Ignorant seed predators and factors affecting the seed survival of a tropical palm

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In addition to acting as seed predators, some terrestrial mammals bury seeds via scatter hoarding. This study system used two permanent plots in examining the interaction between small rodents and the seeds of the palm *Astrocaryum mexicanum*. We tested how experimental burial, and fruiting status of the parent, distance to the parent, seed size, and microsite characteristics affect the survival of these seeds. Up to 34% of the buried seeds that were exposed only to ignorant rodent foragers (individuals not responsible for burial) survived. In comparison, less than 1% of seeds buried by scatter hoarding rodents survived in previous studies, a percentage that is comparable to the low survival of unburied seeds in this study (< 2%). Although unburied seeds had very low survival, increasing distance and/or seed density positively affected survival of unburied seeds. Distance to parent had no effect on buried seed survival.
Buried seed survival was most strongly and significantly determined by the fruiting status of the trees under which they occurred. Seeds experienced significantly greater predation if buried under "parent" trees that fruited during the experiment. Buried seed survival was also negatively affected by germination, as germination may signal the presence of a seed to foraging rodents. There was some indication of a positive effect of tree density on seed survival between the two plots, whereas differences in rodent abundance appear to have no effect on seed survival. Seed size and microsite characteristics had no significant effect on buried seed survival, likely due to the greater proportional effects of other factors and the longevity of *A. mexicanum* seeds. The results of this study were used to generate a hypothetical causal network showing how comparatively low recovery of buried seeds by ignorant foragers – combined with processes determining the removal of scatter hoarding foragers from their scattered seed caches – may affect seedling recruitment in *A. mexicanum*.

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Recruitment limitation is becoming increasingly recognized as a potent ecological feature of forest dynamics (Clark et al. 1999), especially as it pertains to the maintenance of species diversity in such complex systems as tropical forests (e.g. Tilman 1994, 1999, Hubbell et al. 1999). Seed predation and dispersal by vertebrates are key processes determining the variability in seed survival within forests, particularly in wet tropical forests, where most seeds are handled by vertebrates (Dirzo and Domínguez 1986). The mechanisms by which predation and dispersal of seeds effect variability in seed survival are hard to grasp, for tracking seed fates and the behavior of their associated predators and dispersers is logistically difficult.

Rodents may be especially influential in seed survival because of their high relative abundance and ubiquity (Robinson and Redford 1986, Emmons and Feer 1997), and their tendency to disperse seeds by burying them (e.g. Fleming and Brown 1975, Price and Jenkins 1986, Forget 1991). Burying seeds in dispersed caches, or

scatter hoarding (Morris 1962), is common behavior from spiny pocket mice (e.g. Fleming and Brown 1975, Brewer and Rejmánek 1999) to large caviomorph rodents (e.g. Morris 1962, Smythe 1978). Caching behavior potentially enhances plant recruitment by decreasing the probability of predation of seeds, maintaining seed viability, and promoting seedling establishment (Vander Wall 1990). Scatter hoarding behavior presumably benefits the scatter hoarding rodent by giving that individual better or exclusive access to seed resources compared to a competitor that is ignorant of the locations of cached seeds (Smith and Reichman 1984). Few studies, however, have actually quantified the numbers of seeds buried by rodents (Forget 1990, Vander Wall 1990). Further, whether or not the exposure of seeds exclusively to ignorant foragers results in relatively higher seed survival is poorly understood, for any given species of seed predator and prey. The factors affecting the survival of buried seeds have not been well documented and remain largely unknown (but see e.g. Stapanian and Smith 1986, Vander Wall 1995). The potential effects of distance and/or density of unburied seeds (Janzen 1970, Connell 1971) have been studied for a number of tropical plant taxa (see review in Hammond and Brown 1998), and a small number of studies have attempted to determine the local habitat factors associated with increased mortality of unburied seeds (e.g. Willson 1988, Osunkoya 1994, Forget 1997).

Despite the presumed benefits of burial for seeds, scatter hoarding rodents are remarkably adept at recovering their own caches; the few estimates of recovery often range above 98% of cached seeds (see review by Vander Wall 1990). It is conceivable that scatter hoarding does not enhance seed survival unless forces act to prevent the scatter hoarder from recovering its buried seeds. Therefore, the objectives of this study were to (1) quantify the survival of seeds exposed to ignorant individuals (not responsible for burying the seeds) and compare this survival to the recovery of seeds by scatter hoarders in a previous study, (2) quantify the effect of experimental burial on the survival of seeds exposed to ignorant foragers, and (3) examine the relative importance of several factors on buried and unburied seed survival: distance to parent/seed density, phenology of the parent (i.e. reproductive or not), seed size, and microsite characteristics. Other interactions of the focal species, an understory palm (*Astrocaryum mexicanum*) and its dominant seed predator/disperser, the spiny pocket mouse (*Heteromys desmarestianus*), have been documented (Brewer and Rejmánek 1999).

Methods and materials

Study site and species

This study was conducted from August 1998 to June 2000 in two permanent, 1-ha plots in a lowland, evergreen seasonal tropical forest (Beard 1944) in the Bladen Nature Reserve in southern Belize (16°34′N, 88°43′W, ca 45 m elevation). Annual rainfall is approximately 2500–3000 mm, with a distinct dry season from February through May. Plots 1 and 2 are located in areas of mature-phase forest and are similar in physical structure and richness of tree species, but differ in age of their alluvium substrate, distance to the Bladen River, and the density of the study tree species, *Astrocaryum mexicanum* Liebm. ex Mart. (Palmae) (Table 1).

Fruiting individuals of *A. mexicanum* can be found throughout the year, but *A. mexicanum* fruits are most abundant during the mid-wet season (September–November) and are scarce during the dry season. Infructescences are borne and mature sequentially on each tree (mean 1.6 per tree $\pm$ 0.08 SE, range = 1–4,

Table 1. A comparison of the 1-ha plots used in the seed survival experiment. Mean (SE) numbers and frequencies of *Astrocaryum mexicanum* individuals are derived from counts in six belt transects per plot. Frequency is the proportion of intervals in a belt transect with at least one individual.

	Plot 1	Plot 2
Astrocaryum mexicanum		
Number of individuals*		
[a]Seedlings ($\leq$5 leaves)	12.8 (2.1)	6.7 (0.72)
[b]Stems of reproductive size ($>$1 m)	13.3 (1.5)	7.3 (1.3)
% Individuals of reproductive size in fruit	53	56
Frequency of individuals		
[c]Seedling ($\leq$5 leaves)	0.67 (0.049)	0.47 (0.067)
[d]Stems of reproductive size ($>$1 m)	0.68 (0.070)	0.48 (0.060)
Heteromys desmarestianus (spiny pocket mice)		
[e]Lincoln-Petersen population estimate	66 (15.5)	50 (17.5)
Upper-lower 95% confidence bounds	48–112	32–108
Distance to the Bladen Branch of the Monkey River	250 m (older alluvium)	50 m (young)
Number of stems/species $\geq$10 m dbh	327/91	358/88

* Ratio of mature stems to seedlings = n.s. $t_{1,10} = 0.21$, $P = 0.8$; [a]$t_{1,10} = 3.04$, $P = 0.012$; [b]$t_{1,10} = 2.94$, $P = 0.015$; [c]$t_{1,10} = 2.41$, $P = 0.037$; [d]$t_{1,10} = 2.17$, $P = 0.055$; [e]based on the null model M(0), generated by CAPTURE.

$n = 100$ trees). The nuts are borne together in tight clusters of about 25 nuts per infructescence (mean = 23.5 ± 0.89 SE, range = $10-41$, $n = 60$ trees). Nuts average 4.7 cm in length (± 0.02 SE, $n = 730$ nuts) and weigh on average 14.5 g (± 0.16 SE, $n = 673$). We refer to the *A. mexicanum* nut (technically a nuculanium, Spjut 1994) as a seed throughout this study, since it is the smallest unit of dispersal (i.e. diaspore), and in that sense is equivalent to a seed. *Astrocaryum mexicanum* seeds that have fallen in the wet season readily germinate within 3 to 6 months; germination in the wet season is not enhanced by burial (Brewer unpubl.).

Primary dispersal of *A. mexicanum* seeds is by gravity. The spiny pocket mouse (*Heteromys desmarestianus*) is the dominant handler of *A. mexicanum* seeds in the study area (Brewer and Rejmánek 1999). This burrowing mouse is also the most abundant terrestrial mammal in the study area (Brewer and Rejmánek 1999), and is often the most abundant terrestrial mammal in many of the forests where it is found throughout Central America (Reid 1997). Spiny pocket mice scatter hoard 5–21% of the *A. mexicanum* seeds that they handle, burying the seeds just under the soil surface (i.e. covered with approximately 1–2 cm of soil) (Brewer and Rejmánek 1999). Most of the seeds are scattered and buried less than 5 m from the parent tree (mean distance = 4.3 m ± 0.59 SE, Brewer and Rejmánek 1999). More than 99% of all of these buried seeds are eventually retrieved by the rodents and taken to burrows (Brewer unpubl.).

Seed survival and germination

Thirty-two *A. mexicanum* trees of reproductive size (> 1 m) were randomly selected in each plot for the experiment, and the reproductive status of each tree was recorded. Trees were selected such that the bulk of the seed shadow (a 5-m radius circle, Brewer and Rejmánek 1999, Brewer unpubl.) of an individual did not overlap with that of another experimental tree, although other reproductive individuals of this species might be closer than 5 m. Seeds of *A. mexicanum* were gathered > 500 m away from the plots.

Seed survival of *A. mexicanum* was examined by placing 16 seeds divided equally between two distances, 1 m and 5 m from the "parent" tree, along eight 45° azimuths from the stem. All of the seeds beneath an individual tree were either buried or left on the soil surface ("unburied"), the treatment being randomly assigned to each tree. Seeds were buried in a similar way that spiny pocket mice bury seeds (Brewer pers. obs.): just beneath the soil surface (1 to 1.5 cm) with replacement of the soil and leaf litter (if present). This design more closely resembles the behavior of spiny pocket mice than a design mixing

buried and unburied seeds. When buried by these mice, *A. mexicanum* seeds are taken within 1–3 nights of being left on the forest floor and are not found mixed with unburied seeds.

Care was taken to prevent contact of the seeds with sources of human scent, although direct handling of seeds has no effect on removal rates or fates of the seeds (Brewer pers. obs. and unpubl.). In order to distinguish between experimental and other seeds and in order to follow seed survival, all seeds were tagged with pieces of white Dacron fishing line, not anchored at an end, by sewing the line through the apical pericarp of the nut (Brewer and Rejmánek 1999). The length of each seed was measured with calipers just before placing it on or in the soil.

Microsite characteristics were recorded as categories for each seed location: (1) distance to the nearest fruiting individual of *A. mexicanum*, (2) distance to the nearest log (> 10 cm minimum diameter), (3) distance to nearest buttress, (4) distance to the nearest woody liana > 2 cm diameter, (5) distance to the nearest non-*A. mexicanum* palm, (6) percent herb cover, and (7) litter depth (in 1-cm categories). These categories were chosen to reflect environmental variation that might affect the likelihood of discovery of *A. mexicanum* seeds. For example, categories 1, 6, and 7 represent factors that might affect the detectability of seeds to a forager. Categories 2, 3, 4 and 6 might indirectly influence seed survival via their potential to influence rodent movement. Seed and seedling survival and germination were monitored at three, six, nine, and 21 months.

Astrocaryum mexicanum and spiny pocket mouse abundances

Six 2 m $\times$ 100 m transects were located 20 m apart within each plot in order to estimate population sizes of mature individuals (> 1 m) and seedlings (< 6 leaves, no stem) of the study tree (Sarukhán 1978). Numbers of individuals were counted in 2 m $\times$ 10 m intervals within each transect.

In August of 1998, before the establishment of the seed-survival experiment, small rodents were live-trapped in two sites corresponding to the forests in Plots 1 and 2. The two trapping grids were located next to the respective plots, in order to estimate local densities of small rodents but without interfering with the experiment. Tomahawk (single door, wire mesh 16 $\times$ 5 $\times$ 5 cm) traps were placed in one 4 $\times$ 11 grid per site with 15 m spacing between traps. Traps were baited daily with 10 *A. mexicanum* seeds each and checked at 6.00 and 17.30 hours each day for five days. Trapped individuals were given unique fur-clipping marks, and were sexed, weighed and released.

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Table 2. Multivariate, repeated measures ANOVA of the logit-transformed proportions of seeds surviving per tree. The between subjects effects were plot (1, 2), burial (buried, unburied), and phenology of the parent (fruiting, not fruiting). The within-subjects effect (repeated measure) was distance to parent tree (1 m or 5 m). All interactions with distance were not significant (all $P > 0.20$).

All seeds combined	df	MS	F	P
Within subjects				
Distance	1	0.010	1.245	0.269
Between subjects				
Burial	1	1.133	20.277	<0.0001
Phenology	1	0.206	3.686	0.060
Plot	1	0.163	2.909	0.094
Burial × Phenology	1	0.303	5.417	0.024
Burial × Plot	1	0.007	1.272	0.264
Phenology × Plot	1	0.00007	0.001	0.972
Burial × Phen. × Plot	1	0.010	0.173	0.679
Error	56	0.056		

Separate analyses	Buried seeds				Unburied seeds			
	df	MS	F	P	df	MS	F	P
Within subjects								
Distance	1	0.0003	0.018	0.269	1	0.017	7.865	0.009
Between subjects								
Phenology	1	0.900	8.255	0.008	1	0.003	1.062	0.312
Plot	1	0.400	3.674	0.066	1	0.007	2.133	0.155
Plot × Phenology	1	0.010	0.093	0.762	1	0.003	0.926	0.344
Error	28	0.109			28	0.003		

Data analyses

All data were analyzed using the SPSS 9.0 (SPSS 1999a, b, c) statistical software. The seed survival data are presented only for the 9-month census of seeds, because seed survival was virtually unchanged after 3 months, and changes in seed germination after 6 months were very small. Proportions of seeds surviving per tree were analyzed using repeated measures analysis of variance (ANOVA) with plot, burial, and fruiting status of the tree as the between-subjects effects, including all possible interactions. Distance from the parent tree was the within-subjects effect. The multivariate approach (MANOVA, O'Brien and Kaiser 1985) to repeated measures was employed for all seeds combined, and as separate analyses for buried and unburied seeds, because the burial effect was so strong. All proportions were logit transformed in order to meet the assumptions of the analyses.

The forward stepwise, log-likelihood-ratio procedure (SPSS 1999c) was employed to determine if seed size or any of the microsite variables explained a significant proportion of the survival and germination of the *A. mexicanum* seeds. Only the data for seeds in the 5-m distances after 9 months were used in this analysis. Alpha values of 0.05 and 0.10 for entry and removal in the model were used, respectively. The individual tree for each group of seeds was included as a variable in order to avoid pseudoreplication and to avoid having seeds from one or a few trees biasing the results.

Comparisons of Plots 1 and 2 with respect to *A. mexicanum* populations were examined using *t*-tests with the belt transects within plots employed as replicate subplots. In order to meet the assumptions of the test, counts of individuals were square-root transformed, and proportions and frequencies were logit transformed. Frequency for each size class was defined as the proportion of intervals within a transect that had at least one individual of that size class. Frequency is therefore a proxy for the likelihood that a forager would encounter an individual of *A. mexicanum* when moving across the forest.

Mark recapture data were used to estimate the abundance of spiny pocket mice in the trapping grids. The software CAPTURE was used to select the most appropriate model for generating Lincoln-Peterson estimates of *N* and associated 95% confidence intervals (Otis et al. 1978, Pollock et al. 1990) for each grid.

Results

Seed survival

No buried seeds that were removed were found re-buried within 10 m of their locations. Reburying seeds is uncommon behavior for spiny pocket mice (*H. desmarestianus*), at least for *A. mexicanum* at this site (<1% of buried seeds, Brewer unpubl.).

Whether or not the seeds were buried had a significant and dominant effect on seed survival ($P < 0.00001$,

Table 2). After 9 months, buried seeds had 15–34% survival compared to 0–2% for unburied seeds (Fig. 1). This does not account for the proportion of buried seeds that were attacked by rodents after germination (12%), because the resulting seedlings did not appear to be immediately damaged. At 21 months, all seeds that were not removed had either germinated or were rotting, presumably due to insect damage.

For unburied seeds, the distance-to-parent effect on seed survival was significant ($P = 0.009$, Table 2): seeds at 1 m from the parent had 0–0.7% survival compared to 2.1–3.7% at 5 m (Fig. 1). Distance did not significantly affect survival, however, of buried seeds ($P = 0.90$, Table 2). No significant interactions including the distance effect were detected (all $P > 0.15$).

Whether or not the parent tree fruited during the experiment had a significant effect on survival of buried seeds ($P = 0.008$, Table 2, Fig. 2). Seeds buried beneath trees that bore fruit during the wet season had 43% survival compared to 16% survival of seeds buried beneath trees that did not bear fruit (Fig. 2). Fruiting status had no detectable effect on unburied seed survival ($P > 0.25$ for both Plots, Table 2).

Overall, seed survival was higher in Plot 1 than in Plot 2 (Fig. 1). The difference was on the margin of significance for buried seeds ($P = 0.066$, Table 2, Fig. 1) and was not significant for unburied seeds ($P = 0.16$). No significant interactions including the Plot effect were detected (all $P > 0.34$). The plot effect was significant, however, for seeds buried beneath fruiting individuals ($P = 0.024$) and was not significant for seeds buried beneath nonfruiting individuals ($P = 0.12$) (Fig. 2).

Unburied seeds were not used in the analyses of seed size and microsite effects, due to very low survival for
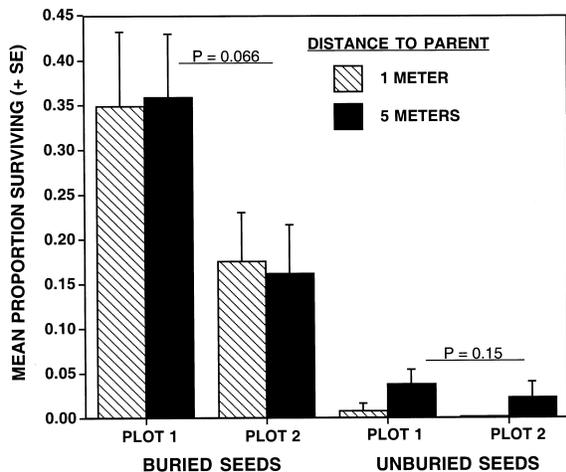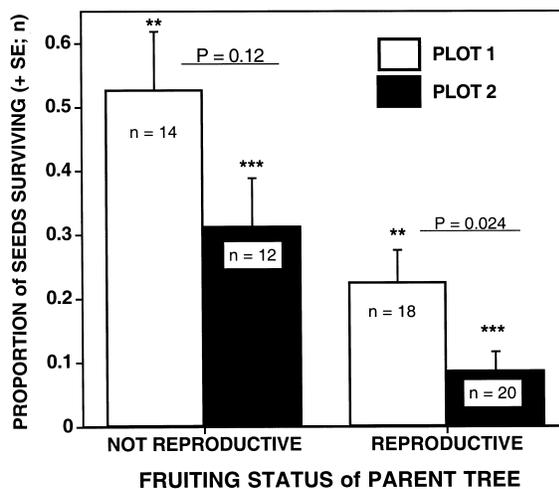

Fig. 2. Per-tree survival (untransformed means + SE bars, and n trees) of buried *Astrocaryum mexicanum* seeds. Underlined *P*-values indicate significance of differences between plots. Within plots, seed survival was significantly different between trees that did and did not fruit during the experiment (**$P = 0.012$; ***$P = 0.004$).

this treatment. Seed size did not explain a significant proportion of the variation in seed survival of buried seeds in either plot ($P > 0.50$). Likewise, none of the microsite variables significantly explained the variation in seed survival (all $P > 0.3$).

Seed germination and seedling survival

Due to the very low numbers of surviving unburied seeds, the effect of burial on germination could not be tested in this study, although *A. mexicanum* germination of intact seeds, in the field during the wet season, approaches 100% – whether or not the seeds are buried (Brewer unpubl.). Two of the surviving seven unburied seeds germinated. For those buried seeds that survived, the largest increase in total germination occurred between 3 and 6 months (from 22% to 61%) after the start of the experiment (Fig. 3). Germination at 21 months (66%) likely represents the maximum possible, because pre-dispersal attack by insects kills nearly one-third (mean $= 32\% \pm 4.16\%$ SE, $n = 45$ trees) of *A. mexicanum* seeds per tree (Brewer unpubl.). The remaining, ungerminated seeds in this experiment were rotting and showed signs of insect attack at 21 months. At 6 months, 9 (12% overall) of the buried seeds that germinated were partially or completely eaten. This proportion did not change after 6 months. Small rodents, which left their distinctive bite-marks in the endosperm or seed coat, had dug up these seeds and/or seed remains. These seedlings survived 9 months, but 6 seedlings died within 21 months, twice the overall seedling mortality of 33% (Fig. 3).

Fig. 1. Per-tree survival of *Astrocaryum mexicanum* seeds placed 1 m and 5 m away from the parent tree and either experimentally buried or left on the soil surface ("unburied"), in the two 1-ha plots. Untransformed means + SE bars are shown. Underlined *P*-values indicate significance of differences between plots.

For buried seeds, there was no effect of distance to the parent on the proportion of seeds germinating (paired $t = 0.076$, df $= 18$, $P = 0.94$). In the logistic regression, seed size did not explain a significant amount of variation in the germination of seeds ($\chi^2 = 0.077$, df $= 1$, $P = 0.78$).

Astrocaryum mexicanum and spiny pocket mouse abundances

Total *A. mexicanum* recruitment was higher in Plot 1 than Plot 2. Plot 1 had a significantly larger number of *A. mexicanum* trees of reproductive size (> 1 m) than Plot 2 ($P = 0.015$, Table 1). Plot 1 also had a higher frequency of stems of reproductive size than Plot 2, but the difference was on the margin of statistical significance ($P = 0.055$, Table 1). Plot 1 also had a significantly larger number ($P = 0.012$) and frequency ($P = 0.037$) of *A. mexicanum* seedlings (≤ 5 leaves) than Plot 2 (Table 1). The two plots were not significantly different, however, with respect to the ratio of mature trees to seedlings ($t_{1,10} = 0.206$, $P = 0.84$, Table 1).

Grid 1, representing the forest in Plot 1, captured more individuals over 5 d than grid 2 (38 to 23), and had higher mean daily numbers of captures, recaptures, and new captures, but the differences were not significant (all $P > 0.09$, Table 1). The most appropriate model generated by CAPTURE for each of the two plots was the null model M(0) that assumed equal probability of capture among individuals. The two plots had similar Lincoln-Petersen estimates of abundance, with overlapping 95% confidence intervals (Table 1).
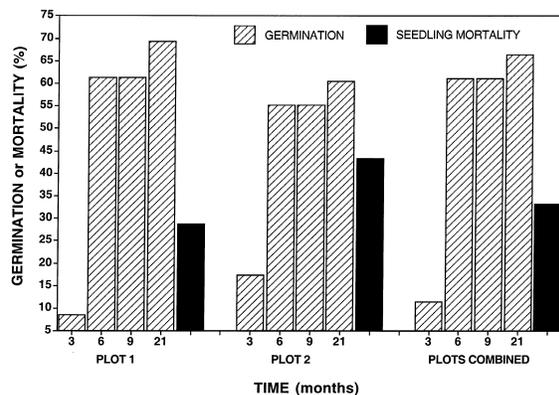

Fig. 3. Percent germination of buried *Astrocaryum mexicanum* seeds and mortality of the resulting seedlings over 21 months.

Discussion

The survival of buried and unburied seeds

Artificial burial greatly increased the probability of *A. mexicanum* seeds surviving to the seedling stage. Whether or not *A. mexicanum* seeds were buried accounted for most of the variation in seed survival in this study (Table 2, Fig. 1). The seeds of *A. mexicanum* and other tree species left on the forest floor of the study area are removed rapidly (within 6–10 d) and completely by spiny pocket mice during the rainy season (Brewer and Rejmánek 1999, Brewer unpubl.). In fact, so few unburied seeds survived (1.4% or 7/512) in this experiment, that the relative importance of other factors that influence the total survival of unburied *A. mexicanum* seeds would be difficult to test. Microsite variables, such as distance to the nearest log or herb cover could have significant effects on the *rate* of seed removal, but given the life span of *A. mexicanum* seeds before they germinate (months), the search for microsite and other variables that influence overall survival of unburied seeds may be an unrealistic and fruitless task for this species. Longer exposure to potential predators increases the likelihood of discovery of seeds (Hammond 1999), and increases the likelihood that seeds will be available when food is limiting to foragers. This increased exposure raises the profitability of a seed as food becomes limiting and reduces the relative importance of microsite, seed size, or other variables that might otherwise reduce the risk of predation for any given seed.

Unburied seed survival was significantly higher at the lower density (and farther distance) in this study (Fig. 1), in contrast to seed survival for other long-lived, large seeds (Hammond 1999). In Mexico, unburied *A. mexicanum* seeds at higher densities have also been shown to experience greater predation than those at lower densities (Sánchez-Cordero and Martínez-Gallardo 1998). The proposed effect of distance to the parent on seed predation (Janzen 1970, Connell 1971) has been explored through a number of studies. The results of the studies of seed predation by terrestrial vertebrates, however, generally do not support the Janzen-Connell model (see Hammond and Brown 1998). The context in which seeds are dispersed, for example dispersal by burial, may modify the impact of any density/distance effect that may exist. As ignorant (i.e. individuals that are not the agents of burial of a cohort of seeds), nocturnal seed predators such as spiny pocket mice forage by olfaction (Vander Wall 1990), increasing densities of seeds should raise the density of the scent cue(s) above the threshold necessary for detection. That density/distance had a significant effect on unburied but not buried seeds are therefore not unexpected. Burial should substantially weaken the scent signal from the source seed (Reichman 1981, Vander

Wall 1993), thereby diminishing any effect of seeds buried near each other.

Like other, temperate-zone scatter hoarding mice and squirrels (e.g. Cahalane 1942, Abbott and Quink 1970, Vander Wall 1990), spiny pocket mice are effective at recovering their own cached seeds. Survival of *A. mexicanum* seeds buried by rodents themselves (i.e. by "scatter hoarding" rodents) is less than 1%. Except for the very smallest of *A. mexicanum* seeds, virtually all seeds buried by scatter hoarding spiny pocket mice in other experiments in the same area, covering different years, have been removed within 9 months of deposition (Brewer unpubl., data for seeds used in Brewer and Rejmánek 1999). This recovery represents predation, since recovered seeds are taken deep into burrows (≥ 40 cm) and are eaten (Brewer unpubl.). In contrast, up to 34% of buried seeds that were exposed exclusively to ignorant foragers survived, in this study, for a length of time sufficient for germination.

Recovery of naturally buried seeds may reflect predation by both ignorant and scatter hoarding rodents. Nevertheless, a strong difference in survival rates between naturally and artificially buried seeds implicates different mechanisms of seed recovery between ignorant and scatter hoarding rodents. Were scatter hoarding and ignorant foragers to use the same means of retrieving cached seeds, there should be no difference in the survival of seeds buried by scatter hoarding rodents and the seeds buried in this study. Nor would there be any advantage offered by scatter hoarding seeds if competitors could recover them at the same rate as scatter hoarders. Recovery of seeds in mammals and birds has been linked to the use of memory in caching animals (Smith and Reichman 1984, Vander Wall 1990). The advantage to scatter hoarders of using memory is that it gives scatter hoarding individuals exclusive access to a portion of the seeds that are buried (Smith and Reichman 1984). It is therefore likely that ignorant individuals of spiny pocket mice forage via olfaction and caching individuals use memory and olfaction.

Factors affecting survival of scatter hoarded seeds

Once an *A. mexicanum* seed has escaped predation by scatter hoarding individuals, what determines the probability that it will survive ignorant foragers? For buried seeds in this experiment, survival depended on (1) whether the parent tree fruited during the experiment, and to a lesser extent, (2) plot, and (3) whether the seed germinated.

Astrocaryum mexicanum trees develop infructescences sequentially during the rainy season, so seeds drop from the tree in small pulses. These pulses may serve to attract foragers, and perhaps stimulate more intensive, localized foraging (Tinbergen et al. 1967, Lewis 1980) by ignorant predators, thereby reducing the likelihood

that a buried seed will escape predation. One implication for tree reproduction is that dispersal near fruiting trees – of the same or other fruiting species – could significantly change the risk of mortality for buried seeds. The direction in the change in risk of mortality, however, might depend on the amount of seeds produced by the nearby fruiting tree. For example, spiny pocket mice readily consume seeds of *Brosimum alicastrum* (Martínez-Gallardo and Sánchez-Cordero 1993, Brewer unpubl.), a species of very large trees that produces so many seeds beneath its canopy that carpets of seedlings from the uneaten "leftovers" appear during mast years. Such saturating seed levels should be expected to reduce the risk of mortality of nearby buried *A. mexicanum* seeds, which also have a lower dietary value to spiny pocket mice compared to *B. alicastrum* (Martínez-Gallardo and Sánchez-Cordero 1993). Alternatively, below a saturation food level such as that exhibited by *A. mexicanum* trees, seeds might experience increased risk of predation when dispersed near other food sources that attract foragers and/or stimulate intensive foraging by seed predators.

Germination may also signal to the seed predators the presence of a potential seed source. Predators ate 12% of the buried seeds that germinated, but no buried, ungerminated seeds were removed during the same time period. These *A. mexicanum* seedlings did not appear to be affected, after 9 months, by the loss of their attached seeds and its remaining endosperm. Mortality of these seedlings at 21 months, however, was twice the rate of mortality for all seedlings. Herbivory of germinated seeds may affect growth and establishment of seedlings from some species (e.g. Korstian 1927, Shaw 1974) but not others (Mack 1998).

An effect of plot, albeit on the margin of significance ($P = 0.066$), on the survival of buried seeds per tree (Table 2, Fig. 1) points to the higher density of reproductive *A. mexicanum* trees in Plot 1 as potentially having a positive effect on seed survival. This result is congruent with those results for unburied seeds in Schupp (1992). The effect of plot was not significant, however, for unburied seeds in this study. Plot 1 has a greater amount of *A. mexicanum* seeds available, due to the higher reproductive tree density, and a higher probability of encountering a reproductive individual, than does Plot 2 (Table 1). Greater numbers of seeds available on the surface should make foraging for buried seeds less profitable. Plot 1 had significantly more seedlings than Plot 2, but the two plots did not differ significantly in the ratio of the number of reproductive-sized adults to seedlings, indicating that per-tree recruitment in the two plots has been similar in the short term (Table 1). Long-term recruitment dynamics of *A. mexicanum*, however, would be difficult to infer from static population data. It is possible that the plot effect on seed survival could be due to some location-specific condition other than tree density (e.g. higher alternative food source) not apparent during the experiment.
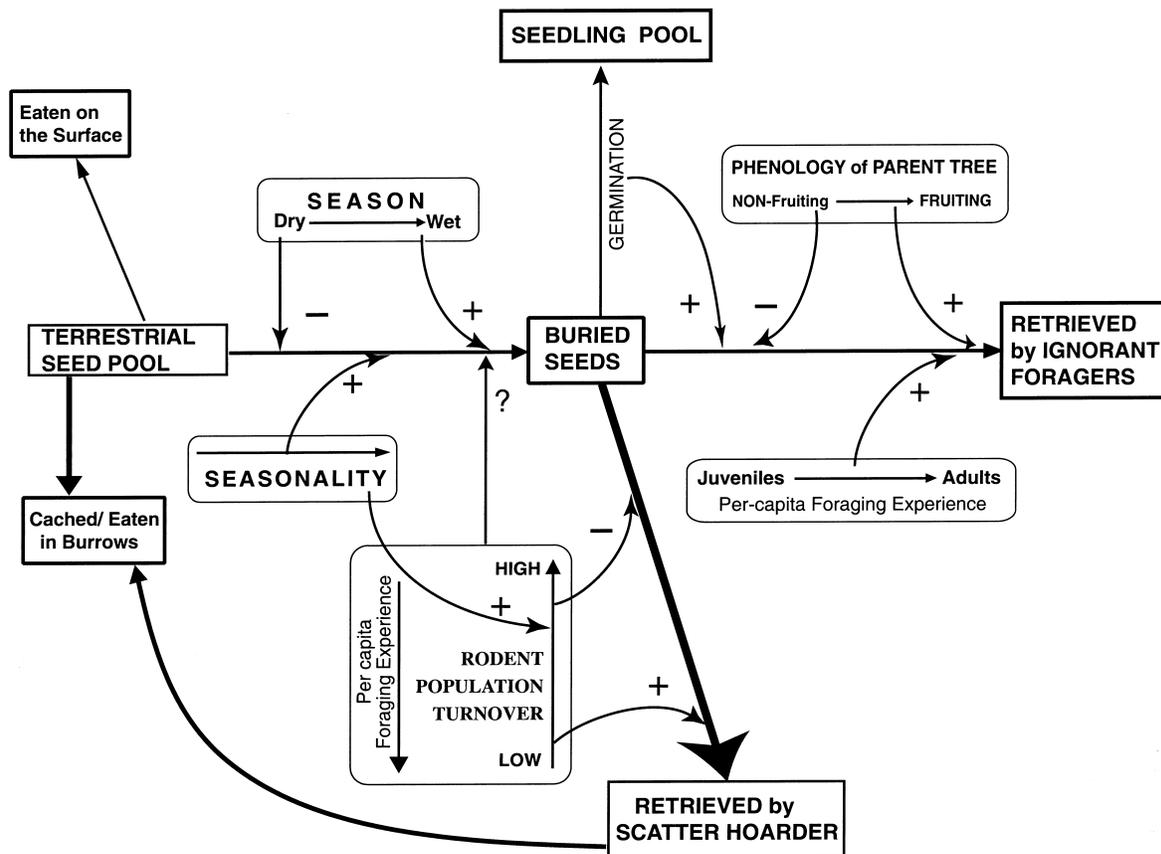
38

Fig. 4. Hypothetical causal relationships among factors contributing to actual fates of *Astrocaryum mexicanum* seeds that have been handled by spiny pocket mice (*Heteromys desmarestianus*). Plus signs (+) indicate positive effects and minus signs (−) indicate negative effects on the flows of seeds. Wider arrows indicate relatively more seeds flowing to their respective fates; however, width is not proportional to numbers of seeds because the seed fates depend on different factors such as season (Brewer and Rejmánek 1999) or phenology (this study). Ignorant foragers are those that are ignorant of the locations of buried seeds; scatter hoarders are responsible for the burial of seeds.

Factors not explaining a significant proportion of the variation in seed survival were microsite, seed size, and absolute rodent abundance in the plots. The relative importance of microsite characteristics and seed size variation on seed survival seems to be low for long-lived seeds that remain available to predators for long periods of time, for less preferred seed species (Hay and Fuller 1981), and may be relatively high for fast-germinating seeds. Studies of microsite on seed survival are few in the tropics, however, and do not demonstrate any consistent trends among the habitats that have been studied (Schupp 1988, Willson 1988).

Hypothetical relationships among factors of seed survival and their implications

What explains the high abundance of *A. mexicanum* trees and seedlings in the study site, if recovery of buried seeds by scatter hoarding small rodents and overall predation on unburied seeds are so nearly com-

plete? One possible explanation is that the observed seed survival is consistently low over a long time scale, but it provides just enough recruitment for this shade tolerant palm to become dominant in the understory. If this explanation alone is true, however, dispersal by small rodents does not necessarily promote recruitment of *A. mexicanum*. All else being equal, scatterhoarded seeds are no more likely to survive predation than seeds that are not handled by spiny pocket mice. Furthermore, burial of these seeds does not promote germination. A second explanation, however, includes the possibility that scatterhoarding of *A. mexicanum* seeds could interact with rodent population dynamics in the recruitment of seedlings (Fig. 4).

For some seed-dispersing animals such as small rodents, the probability of intra-annual mortality can be high (Promislow and Harvey 1990, Adler 1998, Tkadlec and Zejda 1998). Moreover, increased population turnover might be the result of seasonal changes in food supply (e.g. Adler 1998) or from severe disturbances such as drought or flooding. Therefore, the

number of cached seeds left by scatter hoarders and exposed to ignorant foragers may be significant for tree recruitment over long periods of time. If a scatter hoarding individual dies or emigrates from its territory of buried seeds, then ignorant (and thus less effective) foragers will determine the fates of those buried seeds left behind.

As the age structure and mortality of small rodents fluctuate in short time periods in seasonal environments (Fleming 1971, Gliwicz 1984, Tkadlec and Zejda 1998, Adler 2000), so should the proportion of younger, naïve foragers in that environment. Assuming that foraging efficiency increases with age (Caldow et al. 1999) and experience in a territory (Bell 1990), and given that foraging rates increase with age and size (Persson et al. 1998), the probability of buried-seed survival should decrease in the territories of an aging population of rodents (Fig. 4).

Other factors, such as season, may also affect seedling recruitment by directly or indirectly determining the proportion of seeds that are scatter hoarded and retrieved by rodents (Fig. 4). For example, more seeds of *A. mexicanum* are scatter hoarded by spiny pocket mice in the wet than dry season (Brewer and Rejmánek 1999). More seasonal forests should be expected to have greater amounts of seeds cached by foragers, since seasonal food scarcity promotes caching behavior (Smith and Reichman 1984, Jenkins and Peters 1992). The environmental context and particular biological characteristics of the tree species will ultimately manifest variation in the dispersal and survival of seeds. The hypothetical causal network (Fig. 4) may therefore be instructive in generating hypotheses about how scatter hoarding affects recruitment in other tropical trees and in other tropical forests.

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