



## Postdispersal Seed Fate of Tropical Montane Trees in an Agricultural Landscape, Southern Costa Rica

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### ABSTRACT

Variation in postdispersal seed fate is an important factor driving patterns of forest regeneration. Because most previous studies have not tracked final seed fate and have commonly equated seed removal with predation without considering the possibility of secondary dispersal, little is known about individual seed mortality factors in successional and degraded habitats. This study tracked the postdispersal fate of large-seeded tropical montane trees in abandoned pasture, young secondary forests, and small forest fragments during two consecutive years in an agricultural landscape in southern Costa Rica. The incidence of secondary dispersal by animals, scatterhoarding in particular, and the effects of seed burial on germination were measured. Overall, seeds survived through germination more often in secondary forests with high levels of mortality occurring in abandoned pastures and forest fragments. The majority of seed mortality was caused by rodent predation in forest fragments, insects and fungal pathogens in secondary forests, and a combination of desiccation, insects, and fungal pathogens in pastures. Seeds were frequently secondarily dispersed in larger forest fragments, whereas they were only rarely moved in pastures and secondary forests. Burial tended to improve germination in pastures and was important for an often scatterhoarded species, *Otoba novogranatensis*, in all habitats. The results of this study suggest that: (1) seed mortality factors differ in response to the type of habitat degradation; (2) large-seeded species have high potential for survival when dispersed to young secondary forests; and (3) seed removal is not a reliable proxy for seed predation, particularly in less degraded forest fragments.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

*Key words:* scatterhoarding; secondary dispersal; seed predation; tropical forest succession.

VARIATION IN BIOTIC AND ENVIRONMENTAL CONDITIONS among degraded tropical habitats may strongly influence seed fate with important consequences for patterns of forest succession. Postdispersal seed fate plays a large role in determining the rate of tree recruitment following anthropogenic activities (Uhl *et al.* 1988, De Steven 1991, Whelan *et al.* 1991, Myster 1993, Hammond 1995) and can act as a selective filter for which species are able to establish during forest succession. The conditions that cause seed mortality, however, are likely to differ in intensity and frequency depending on the type of habitat alteration (Hammond 1995). To effectively manage the increasingly large area of land that has been altered through human activity, it is necessary to understand the ecological processes that mediate natural tree establishment at the habitat level. Unfortunately, most past studies of seed fate in anthropogenically impacted landscapes have not identified individual mortality factors and have commonly equated seed removal with seed predation, without considering other seed fate pathways such as secondary dispersal by animals (*e.g.*, Vander Wall *et al.* 2005).

Seeds can experience a variety of different fates that are mediated by abiotic and biotic agents. Changes in habitat structure due to human activities can alter environmental conditions such as exposure to light, humidity, and quantity of leaf litterfall (Guariguata & Ostertag 2001). Seeds dispersed to harsh microclimates common in successional habitats can be exposed to inundation or desiccation (Howe 1990). For example, Notman and Gorchoy (2001) found that desiccation was an important source of seed mortality in lowland swidden fallows.

Predation by vertebrates or insects (Schupp 1988) and infection by pathogens (Augsburger 1984) can have a particularly strong impact on rates of forest succession. Previous studies examining seed predation in agricultural landscapes indicate that mortality rates are high and rodents are the primary predators (Uhl 1987, Hammond 1995, Notman & Gorchoy 2001). Comparisons of seed removal between large forests and abandoned pastures (Uhl 1987) and secondary forests (Hammond 1995, Notman & Gorchoy 2001, Peña-Claros & De Boo 2002) suggest that seed predation is elevated in the successional habitats, although a few studies have reported the opposite (Aide & Cavelier 1994) or no trend (Holl & Lulow 1997). The importance of insect predation relative to other factors in successional habitats has been examined less frequently and the few existing studies have reported different trends. Holl and Lulow (1997) found uniform rates of insect predation between montane pastures and primary forest, while Notman and Gorchoy (2001) saw higher rates of insect predation in lowland forests compared to swidden fallows. The causes of seed mortality can often be difficult to identify. Infection by fungal pathogens is not always readily visible and insect predation does not always result in seed death (Marin *et al.* 2006). The incidence and causes of seed death may be overlooked unless seeds are exposed for a sufficient amount of time to germinate or are opened and inspected.

It is possible that the levels of seed mortality in early- and mid-successional habitats have been overestimated because seed removal is generally considered to be a proxy for seed predation, even though some seeds may be secondarily dispersed by animals (Forget & Milleron 1991, Jansen *et al.* 2004, Vander Wall *et al.* 2005). Secondary dispersal (any significant movement of viable seeds following the initial or primary dispersal) has been increasingly

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recognized as a key factor affecting the establishment of many temperate and Neotropical trees (Chambers & MacMahon 1994, Jansen *et al.* 2004, Vander Wall & Longland 2004). Although a lack of primary dispersal clearly slows forest regeneration (Aide & Cavelier 1994, Nepstad *et al.* 1996, Holl 1999, Zimmerman *et al.* 2000), reduced secondary dispersal may also be an important limiting factor, especially for large-seeded species.

An important type of secondary dispersal in both temperate and tropical systems is scatterhoarding (burying seeds in many small depots for future consumption) (Forget & Milleron 1991, Forget 1993, Vander Wall *et al.* 2001, Wenny 2001). Scatterhoarding is a widespread behavior among medium-sized (Forget & Vander Wall 2001) and small mammals (Brewer & Rejmanek 1999). Cached seeds that are not retrieved are more likely to avoid predation than seeds on the surface and may have higher rates of germination and establishment (*e.g.*, Vander Wall 1990, Vander Wall *et al.* 2001). Large-seeded species are often preferentially cached by granivores (Jansen *et al.* 2004,) and are of particular interest for forest restoration because they have been shown to establish well in degraded habitats if they survive through germination (Hooper *et al.* 2002).

The goal of this study was to examine factors influencing the seed fate of montane tropical forest trees in degraded and successional habitats common to agricultural landscapes. Extensive forest clearing has created mosaic landscapes with areas of active agriculture, grazed and abandoned pastures, fallow and successional forest, and small forest remnants. Three of these habitats are of focal dispersal interest for conservation and/or restoration efforts: forest remnants that harbor the majority of remaining biodiversity and function as sources of seeds for restoration; secondary forests and fallows that are increasingly valued for providing ecological services (Brown & Lugo 1990, Guariguata & Ostertag 2001); and extensive areas of abandoned pasture. I conducted the study over a relatively large area of agricultural matrix (60 km<sup>2</sup>) over two consecutive years to better evaluate seed survival across a range of sites and compare patterns in different years. Biotic and abiotic sources of mortality were tracked for 3780 individual seeds and rates of secondary dispersal and germination success were compared among habitats. The specific objectives of this research were to: (1) identify and compare mortality factors limiting seed survival in each habitat; (2) assess the incidence of secondary dispersal relative to seed predation by animals; and (3) test whether seeds buried to mimic scatterhoarding experienced different rates of germination success compared to those left on the surface.

## METHODS

**STUDY AREA.**—The study was conducted near Agua Buena de Coto Brus (8°47' N, 82°57' W) in southern Costa Rica. The forest is classified as a tropical montane rain forest by Holdridge *et al.* (1971) with elevation range of 1000–1300 m asl in the sites studied; mean annual rainfall is *ca* 3500 mm with a distinct dry season from December to March. In the last 50 yr all but 25 percent of the forest cover was cleared for agriculture (Daily *et al.* 2001). Changes

in the global coffee market over the last 10 yr have precipitated an increase in conversion of coffee plantations to pasture and land abandonment resulting in numerous patches of successional forests (Rickert 2005). As is typical in much of Central America, remnant forests are small and located along waterways or on steep slopes and hilltops that are unsuitable for agriculture.

Four replicates of each of three habitat types were studied: abandoned pasture (3 yr since abandonment), secondary forest (8–10 yr since abandonment), and primary forest fragments. All sites were separated by at least 1 km from other sites of the same habitat type and were surrounded by a matrix of pasture, coffee, and secondary forest. The four forest fragments were the largest remaining in the region and included the Las Cruces Biological Station (LCBS) of the Organization for Tropical Studies (200 ha of relatively undisturbed primary forest), Las Cascadas (25 ha of primary forest), Loma Linda (19 ha of primary forest with adjacent secondary forests) and La Reserva (12 ha of primary forest with areas previously selectively logged). Prior to abandonment, the secondary forest patches had land-use histories common to the region including coffee agriculture (two sites), and a mix of coffee and grazing (two sites) and were > 2 ha in size. The structural characteristics of the secondary forests were heterogeneous. Canopy height ranged from 5 to 15 m, overhead cover ranged from 40 to 100 percent, and stem density (dbh ≥ 2 cm) ranged from 1406 to 6875 stems/ha. Dominant tree species included *Cecropia obtusifolia* Bertol., *Conostegia xalapensis* (Bonpl.) D. Don ex DC., *Croton draco* Schltld., *Heliocarpus appendiculatus* Turcz., and *Psidium guajava* L (R. J. Cole, pers. obs.). Grazing in all the pastures had ceased at least 3 yr prior to the study and these sites were dominated by a mix of introduced pasture grasses, primarily *Axonopus scoparius* (Flugge) Kuhl., *Paspalum* spp., *Pennisetum purpureum* Schumach, and *Urochloa brizantha* (Hochst. Ex. A. Rich.) R. D. Webster, and ruderal herbs, such as *Heterocondylus vitalbae* (D.C.) King & H. Robins., *Pteridium arachnoideum* (Kaulf.) Maxon, and *Spermacoce assurgens* Ruiz & Pav. (K. D. Holl & R. A. Zahawi, pers. comm.). All pastures were cleared with machetes or mechanical trimmers *ca* 6 weeks prior to the initiation of this study in 2006 to achieve similar initial conditions. The pastures were allowed to regenerate naturally thereafter. The same sites and transect locations were used in both years of the study with the exception of the substitution in 2007 of one pasture and one secondary forest for nearby habitats of the same type and similar land-use histories due to vegetation clearing for agriculture.

Surveys of mammal species in the study area near the LCBS suggest that although populations have been reduced, the majority of medium and small native mammal species were present in forest fragments and adjacent agricultural areas (Daily *et al.* 2003). The agouti *Dasyprocta punctata* (Dasyproctidae), an important scatterhoarding tropical rodent (Hallwachs 1986, Forget & Milleron 1991, Forget 1993), was reported in a recent study (Pacheco *et al.* 2006) to be common in local forest fragments, coffee plantation, and pastures adjacent to forests. An earlier survey (Rodríguez & Chinchilla 1996) confirmed the presence of a small scatterhoarding rodent, the spiny mouse *Heteromys desmarestianus* (Heteromyidae) in the region.

TABLE 1. Species used in this study including family name, mean fresh seed weight, maximum seed width, and some tree and fruit characteristics. Values are means  $\pm$  SD. N = 40 for each species.

Species	Family	Fresh weight (g)	Maximum length (cm)	Tree and fruit characteristics
<i>Persea americana</i> (Ruiz & Pav.)	Lauraceae	1.43 $\pm$ 0.24	1.43 $\pm$ 0.16	Canopy tree, fleshy drupe
<i>Pseudolmedia oxyphyllaria</i> Donn. SM.	Moraceae	6.30 $\pm$ 1.51	2.67 $\pm$ 0.21	Mid-canopy tree, fleshy drupe
<i>Pseudolmedia spuria</i> (Sw.) Grisebach	Moraceae	1.92 $\pm$ 0.44	1.62 $\pm$ 0.13	Canopy tree, red ellipsoidal berry
<i>Ocotea endresiana</i> (Mez.)	Lauraceae	5.29 $\pm$ 1.12	3.13 $\pm$ 0.21	Canopy tree, fleshy drupe
<i>Cinnamomum triplinerve</i> (Ruiz & Pav.)	Lauraceae	1.76 $\pm$ 0.55	1.63 $\pm$ 0.15	Lower canopy tree, fleshy drupe
<i>Otoba novogranatensis</i> Moldenke	Myristicaceae	4.61 $\pm$ 0.76	2.36 $\pm$ 0.15	Mid-canopy tree, capsule, dehiscent, seed covered with aril

SEED SELECTION AND PREPARATION.—Six large-seeded tree species (three in 2006 and four in 2007 including *Otoba novogranatensis* which was tested both years) were used in the experiment (Table 1). Species were selected based on the local abundance of the tree species in forest fragments and the availability of seeds at the time of the study. Due to natural fruiting cycles, the selection of species differed between years. Seeds were collected from at least two forest remnants and a minimum of three parent trees and then mixed. Areas below fruiting trees were checked regularly and only freshly fallen fruits and nondiscolored seeds were collected.

Seeds were cleaned and visually inspected for signs of insect or pathogen damage. All fleshy tissue was removed, as the goal of this study was to quantify postdispersal predation and flesh would be removed during primary dispersal. Seeds that floated in water were rejected, as floating is often a sign of insect infestation. Seeds were stored at ambient temperature for < 4 d. To track seed movement, a 50-cm length of neon-colored nylon thread was attached to the seed surface with quick bonding gel glue. Similar marking procedures have been tested before with no evidence of effects on seed removal (Forget 1993, Notman & Gorchoy 2001, Xiao *et al.* 2006).

EXPERIMENTAL DESIGN.—Seeds of each species were placed along three 50-m transects at each site (Fig. 1). Transects in the forest fragments were located > 50 m from the edge of the forest to minimize edge effects. Transects in secondary forests were placed > 50 m away from habitats of a different type, and those in abandoned pasture were located a minimum of 10 m from the edge of a recently cleared area. All transects were separated by > 20 m. Three seed stations were located along each transect (N = 9/treatment/site). A seed station consisted of three (2006) or four (2007) depots (one for each species) spaced 5 m apart. In each depot, five seeds with attached threads were placed in a circular array inside a wire mesh disk with an open top (1-cm high  $\times$  10-cm diam) to prevent movement by abiotic factors but not seed predators. Threads were covered by a light layer of litter so that only the seed remained visible. Germination trials were placed 1 m to each side of the threaded seed disks and consisted of two secured wire-mesh rodent exclosures (20  $\times$  20  $\times$  10 cm) covering seeds and placed either on the surface or buried 2 cm deep to mimic scatterhoarding (Forget

1993). Either three (*Pseudolmedia spuria*) or five (*O. novogranatensis*, *Ocotea endresiana*) seeds were placed in each germination treatment. Seeds placed on the surface were covered by one leaf to simulate litterfall. Subsequent leaf litter that accumulated on the surface of the cage was removed at each census. In all, 180 threaded seeds of each species and 108–180 germination trial seeds of each species were placed in each habitat type.

DATA COLLECTION.—Seeds were set out at each site to coincide with peak fruiting periods of each species. Stations were checked approximately every 8 d in 2006 and every 15 d in 2007 after it was determined that seeds could be reliably relocated within this time frame. The seeds were monitored for *ca* 10 weeks in 2006 and *ca* 12 weeks in 2007. At each census, seeds were inspected and the number still present and the number germinated were recorded. Germination was defined as the emergence of a 1-cm long radicle. When a seed was missing from the disk, the surrounding

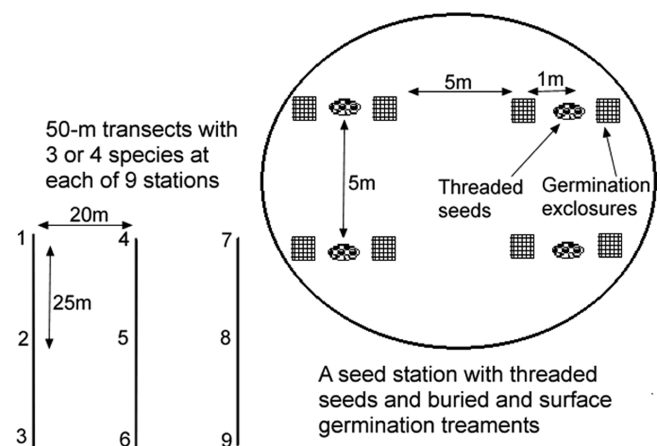


FIGURE 1. Diagram representing an experimental site. Each number represent an individual seed station (see insert). The circles represent seed disks holding five threaded seeds of a species. The squares represent rodent exclosures over seeds in each of two treatments: placed on the surface or buried 1–3 cm deep in soil to mimic scatterhoarding.

20-m radius area was searched. All but eight seeds of a total of 3780 seeds were relocated in this way. This criterion was applied as virtually all seeds cached by scatterhoarding rodents are buried within this distance (Forget 1990, Asquith *et al.* 1997, Peres *et al.* 1997), however, it is possible that the lost seeds were dispersed further than 20 m or taken into deep burrows (Brewer & Rejmanek 1999).

If the thread was relocated with the intact seed still attached, it was recorded as secondary dispersal. To relocate secondarily dispersed seeds, a small stick was placed 20 cm from the new location. The initial distance moved, subsequent recaching, predation, or germination was recorded. If only the thread was located, I assumed that a rodent had preyed upon the seed. In the majority of cases, seed fragments were found still attached to the thread, indicating that the seed had been at least partially consumed, although it is possible that some of the threads became detached and the seed was actually cached. Therefore, seed predation may have been slightly overestimated.

Because seed damage due to insects, fungi, or desiccation was not readily visible to external examination in the field, a final determination of seed fate was made at the end of the study each year. All remaining seeds, including those that had been secondarily dispersed, were opened and inspected for insect larva, fungal infection, or other damage. Because it was not always possible to differentiate between attack by insects and fungal pathogens, these causes of mortality were included into one category. Desiccation was identified by obvious peeling, splitting, and discoloration of the seed coat, and mealy, dry seed tissue. Seeds that were germinated or appeared to be healthy inside were considered to have survived.

**STATISTICAL ANALYSIS.**—Each habitat was considered a replicate ( $N = 4$ ). Only data from the final censuses in which overall seed fate was determined were used in analyses. Two-way Analyses of Variance (ANOVAs) with interaction terms were used to test whether the proportion of surviving seeds varied with respect to habitat and species. Tukey's HSD multiple comparisons procedure was used to separate habitat groups when habitat or species were found to be significant factors. These data were arcsine-square root transformed and the residuals were examined to determine that the data met assumptions of normality and homogeneity of variances (Zar 1996). A contingency table analysis was used to assess whether habitat type affected the relative importance of rodent, insect/fungus, and desiccation-related seed mortality. Differences in germination by burial treatment and habitat and their interaction were tested with a two-way ANOVA followed by Tukey's HSD *post hoc* tests. Germination percentage data were arcsine transformed to meet assumptions of normality. Only *O. endresiana* (2006), *O. novogranatensis*, and *P. spuria* (2007) were included in the germination analysis because the other species had not germinated by the end of the study. A contingency table analysis was used to determine if the incidence of secondary dispersal varied among forest fragments as seed movement in the other habitats was negligible. Standard deviations are reported throughout. Analyses were conducted using Systat version 10.2 (SYSTAT Software Inc. 2002).

## RESULTS

**SEED FATE BY HABITAT AND SPECIES.**—Overall seed survival was 65 percent in 2006 and 66 percent in 2007. The number of surviving seeds varied significantly by both habitat and species but there was no habitat  $\times$  species interaction in either year. Habitat type strongly affected overall survivorship in both 2006 ( $F = 11.7$ ;  $df = 2$ ;  $P = 0.0002$ ) and 2007 ( $F = 12.9$ ;  $df = 2$ ;  $P < 0.0001$ ) (Fig. 2). In 2006, the proportion of seeds surviving after 10 weeks was significantly lower in pastures than in either forest fragments or secondary forest. In 2007, the proportion of seeds surviving to 12 weeks was significantly lower in both forest fragments and pastures compared to secondary forest (Fig. 2).

Overall survivorship also differed among species (2006:  $F = 4.0$ ,  $df = 2$ ,  $P = 0.03$ ; 2007:  $F = 23.9$ ,  $df = 3$ ,  $P < 0.0001$ ; Fig. 3). In 2006 *Pseudolmedia oxyphyllaria* seeds (45%) survived more often than *O. endresiana* (29%), whereas *O. novogranatensis* (31%) had intermediate survivorship. In 2007, the proportion of surviving *Persea americana* (42%), *P. spuria* (49%), and *O. novogranatensis* (39%) were similar but *Cinnamomum triplinerve* (7%) suffered far higher levels of mortality. *Otoba novogranatensis*, the only species to be tested in both years, survived at higher rates in pastures in 2007 than in 2006 (40% compared to 16%) likely due to increased vegetation cover that reduced desiccation.

**CAUSES OF SEED MORTALITY.**—Overall, insects and fungal pathogens killed the most seeds (35% in 2006 and 31% in 2007), followed by rodent predation (18% in 2006 and 27% in 2007) and desiccation (17% in 2006 and  $< 1\%$  in 2007; Fig. 3). The proportion of seed mortality due to insects or fungi was greater than rodent predation for all species in pastures, whereas rodent predation was more important in forest fragments. Desiccation only occurred in pastures and was less important in the second year. Of all species, *C. triplinerve* suffered the highest levels of rodent and insect and fungal attack (46% and 42% respectively). *Otoba novogranatensis* was highly susceptible to insect and fungal attack but was

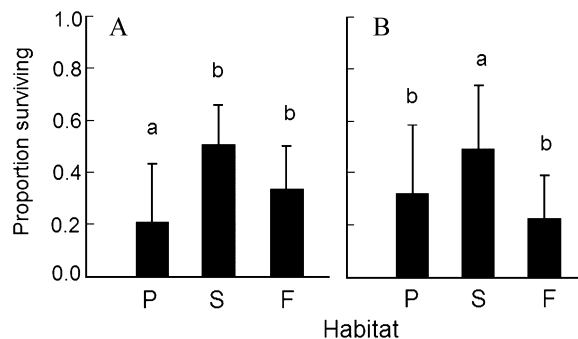


FIGURE 2. Mean proportions of seeds surviving at the end of the experiment in each habitat type (P = pasture, S = secondary forests, F = forest fragments) in (A) 2006 and (B) 2007. Habitats with the same letter are not significantly different ( $P < 0.05$ ) based on Tukey's HSD multiple comparisons. Error bars represent one standard deviation.

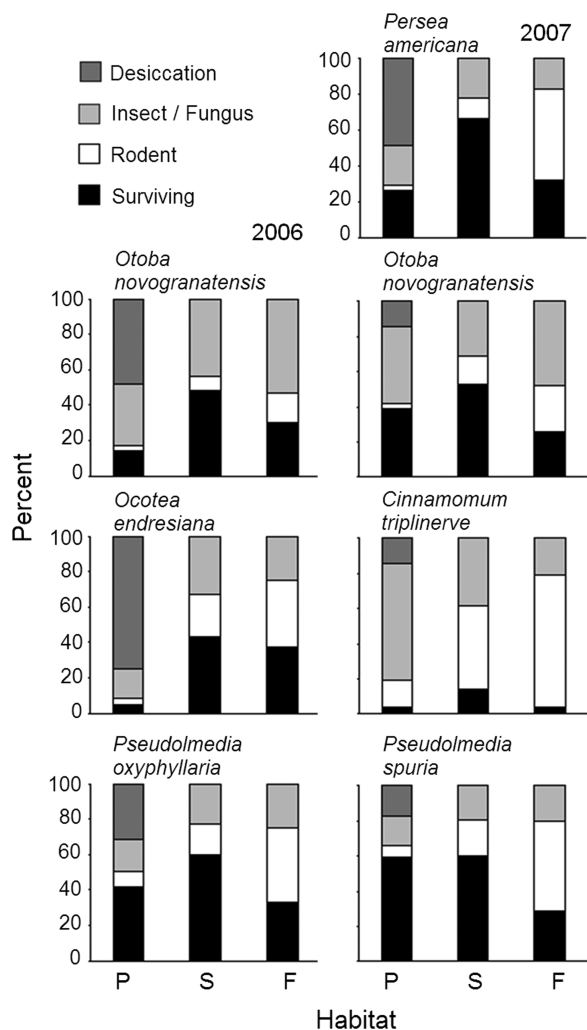


FIGURE 3. Percent of seeds falling into each fate category by year (2006 left, 2007 right) and habitat type (P = pasture, S = secondary forests, F = forest fragments).

consumed less frequently by rodents than any other species. This trend was most marked in pastures where the ratio of rodent to insect and fungal attack on *O. novogranatensis* was > 1:19 in both years (Table 2).

**SECONDARY DISPERSAL.**—In 2006, a total of 90 seeds (5.5%) were secondarily dispersed either by being scatterhoarded or moved and left on the surface (Table 3). Twenty-five of the 59 scatterhoarded seeds survived through germination compared to 15 of 32 surface-dispersed seeds. In 2007, a total of 81 seeds (3.8%) were secondarily dispersed. Twenty-two of 50 scatterhoarded seeds survived compared to only four of 31 seeds dispersed to the surface. All the remaining dispersed seeds were either retrieved and consumed or were killed by insects and fungi. *Otoba novogranatensis* seeds were most frequently scatterhoarded (19–22% each year). *Cinnamomum*

*triplinerve* seeds were also moved (11% of seeds in placed fragments) but were left on the surface rather than buried and survived < 1 percent of the time.

The vast majority of seed movement occurred in forest fragments (86% in 2006, 81% in 2007). The number of seeds that were secondarily dispersed, however, varied greatly among the four forest fragments ( $\chi^2 = 37.0$ ,  $df = 3$ ,  $P = 0.001$ ). Most seed movement occurred in the two larger and least-disturbed forest fragments, Las Cruces (68% in 2006, 35% in 2007) and Las Cascadas (26% in 2006, 50% in 2007), whereas only 14 total seeds were moved at Loma Linda and La Reserva.

**GERMINATION.**—Habitat was a significant factor for the germination success of all species tested with a trend for higher germination in secondary forest (Fig. 4). *Pseudolmedia spuria* germinated more often in secondary forests compared to pasture whereas germination in fragments was intermediate ( $F = 6.5$ ,  $df = 2$ ,  $P = 0.008$ ). Similarly, *O. endresiana* had a higher percent germination in secondary forests compared to pasture ( $F = 3.8$ ,  $df = 2$ ,  $P = 0.042$ ). A significant habitat  $\times$  treatment interaction arose for *O. endresiana* ( $F = 3.9$ ,  $df = 2$ ,  $P = 0.384$ ) where burial enhanced germination of seeds by over 40 percent in pastures but had no effect in the other habitats. Both habitat type ( $F = 6.96$ ,  $df = 2$ ,  $P = 0.006$ ) and burial treatment were significant for *O. novogranatensis* ( $F = 9.48$ ;  $df = 1$ ;  $P = 0.006$ ) but not the interaction. *Otoba novogranatensis* germinated more often in secondary forest compared to pasture and forest fragments. Its buried seeds germinated 14 percent more often than seeds left on the surface.

## DISCUSSION

**GENERAL OVERVIEW.**—These results concur with those of previous studies showing that postdispersal seed mortality in human-altered tropical forest habitats is high (49–93%) (Uhl 1987, Osunkoya 1994, Holl & Lulow 1997). The levels of seed mortality and causes of seed death were relatively consistent across the 2 yr of the study. However, these observed patterns of seed fate contrasted with previous work in several key ways. First, I found that the causes of seed mortality differed significantly among habitats and that rodent predation in the abandoned pastures and secondary forests was low compared to forest fragments. Second, seed survival and germination were generally higher in secondary forests than in either forest fragments or abandoned pastures. Finally, seeds of several species were frequently moved by animals in the larger forest fragments and subsequently survived, whereas secondarily dispersal in the abandoned pastures and secondary forests was rare.

**CAUSES OF SEED MORTALITY AMONG HABITATS.**—In contrast to most previous studies, I found that rodent predation in abandoned pastures and secondary forests was lower than in primary forests (Fig. 3). This result was unexpected because the majority of tropical studies have reported higher levels of seed predation in successional habitats (pastures and secondary forests) relative to mature forest

TABLE 2. Changes in the relative contributions of rodent versus insect/fungal attack and biotic (combined rodent, insect and fungi) versus desiccation to seed death among habitats. The relationships are expressed as ratios ( $df = 2$  in each case). Rodent predation was more important in fragments while insect and fungal attack was higher in pasture and secondary forests. Desiccation only occurred in pastures. \* $P < 0.001$ .

Species		Pasture	Secondary	Fragment	
<i>Pseudolmedia oxyphyllaria</i>	Rodent:Insect/Fungi	1:2	1:1.3	1.7:1	$\chi^2 = 144^*$
	Biotic:Desiccation	1:1.2	–	–	
<i>Ocotea endresiana</i>	Rodent:Insect/Fungi	1:4.8	1:1.4	1.5:1	$\chi^2 = 278^*$
	Biotic:Desiccation	1:3.9	–	–	
<i>Otoba novogranatensis</i> (2006)	Rodent:Insect/Fungi	1:21	1:5.6	1:3.1	$\chi^2 = 169^*$
	Biotic:Desiccation	1:1.3	–	–	
<i>Persea americana</i>	Rodent:Insect/Fungi	1:8.2	1:1.9	2.6:1	$\chi^2 = 64.9^*$
	Biotic:Desiccation	1:1.9	–	–	
<i>Pseudolmedia spuria</i>	Rodent:Insect/Fungi	1:2.6	1:1.1	2.6:1	$\chi^2 = 27.8^*$
	Biotic:Desiccation	1.4:1	–	–	
<i>Cinnamomum triplinerve</i>	Rodent:Insect/Fungi	1:4.4	1.2:1	3.6:1	$\chi^2 = 113^*$
	Biotic:Desiccation	5.4:1	–	–	
<i>Otoba novogranatensis</i> (2007)	Rodent:Insect/Fungi	1:19.8	1:1.93	1:1.8	$\chi^2 = 28.3^*$
	Biotic:Desiccation	3.2:1	–	–	

(e.g., Uhl 1987, Hammond 1995, Asquith *et al.* 1997, Notman & Gorchoy 2001, Peña-Claros & De Boo 2002, Andresen *et al.* 2005) and small mammals were cited as the key predators (Osunkoya 1994, Hammond 1995, Holl & Lulow 1997, Notman & Gorchoy 2001). Although direct comparison with the results of other studies is complicated due to the use of different methods and differences in land-use histories, several explanations for the low rates of rodent predation in the pasture and secondary forests are possible. First, the seeds used were relatively large and some studies have shown a trend for higher levels of predation on smaller seeds (Osunkoya *et al.* 1994, Blate *et al.* 1998, Myster 2004). Dirzo *et al.* (2007) suggests that the larger granivores that prefer larger seeds are often absent from heavily impacted landscapes whereas small rodents are abundant (*sensu* Terborgh 1992) and preferentially attack smaller-seeded species. Second, it is possible that levels of seed predation are elevated in the forests because of the high degree of fragmentation. Elevated levels of granivory have often been reported in small fragments when compared to large fragments or intact forests (Sork 1987, Asquith *et al.* 1997, Donoso *et al.* 2004, Fleury & Galetti

2006). Finally, mammalian seed predators may simply be less abundant in successional habitats with a history of intensive land use and in agricultural landscapes that lack nearby intact forests (Stevens & Husband 1998).

The ultimate fate of seeds also differed among the habitats with a trend for higher survival in young secondary forests. In contrast, research in moist lowland tropical forests (Uhl 1987, Notman & Gorchoy 2001, Peña-Claros & De Boo 2002) and in dry tropical forest (Hammond 1995) reported lower levels of mortality in mature compared to secondary forests. Because the cause of mortality was determined for each seed, a mechanistic understanding of this result is possible. First, desiccation contributed to high seed mortality in pastures although the number of desiccated seeds decreased in 2007 as the pastures grew and vegetation cover increased. This is not surprising given that many primary forest species have a low tolerance for desiccation. Second, insect predation and fungal infection, which accounted for the majority of overall seed death, were relatively constant in magnitude across all the habitat types. Mortality in secondary forests was therefore lower because

TABLE 3. Number and percent of seeds secondarily dispersed to the surface and buried (scatterboarded) and total number surviving in each habitat type ( $P =$  pasture,  $S =$  secondary forests,  $F =$  forest fragments). A total of 540 seeds in 2006 and 720 seeds in 2007 were experimentally placed in each habitat.

Seed fate	2006			2007		
	P	S	F	P	S	F
Total moved	1 (> 1%)	11 (2%)	78 (13%)	0	15 (2%)	66 (9%)
Moved to surface	0	11 (2%)	21 (4%)	0	7 (1%)	24 (4%)
Moved and buried	1 (> 1%)	0	57 (11%)	0	8 (1%)	42 (8%)
Total moved and surviving	1 (> 1%)	7 (1.3%)	32 (6%)	0	3 (> 1%)	23 (3%)
Mean distance moved (cm)	80.0	26.4 ± 13.3	170.2 ± 167.5	0	107.8 ± 80.3	80.1 ± 77.3

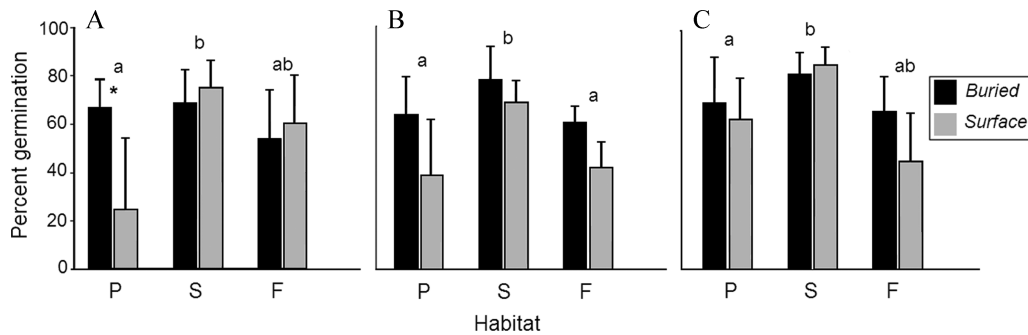


FIGURE 4. Mean proportion of germinated seeds after 10 weeks (A: *Ocotea endresiana*) and 12 weeks (B: *Otoba novogranatensis* and C: *Pseudolmedia spuria*) by habitat and burial treatment. Total germination (combined buried and surface treatments) by habitat with the same letter are not significantly different ( $P < 0.05$ ) based on Tukey's HSD multiple comparisons. Overall germination of *O. novogranatensis* is higher in buried treatment. \*Germination of buried *O. endresiana* seeds is higher only in pasture.

seeds were protected from desiccation and rodent predation was relatively low.

**SECONDARY DISPERSAL.**—Although secondary dispersal has been shown to be an important factor in the establishment of some tropical tree species (Asquith *et al.* 1999, Jansen *et al.* 2004), seed removal has often been equated with seed mortality, especially in successional habitats (*e.g.*, Vander Wall *et al.* 2005). This study found that secondary dispersal of large seeds was rare in pastures and secondary forests but occurred frequently in some of the forest fragments (Table 3). The amount of scatterhoarding differed markedly among the four forest fragments tested: over half the seeds of several species were scatterhoarded in larger fragments, whereas almost no seeds were scatterhoarded in the two smaller and more isolated fragments. This lack of secondary dispersal may be due to a reduction in populations of agoutis that can occur in smaller fragments and areas where there is hunting pressure (Cullen *et al.* 2000, Peres 2001). For example, Asquith *et al.* (1999) found that burial of *Hymenaea courbaril* seeds occurred frequently on islands where agoutis were present but was rare on islands where they had been eliminated. The surveys of mammals in the area surrounding the LCBS indicated that although the majority of species still persist in this landscape, abundances of large- and medium-sized species were relatively low (Daily *et al.* 2003, Pacheco *et al.* 2006). Although smaller scatterhoarding rodents, such as spiny mice *H. desmarestianus* (Heteromyidae), may persist in small fragments and degraded forests, the low level of seed movement suggests that this important dispersal pathway is largely disrupted in this agricultural landscape.

**GERMINATION.**—Seeds of all three species germinated at significantly higher levels in secondary forests compared to pasture and *O. novogranatensis* germinated more often in secondary forest than in either of the other habitats (Fig. 4). Burial had a positive effect on germination of two of the species tested although the effect varied by habitat. Seed burial can improve germination by reducing fluctuations in temperature and moisture and hide seeds from some predators. Buffering of harsh surface microclimate conditions ap-

pears to have been important for *O. endresiana*, for which burial greatly increased germination in pastures but not in other habitats. Germination of *O. novogranatensis* was improved by burial in all habitats, perhaps because of reduced insect predation (Vander Wall 1993). The importance of seed burial mimicking scatterhoarding by rodents has been demonstrated in several other studies. For example Wenny (1999) found that burial improved germination of *Guarea glabra* seeds under green house conditions. Similarly, buried *H. courbaril* pods and seeds in forest habitat in Venezuela germinated more often than those left on the surface (Asquith *et al.* 1999). The finding that *O. novogranatensis* was frequently scatterhoarded and germinated more often when buried suggests it may be adapted for a secondary dispersal phase.

**IMPLICATIONS FOR TROPICAL FOREST RECOVERY AND RESTORATION.**—Agricultural landscapes cover vast areas that until recently were largely forested. Because these landscapes now play a critical role in the conservation of remaining biodiversity and maintenance of environmental services, there is a great deal of interest in encouraging the growth of native trees on former agricultural land and in managing forest succession. Previous studies suggest that the low recolonization potential of many primary forest species due to disrupted dispersal pathways, especially those with larger-seeds, may alter normal successional trajectories and lead to landscapes dominated by pioneer species (Finegan 1996, Martinez-Garza & Howe 2003). Understanding the ecological processes that limit tree establishment in these areas is therefore important for developing effective management approaches.

The results of this study suggest that a lack of seed dispersal is a more important barrier to forest succession than predation because seeds that are successfully dispersed to successional habitats have a reasonable chance of escaping predation and surviving. The apparent loss of scatterhoarding activity from more degraded habitats and forest fragments is a concern because it reduces the regeneration potential of tree species adapted for secondary dispersal. The lack of secondary dispersal also has implications for the rate of tropical forest recovery because it affects overall patterns of seedling distribution, and as the germination experiment suggests, burial can

enhance germination in degraded habitats. From a management perspective, protecting remaining forest fragments and populations of animal seed dispersers is clearly a priority. Moreover, the high levels of seed mortality in forest fragments observed here and elsewhere suggest that active management of fragments and restoration of abandoned land is necessary to conserve the plant species remaining in agricultural landscapes. A common restoration technique is to plant tree seedlings (Holl *et al.* 2000, Ruiz-Jaen & Aide 2005); however, this approach can be both expensive and labor intensive. The findings of this study suggest that some large-seeded primary forest species have good potential to survive and germinate if they are dispersed into early stages of succession, especially young secondary forests. Direct seeding of larger-seeded species into successional habitats may therefore be a viable, low-cost alternative to planting seedlings and merits further testing as a restoration strategy.

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