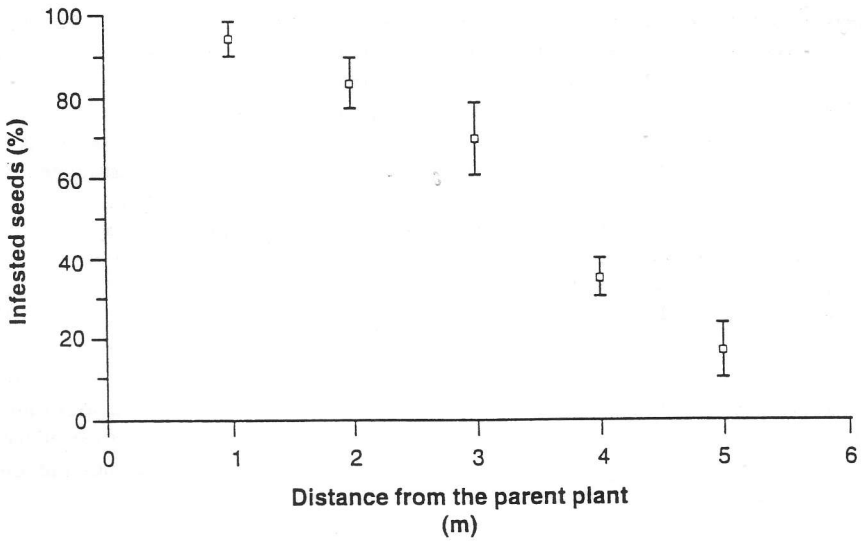
8. Seed infestation by scolytid beetles as a function of distance from the parent plant. Points represent the average percentage of seeds infested by scolytid beetles inside successive 1×1 m plots, at varying distances from parent plants. Error bars are ± 1 SE, $N = 30$.

square (χ^2) goodness of fit analysis showed a significant association between seed removal and treatment at the 27th ($\chi^2 = 9.12$, df $= 3$, $p < 0.05$), 32nd ($\chi^2 = 12.11$, df $= 3$, $p < 0.01$), and 50th ($\chi^2 = 16.32$, df $= 3$, $p < 0.01$) census days (Fig. 9). This significant association appears to be due to the effect of the closed canopy with no *Dyp-*

sis decaryi cell. Seed removal underneath the canopy was significantly greater than in the gap area from the 27th day of census onward.

The effect of insect herbivory on non-seed stages also appears to be significant in *Dypsis decaryi*. Seedlings and juveniles were susceptible to rhinoceros beetle (*Oryctes pyrrhus*, Scarabeidae)
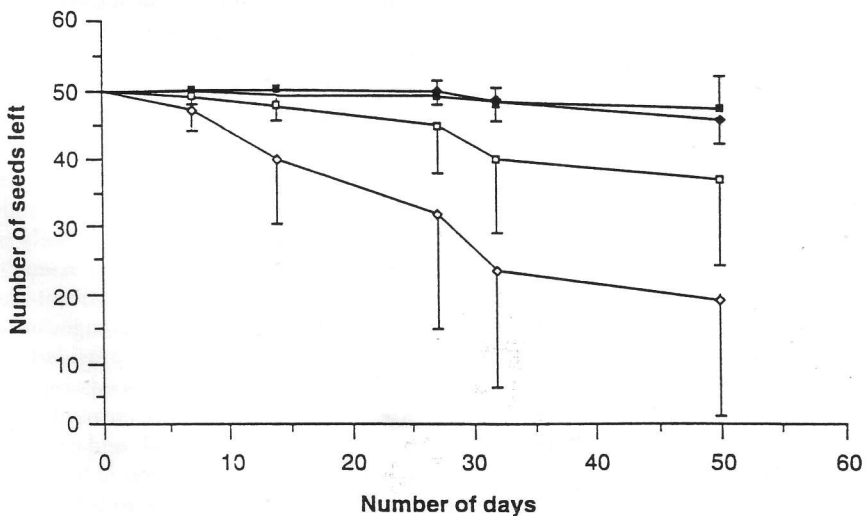
9. Seed removal by mouse lemurs (*Microcebus murinus*). Points represent the number of remaining seeds at different census periods. The four treatments were: seeds placed under a closed canopy, without *Dypsis* present (filled squares (■); seeds placed in an open gap, with *Dypsis* nearby (filled diamonds ◆); seeds placed under a closed canopy, with *Dypsis* (open squares □) and seeds placed in an open gap, without *Dypsis* (open diamonds ◇). Error bars are 1 SE.

attack. The beetles dig into the plant, consume the sap, and destroy the apical meristem. Approximately 95% of juvenile, and 20% of seedling mortalities are caused by rhinoceros beetles (Ratsirarson 1993a, b).

Human Disturbance. Human activity is one of the most important factors controlling the current viability and the distribution of *Dypsis decaryi* (Ratsirarson 1993a). Local people cut and frequently burn much of the area outside the protected reserve for agricultural practices (mainly tobacco and maize plantations). Few or no seedlings and juveniles are to be found outside protected areas (Ratsirarson 1993b). Although adult individuals are resistant to fire (Fig. 10), seedlings and juveniles are very sensitive (Ratsirarson 1993a, b). The absence of younger stages (seedlings and juveniles) in the unprotected populations limits natural regeneration. In addition, *Dypsis decaryi* does provide important needs for local people. Leaves and seeds of most individuals outside the reserve and some individuals inside the reserve are heavily harvested (Ratsirarson 1993a, Ratsirarson et al. 1996).

Discussion

Poorest germination occurred when seeds were neither pretreated nor given supplemental watering, which is most likely the conditions of the seeds in their natural habitat. Soil moisture and light resources seem to be important keys to understanding the distribution of *Dypsis decaryi*. In semi-arid zones, like the site occupied by *Dypsis decaryi*, a moderate level of shading may provide that critical moisture level for germination that otherwise would be low in full sunlight. Partial shading under some tree or shrub cover with some moisture supply appears to be the optimal environmental situation for *Dypsis decaryi* establishment. Seeds in full sunlight may desiccate rapidly and fail to germinate. This is perhaps why individuals are largely excluded from the drought-stressed conditions of the drier spiny forest region. In the eastern edge of the spiny forest zone, *Dypsis decaryi* is found only along ephemeral watercourses. Locally, individual palms tend to be concentrated either on rocky slopes in which water seepage is sometimes available or along temporary watercourses. In the adjacent rain forest, *Dypsis decaryi* seeds may germinate readily but seedlings may be poor competitors under the continuous low light levels found there. This may explain the

absence of *Dypsis decaryi* from the nearby wet forest communities. Interspecific interactions (e.g., competition for light resources) were not explicitly examined in this study but may play important roles in the distribution of this palm.

The low mean dispersal distance (about 3 m) in *Dypsis decaryi* probably reflects (1) the limited availability of dispersal agents (seeds tend to passively fall below parent) or (2) the very limited effective range of dispersal agents (Hubbell 1979, Howe and Smallwood 1982, Howe 1990). Observations on the main dispersal agents indicate either narrowly restricted territories or home ranges (i.e., *Lemur catta* and *Microcebus murinus*), or a tendency to feed on the fruit mesocarp and drop the seeds below local foraging sites, near the parent plants.

In the past longer distance dispersal may have been accomplished by now extinct megafauna dispersal agents, including the giant lemurs (*Archaeolemur* spp.) and the elephant birds (*Aepyornis* spp.). Bone and egg fragments of *Archaeolemur* spp. and *Aepyornis* spp., respectively, have been reported from a cave (Andrahomana), within the current distribution of *Dypsis decaryi* in the southeast of Madagascar (Walker 1967). Based on the cranial and dental morphology of *Archaeolemur* spp., they appear broadly convergent with *Papio* baboons, and were likely to have preferred a wooded habitat, had a frugivorous diet, and possessed a greater home range than the present lemur species (Martin and Wright 1967, Tattersall 1973, Dewar 1984). *Aepyornis* spp. were reported to be mainly vegetarian (Wetmore 1967). These elephant birds were likely generalist herbivores and frugivores (Dewar 1984). Cracraft (1974) interpreted the robustness of *Aepyornis* as evidence of forest habitat preferences. These extinct megafauna species (*Aepyornis* spp. and *Archaeolemur* spp.) and *Dypsis decaryi* likely occurred in the same ecological communities, and the fruits of *Dypsis* may have been a significant component of their diet. The larger home ranges or territories of these megafauna may have provided a greater dispersal range for the palm seeds in the past, and a wider distribution than is currently observed.

Most of the seeds fall underneath the parent plant where seed predation is high. Seed dispersers play an important role in the escape from seed predation (Janzen 1971, 1972). The removal of seeds from the vicinity of the parent may thus increase the probability of recruitment since seed predators concentrate their activities under the

parent plant (Howe et al. 1985). Palms appear to be more susceptible to seed predation than other flowering plants, not only because of the size of the seed resource, but also apparently because of more limited dispersal (Vandermeer et al. 1979, Tomlinson 1990). In *Euterpe globosa,* Janzen (1971) reported that when the densities of the scolytid beetle *Cocotrypes carpophagus* were at their maximum, the beetles may destroy all the seeds produced. Willson and Janzen (1972) also found that more than 80% of *Scheelea rostrata* seeds near parent plants were destroyed by a species of bruchid beetle.

Seed removal by nocturnal lemurs appears to be greater underneath a closed canopy than elsewhere. This result may be related to the arboreal behavior of *Microcebus murinus,* which may be better protected from potential predators underneath closed canopies (Richard and Dewar 1991). Removal of seeds left in a gap area was very low. Mouse lemurs (*Microcebus murinus*) are reported to have a wide range in diet (Richard and Dewar 1991), from plant parts (e.g., fruits, seeds, flowers, leaves) and insects (moths, mantises, spiders) to small vertebrates (birds, chameleon, mice) (Petter et al. 1977). Seeds may be an important dietary component of these lemurs during certain periods of the year. More than 5% of *Dypsis decaryi* seeds were seen destroyed by lemurs (as evidenced by seed fragments remaining) within 1 m of the parent plant (Ratsirarson, unpublished data). The lower seed removal rate observed under *D. decaryi* canopies, compared to other closed-canopy conditions, undoubtedly reflects the fact that seeds present naturally underneath the parent plants were not removed prior to the experiment. This inflated the local density of seed in the *D. decaryi* canopies treatment. Here lemurs were probably removing experimental as well as resident seeds.

There was a clear survival advantage to dispersal of *Dypsis decaryi* away from the parent plant. However, the advantage of dispersal is related to the habitat in which the seed is deposited (Howe et al. 1985). The optimal environment for seed survival does not appear to be the optimal environment for germination. Seeds dispersed and deposited in a completely open area may desiccate

and fail to germinate, while seeds deposited below a closed canopy are less likely to survive given the lower light level and the higher predation levels by mouse lemurs. The trade-off between dispersal and predation depends mainly on the microhabitat of the sites where the seeds are deposited which in turn determines the distribution of the palm. In addition, *Oryctes pyrrhus* beetle herbivory appears to have an important effect on early stages (seedling and juvenile) of development of *Dypsis decaryi* populations. Rhinoceros beetles are reported to be a common cause of mortality in many palm species. For example, one of the main threats to the *Borassus aethiopium* palm population in Senegal has been reported to be the large-scale attack by rhinoceros beetles (*Oryctes* spp.) (Sambou et al. 1992). Risk of adult *Dypsis decaryi* mortality to rhinoceros beetle attack appears to be very low (much less than 1%) in contrast (Ratsirarson, unpublished data). Human activities also severely limit the current distribution of this palm. Intensive leaf harvest (up to 100% of leaf number in each adult individual) and the heavy seed collection (up to 100% of seed produced per individual) significantly limit growth and the natural regeneration of *Dypsis decaryi* (Ratsirarson et al. 1996).

In sum, the limited natural distribution of *Dypsis decaryi* in southeast Madagascar seems to be due to the complex interaction of environmental requirements, human disturbance, and the effects of seed dispersers, seed predators, and herbivores. The widespread human destruction of natural habitat (cutting and burning) associated with the local intense harvesting of palm resources (leaves, seeds) limits the growth as well as the recruitment of new individuals. Although adult individuals are resistant to the effect of fire, early stages of the life cycle are very sensitive. Fruit and seed dispersal are limited and seedling recruitment is concentrated underneath the parent plant. The current main animal dispersal agents (lemurs, parrots) deposit seeds near their foraging sites close to adult palms. Seed mortality by seed predators (scolytid beetle, mouse lemurs) is higher underneath parent plants and under closed canopy than elsewhere. Thus, seeds dispersed away from adult

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2. *Dypsis decaryi* leaves used in thatching local village homes. View is east toward the wet, montane forest zone. 3. Population of *Dypsis decaryi* in the third parcel of Andohahela Reserve. 4. Emergent canopy of *Dypsis decaryi* over the spiny shrub understory in Andohahela Reserve. View is west toward the arid zone.
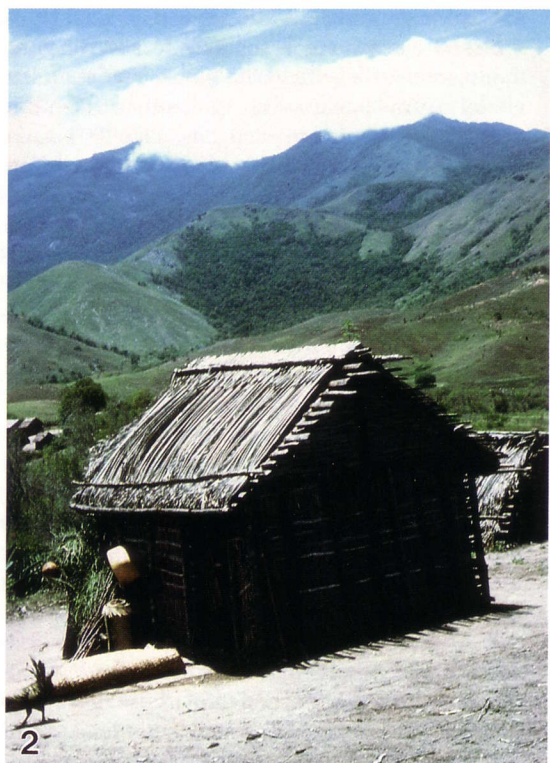
5. Oviposition holes by scolytid beetles (*Lanurgus* sp.) in *Dypsis decaryi* seeds. On the right are seeds cracked open with an adult *Lanurgus* sp. indicated by the arrow. Mature seed size is approximately 1.40 cm in diameter. 6. The mouse lemur *Microcebus murinus* is the main vertebrate seed predator and disperser. 10. Effects of human disturbance on *Dypsis decaryi*. Repeated burning at this site has left charcoal scars on the trunk of this individual. Adults can tolerate a moderate level of repeated fires, seedlings and juvenils cannot.

Dypsis decaryi may have a higher chance of survival. Subsequent to dispersal, successful germination and recruitment depend on the microhabitat where seeds are deposited.

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PALM LITERATURE

SUBHADRABANDHU, S. AND S. SDOODEE (eds.) *Fifth International Sago Symposium*. Hat Yai, Songkhia, Thailand, 27–29 January 1994. *Acta Horticulturae* 389. June 1995. 278 pp. Dfl. 88.00 softcover.

Eleven of the 19 papers in this fifth symposium proceedings are devoted to sago starch as an industrial raw material and to secondary palm products. Ethanol, protein-enriched sago starch, and glucose syrups are examples of starch products discussed. Sago leaf pulp for papermaking and sago pith residue as a green manure represent the latter product group. Various aspects of sago palm cultivation are dealt with in six papers on topics such as research needs, agroforestry, and seedling production. Two presentations covered economics: a cost-benefit analysis of sago production and a study of starch productivity.

This excellent volume represents another milestone in the ongoing attempt to transform the sago palm (*Metroxylon sagu*) into a major commercial species. Prospects of achieving that goal are promising.

To enhance the utility of this review, information on the four preceding international sago symposia, held between 1976 and 1990, is given below[1]; a sixth symposium took place in 1996[2]. Since 1990, periodic information on sago palm developments has also been furnished by a sago newsletter[3].

1. Tan, K. (ed.) *Sago-76: Papers of the First International Sago Symposium*. 330 pp. Kemajuan Kanji, Kuala Lumpur, Malaysia, 1977; Stanton, W.R. and M. Flach (eds.) *Sago: The Equatorial Swamp as a Natural Resource*. Proceedings of the Second International Sago Symposium. 244 pp. Martinus Nijhoff, The Hague, Netherlands, 1980 (see review in *Principes* 27(1):49–50, 1983); Yamada, N. and K. Kainuma (eds.) *The Third International Sago Symposium: Sago-'85*. 233 pp. Tropical Agriculture Research Center, Yatabe, Tsukuba, Ibaraki, Japan, 1986; Ng Thai-Tsiung, Tie Yiu-Liong and Kueh Hong-Siong (eds.) *Towards Greater Advancement of the Sago Industry in the '90s*. Proceedings of the Fourth International Sago Symposium. 225 pp. Ministry of Agriculture, Sarawak, Malaysia, 1991.

2. The Sixth International Sago Symposium was convened December 9–12, 1996 in Pekanbaru, Indonesia. The theme of the symposium was "Sago: The Future Source of Food and Feed." Proceedings will be published.

3. *Sago Communication* is published three times per year by Tsukuba Sago Fund, 791–27 Inaoka, Tsukuba, Ibaraki 305 Japan.

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