Variation in Post-dispersal Seed Predation in Mature Peruvian Lowland Tropical Forest and Fallow Agricultural Sites¹

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ABSTRACT

Variation in post-dispersal seed predation between mature forest and fallow swidden agriculture sites (young forest) was examined for 26 tree and liana species in Peruvian lowland tropical forest. Exclosures were also used to determine the relative importance of vertebrate and invertebrate seed predators. Although species differed significantly in levels of predation, predation of seeds exposed to vertebrates was high (>75%) for all species, while seed predation by invertebrates was lower and more variable. Seed and seedling predation by insects was significantly higher in mature forest, while seed predation by rodents was higher in fallow areas. Other sources of mortality (primarily desiccation) were higher for seeds in fallow areas. The percentage of seeds moved was significantly different among species but not between forests.

RESUMEN

La variación en depredación de semillas, después de dispersadas, se examinó en el bosque maduro y la purma (áreas de agricultura en sucesión) para 26 especies de árboles y lianas en un bosque tropical de bajura en Perú. Se utilizaron tratamientos de exclusión para determinar la importancia relativa de depredadores de semillas vertebrados e invertebrados. Aunque las especies difirieron significativamente en niveles de depredación, la depredación de las semillas expuestas a vertebrados fue alta (>75%) para todas las especies, mientras que la depredación de semillas por invertebrados fue más baja y más variable. La depredación de semillas y plántulas por insectos fue significativamente mas alta en el bosque maduro, mientras que la depredación de semillas por roedores fue más alta en purmas. Otras causas de mortalidad (principalmente desecación) fueron más comunes en las purmas. El porcentaje de semillas movidas difirió significativamente entre especies pero no entre los dos tipos de bosque.

Key words: forest regeneration; Peru; seed dispersal; seed predation; swidden agriculture; tropical wet forest.

An important source of disturbance to tropical forests in Latin America and worldwide is slashand-burn (swidden) agriculture (Gomez & Tamirez, Coomes et al. 2000). Because land is generally used for only a short period before it becomes fallow, large areas of young secondary forest in various stages of regeneration are common in forested areas near human settlements (Coomes et al. 2000). Understanding factors that influence seedling establishment in these areas will be important in any efforts to manage forest regeneration. Fallow areas represent distinct habitats from mature forest and may favor the establishment of distinct species groups (Uhl 1987, Nepstad et al. 1991). Escaping seed and early seedling mortality is likely to be an important first step for establishment in these habitats. Relatively little work, however, has investigated seed mortality in young, fallow agricultural sites.

Among the few studies that have looked at seed predation in young, fallow agricultural areas, seed mortality was generally found to be high, and seed predation was a major cause of mortality (Uhl 1987, Hammond 1995). These studies also suggest that seed predation may be higher in these very young forests compared to older forests. Hammond (1995) found that seed predation in two-tofour-year-old abandoned agriculture sites was greater than seed predation in the forest for three of four species studied in dry forest of Mexico. Uhl (1987) found that seed predation was consistently higher in young abandoned agriculture than in forest gaps for seeds of five species.

Levels of seed predation have frequently been found to differ among plant species (Janzen 1969, Uhl 1987, Myster & Pickett 1993, Terborgh *et al.* 1993, Osunkoya 1994, Holl & Lulow 1997, Blate *et al.* 1998, Hulme & Borelli 1999, Guariguata *et al.* 2000). In areas in which seed predation is high, species with low predation may have a major competitive advantage over species that suffer high predation. Because of the high diversity of species in

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tropical forests, the elucidation of general patterns of seed predation may be particularly important for improving efforts to encourage forest regeneration in tropical areas disturbed by human activities.

Disturbed habitats, either natural such as forest gaps or human-caused such as agricultural areas, may differ in the abundance and identity of seed predators as well as in the conditions that affect the ability of predators to find and consume seeds. Light levels, humidity, leaf litter, fallen branches, ground cover, and number of seeds, all may influence the occurrence of particular seed predators in a given habitat (Emmons 1982, Schupp & Frost 1989, Tomblin & Adler 1998, Manson et al. 1999, Guariguata et al. 2000). These same conditions may also influence the ability of seed predators to find seeds (Schupp 1988, Willson 1988, Whelan et al. 1991). Differences in these conditions may also exist within the same general habitat type due to spatial variation and the effects of distance from habitat ecotones, thus resulting in greater withinhabitat heterogeneity of seed predator communities (Didham 1997).

The composition of the seed predator community is important because not all predators consume the same seed species or may consume them in different quantities. Although seed predation by similar animals, such as small versus medium-sized rodents, may differ (Brewer & Rejmanek 1999), differences in seed predation patterns by two broad categories of seed predators, vertebrates and invertebrates, are likely to be greater and more consistent (Hammond & Brown 1996). These two predator taxa differ in size as well as metabolism and may respond to seed characters such as size or secondary compounds quite differently (Rhoades 1979, Davidson 1993). Many invertebrate seed predators are specialists and are able to tolerate high levels of specific toxins such as alkaloids, which vertebrate generalists cannot (Rhoades 1979). Vertebrate and invertebrate predators may also respond distinctly to seed distributions (Janzen 1970, Wilson & Janzen 1972). Studies by Howe (1993) and Terborgh et al. (1993) have found that seeds or seedlings attacked by insects showed distance-dependent predation, whereas those attacked by mammals did not. The distribution of individuals (or colonies) also may not be the same in these two groups. The seed shadow of a single tree may exceed the home or foraging range of an individual insect or colony, whereas the home range of most vertebrate seed predators is likely to encompass the seed shadows of many trees. Understanding differences in seed predation between these two taxa may have important management implications because the effect of human disturbances can have a large impact on vertebrate seed predators (Wright *et al.* 2000) but is likely to have less influence on populations of invertebrate taxa.

Vertebrate seed predators may also function as important seed dispersers by leaving uneaten scatter-hoarded seeds (Forget 1990, 1993; Brewer & Rejmanek 1999). This source of secondary dispersal has been shown to be important for a variety of species in different habitats (Forget 1991, Asquith *et al.* 1997). As with seed predation, patterns of seed dispersal are likely to differ depending on the seed species and the animal dispersing the seeds, as well as the habitat in which they occur. Variation in dispersal may have an important influence on subsequent seed survival.

Although survival at the seed stage may be an important early determinant of successful establishment, mortality continues at all stages of plant development, and patterns of later mortality may not be the same as those of mortality at the seed stage (Jordano & Herrera 1995, Schupp 1995). During germination and subsequent seedling growth, seed characteristics such as the strength of the seed coat or endocarp that may have influenced predation change; thus, germinated seeds potentially become vulnerable to a different set of predators. Chemical changes in the quantity of defensive compounds such as cyanide and tannins may also change during germination (Ahmed et al. 1996). During seedling development, abiotic conditions may play a greater role in survival and may also affect biotic interactions by influencing seedling growth rate and ability to produce defensive compounds. It is thus important to examine patterns of mortality at different stages of development and understand how these patterns interact with habitat.

This study examined factors influencing seed and early seedling predation in non-flooded lowland tropical rain forest in Peru. Levels of predation were compared in forests of different ages: young, fallow agricultural sites and mature forest. In addition, exclosures were used to determine the relative importance of invertebrate and vertebrate seed predators in these two forests. Seed movement was also quantified and compared between habitats.

The specific objectives of this study were to address the following questions: (1) Do levels of seed predation differ between young and mature forest? (2) Does forest age affect seed predation in a similar manner for different tree species? (3) Do vertebrate seed predators differ from invertebrate predators in the identity of seeds they prey on, and

	Species	Family	Dates (start–finished)	No. of weeks	No. of trees; Forest type*; Habit**
1	Licania urceatoris	Chrysoblanaceae	23/08/96-30/11/96	14	14; Mature; T
2	Inga sp.	Mimosoideae	04/09/96-21/11/96	11	3; Mature; T
3	Garcinia sp.	Clusiaceae	16/09/96-19/02/97	22	3; Mature/Young; T
5	Minquartia guianensis	Olacaceae	24/10/96–19/02/97	18	10; Mature; T
6	Ormosia sp.	Papilionoideae	04/09/96–04/06/97	39	3; Mature; T
7	Telitoxicum sp.	Menispermaceae	16/09/96-26/01/97	19	2; Mature; L
8	Mendoncia glabra	Acanthaceae	16/09/96-09/03/97	25	ca 20; Mature/Young; L
9	Enterolobium cyclocarpum	Mimosoideae	14/10/96–01/05/97	28	2; Mature/Pasture; Ť
10	Sacoglottis sp.	Humiriaceae	01/11/96–19/07/97	37	4; Mature; T
11	Pouteria sp.	Sapotaceae	20/11/96–16/04/97	21	3; Mature; T
12	Virola elongata	Myristicaceae	26/11/96-19/02/97	12	2; Mature; T
13	Bactris gasipes	Palmae	29/01/97-29/05/97	17	>20; Young-cultivated; T
14	Hevea sp.	Euphorbiaceae	29/01/97-21/03/97	8	5; Mature; T
15	Aniba sp.	Lauraceae	08/02/97-21/05/97	15	5; Mature; T
17	Ocotea sp.	Lauraceae	19/02/97–19/07/97	21	3; Mature/Young; T
18	Virola sp.	Myristicaceae	19/02/97–19/07/97	21	4; Mature; T
20	Sclerolobium sp.	Caesalpinioideae	05/03/97-23/04/97	7	5; Mature; T
21	Leonia glycycarpa	Violaceae	22/03/97-19/06/97	13	4; Mature/Young; T
22	Heisteria duckei	Olacaeae	16/04/97–19/07/97	13	3; Mature; T
23	Licania sp.?	Chrysobalanaceae	23/04/97-19/07/97	12	6; Mature; T
24	Protium sp.	Burseraceae	01/05/97-19/07/97	11	4; Mature; T
25	Salacia sp.	Hippocrateaceae	07/05/97–19/07/97	10	2; Mature; L
26	Wettinia augusta	Palmae	22/05/97-19/07/97	8	3; Mature; T
27	Tapirira sp.	Anacardiaceae	29/05/97-19/07/97	7	3; Mature; T
28	Rhigospira quadrangularis	Apocynaceae	04/06/97–19/07/97	6	3; Mature; T
30	Rourea sp.	Connaraceae	19/06/97–19/07/97	4	4; Mature; L

TABLE 1. Species used in the seed predation experiment; date set out and date collected; total number of weeks in the field; number of parent trees from which they were collected; and forest type in which adult trees were found.

* Young forest was less than 20 years old.

** T = tree; L = liana.

is the relative importance of predation by these groups and the intensity of this predation different in young and mature forest? (4) What is the relative importance of seed and early seedling mortality? and (5) Does seed identity or habitat influence the probability of a seed being moved?

MATERIALS AND METHODS

STUDY SITE.—Research was conducted in and around the area of the Centro de Investigaciones Jenaro Herrera (CIJH), a field station 2.5 km east of the Ucayali River, *ca* 140 km south of Iquitos, Peru (4°55'S, 73°45'W). The forest is tropical rain forest of low terrace and high terrace type (Lopez Parodi & Freitas 1990), and is very diverse (Gentry 1988, Phillips & Miller in press). Mean annual rainfall is 2521 mm, and a weak dry season usually occurs between June and September (Spichiger *et al.* 1989). Land under the management of CIJH is a mix of relatively undisturbed mature forest, regenerating pasture, and forest that was either selectively logged or clear-cut. The area bordering CIJH is a matrix of small (0.5–3.0 ha) swidden agriculture plots and secondary forest of various ages regenerating from past agricultural use, as well as small remnants of mature forest.

This study used areas of mature forest within CIJH and areas of fallow swidden agriculture (hereafter referred to as young forest) owned by residents of the area. Agricultural practices closely resembled the swidden-fallow system described by Coomes et al. (2000). Young forest plots ranged from two to three years since becoming fallow. Swidden areas used for this study are typical in that they were planted with a variety of plants (Padoch & De Jong 1991, Lamont 1999, Coomes et al. 2000), but predominantly with either sugarcane (Saccharum officinarum) or a mixture of yuca (Manihot esculenta) and plantains (Musa acuminata). Canopy openness and height in young forest areas was very heterogeneous; canopy cover ranged from less than 10 to almost 100 percent, with an average height of ca 2.5 to 3.5 m.

SEED SELECTION.—A total of 26 species was selected for use in this experiment (Table 1). The choice of species was not predetermined but based on seed availability. For the purpose of this study, a seed was defined as the dispersal unit and included the structure remaining after any material normally consumed by seed dispersers had been removed. Seeds were chosen using the following guidelines: (1) only tree and liana species were included in this study; (2) only species that occurred in young or mature forest similar to that of study plots (see below) were included; (3) seeds were taken from ripe fruit or collected from the ground below the parent tree after being recently dropped by animals (i.e., monkeys or birds) consuming fruits; (4) in order to follow seed fate, only seeds greater than 5 mm in width were included in this study; (5) whenever possible, seeds were collected from species for which more than one individual was fruiting; (6) the use of seeds of more than one species in the same taxonomic family was avoided whenever possible; and (7) seed species very susceptible to desiccation (visibly shriveled or degraded after air-drying for 24 hours indoors, away from direct sunlight) were not included. By this selection process, the 26 species chosen for the experiment were meant to be a reasonably representative sample of the larger-seeded species in this area. Few of the selected species were found growing in the young forest (Table 1), as many of the young forest species had very small seeds. Because only large seeds were used in this study, the overall importance of seed predators that may focus on smaller seeds, such as many ants (Byrne & Levey 1993, Levey & Byrne 1993) and birds (Diaz 1996) was likely to have been underestimated.

Voucher specimens of all species were deposited in the herbarium at the Centro de Investigaciones de Jenaro Herrera, the Herbarium Amazonense de la Universidad Nacional de la Amazonia Peruana in Iquitos, and the Turrell Herbarium, Miami University.

SEED PREPARATION.—After collection, seeds of all species were removed from their fruit (if fleshy), rinsed with water, and put in loosely closed plastic bags. Seeds were not stored in this manner for more than 48 hours. Once a sufficient number of seeds had been collected, all seeds were rinsed again and any remaining fleshy fruit material was removed by gentle scrubbing with a nylon scouring pad. Seeds were also carefully inspected for signs of insect infestation, and non-floating species were tested for possible insect infestation by putting their seeds in water and rejecting any seeds that floated. In order to glue braided nylon fishing line to the seeds (see experimental design below), they



FIGURE 1. Diagram representing an experimental plot. Numbers represent hypothetical placement of species. Each number represents a site with a pair of treatments (see insert): exposed to all predators (open treatment) or protected by a wire mesh cage to exclude vertebrate predators (cage treatment). Squares marked with an "i" show approximate placement of cages excluding both vertebrate and invertebrate predators. See text for details of design.

were air-dried indoors, away from direct sun. Drying time varied among species depending on their seed coat, but ranged from *ca* 15 minutes to *ca* 4 hours. Seeds were then randomly assigned to one of two treatments: unprotected seeds (open) or protected from vertebrate predators (caged).

EXPERIMENTAL DESIGN.—Seeds of each species were placed along transects within four plots in mature forest and four plots in young forest sites. At least 20 m of similar forest surrounded each plot to avoid the effects of other habitats or habitat edge. Young forest sites ranged in size from $ca 150 \times 80$ to 250×150 m and were fallow for between two and one-half to three years before the start of the experiment. Three of the four plots placed in mature forest were surrounded by large areas of mature forest while one was bordered on one side by younger (<30 years old) forest. All four young forest plots were bordered by a mix of mature and/or secondary forest of varying ages. Plots ranged in distance from each other; the closest plots were ca 500 m and the farthest ca 6000 m apart. Each plot consisted of eight 40 m transects separated by 12 m (Fig. 1). Five stations separated by 10 m were placed along each transect. Four replicate stations were used for each species. Seeds of each species were placed in one station along every other transect. This allowed for a maximum of 10 species to be tested at a time. Seeds were placed in the two treatments at each station. For 25 of the 26 species, five seeds were placed in each treatment replicate; for the largest-seeded species (Licania sp. 1), only three seeds were used per replicate.

In the open treatment, seeds were placed on the ground within a 25×25 cm area cleared of most leaf litter and covered by a thin layer (1–2 leaves) of litter. Seeds in the caged treatment were treated similarly but were covered by a $25 \times 25 \times$ 30 cm cage with a hinged top constructed of hardware cloth with a 1.27 cm mesh. Cages were placed *ca* 1 m from the seeds in the open treatment. The sides of the cage were buried *ca* 5 cm into the soil and staked down with small wire stakes.

To ensure that seeds removed from the open treatment were in fact eaten and not cached, a 50 cm green braided nylon thread was glued to seeds using a five-minute epoxy (Soldi-Mix® 5-minutes), and an 8 cm strip of Day-Glow pink flagging was tied to the other end. Seeds in the caged treatment received either a small amount of epoxy or epoxy and short (10 cm) nylon line. For seeds that were narrower than the mesh of the exclosures, the line was tied to a small stake in the middle of the exclosure to prevent the possibility of seeds being washed away.

Although the addition of line and glue to seeds may influence levels of predation, similar methods have been used in other studies (Schupp 1988, 1989; Bodmer 1991; Forget & Milleron 1991; Forget 1996; Brewer & Rejmanek 1999), and field trials have found no effect of these treatments (Notman 2000).

Estimates of mortality apart from predation were obtained for the final 14 species (Table 1) by placing seeds in exclosures designed to exclude both vertebrate and invertebrate predators. Five seeds of each species were placed into four 1 m \times 1 m \times 35 cm cages (Fig. 1) constructed of aluminum window screening (ca 1 mm mesh) supported by wooden stakes; an insecticide, a solution of Baytroid H 10% P.M. (Bayer Corporation) and OikoNeem CE-75 (Herring Ecologica S.A.) containing a 3 percent solution of Azadirachtin extracted from neem (Azadirachta indica), was applied weekly. Litter was removed and replaced in the cages as in the other exclosure cages. Data from 3 of 32 cages were dropped because the cages were stolen. Because this treatment differed in experimental design, mortality rates were not directly comparable to mortality in the other two treatments, but nonetheless provided an estimate of non-predation mortality.

CENSUS OF SEEDS.—Seeds of each species were placed in the field the day following preparation (Table 1). Seeds were checked approximately every two weeks after placement and the number of seeds still present and the number of seeds germinated were recorded. We searched for seeds removed from the open treatment; we then recorded the distance that the flag (or flag and seed) was moved. Seeds that were moved but not eaten were left in place and checked in subsequent censuses. Buried seeds, or seeds in deep holes, were not dug up until the final census. Seeds removed from their flagging were assumed to have been eaten by vertebrate predators. In both treatments, the remains of dead seeds were examined for teeth marks, insect holes, or fungus to determine the cause of death. For the few cases in which seeds were left partly eaten by rodents and were subsequently eaten further by insects (usually ants), mortality was attributed to rodents.

For most species, seeds were left in the field until the majority had either died or produced their first true leaf (at which point they were considered established seedlings). Due to time constraints, several species were collected earlier; for four species (*Licania* sp. 2, *Ocotea* sp., *Ormosia* sp., and *Rhigospira quadrangularis*) less than 50 percent of remaining seeds had germinated. For the other 22 species, an average of 86 percent of the remaining seeds had at least germinated. Collected seeds that had not yet germinated were cut open and inspected visually, and stained with tetrazolium by soaking opened seeds for approximately two hours (methods modified from USDA 1974) to determine if they were still viable.

DATA ANALYSIS.—Analyses of seed predation and seed mortality were performed on the arcsine transformed (Zar 1984) percent seeds preyed on and arcsine percent total mortality. Seeds that were recorded as dead due to pathogens or abiotic factors were not included as preyed on seeds in the analysis of percent seed predation, but were included in the analysis of mortality. For both predation and mortality, two separate analyses were performed, the first using only seed (pre-germination) predation (or mortality) as the dependent variable and the second using both seed and seedling (post-germination) predation (or mortality), hereafter "total predation" (or "total mortality").

Because not all species were exposed the same amount of time and the percentage of seeds that had germinated and/or produced their first true leaves was not equal among species, analyses of seed predation and mortality including only the first two census periods (four weeks) for all species were also conducted. Because the overall results of these tests were similar to tests including all censuses (only the relative species rank in terms of predation or mortality changed significantly), only tests including all data are presented here.

Four separate analysis of variance (ANOVA) models were used to compare levels of seed predation, total predation, seed mortality, and total mortality among habitat and exclosure treatments. The same independent variables (forest type, exclosure treatment, species, and plot) were used for all four analyses. Forest (young vs. mature) and exclosure treatments (open vs. caged) were considered fixed effects. Species and plot (nested within forest) were considered random effects. All two-way interactions between main effects were also included in the model. The interaction of species and plot (nested within forest) was also included in the model. The three-way interaction among the main effects was left in the model only when significant.

Because all species were not tested at the same time, forest, treatment, and plot (forest) were replicated over time with different species. It was not possible to reasonably account for this time effect, however, because species were replaced one or two at a time. The degrees of freedom used in the error term reflected this replication over time.

Because percent predation and percent mortality were calculated based on number of seeds removed from only five seeds, data are likely to violate assumptions of normality even after arcsine transformation. Analyses of residuals, however, showed that the model met the assumption for equal variance and did not have major deviations from a normal distribution. ANOVAs are fairly robust even when the assumptions of normality are not completely met (Zar 1984).

To determine if the relative rankings of species in terms of predation were similar between different forests and different protection treatments, pairwise nonparametric correlations were done using Kendall's Tau-b coefficients.

ANOVA was also used to determine if there was a difference among species or between forest types in the number of seeds moved from the open seed treatment. Moved seeds were considered to be any seeds that were moved farther than 0.5 m from their original position and either left or eaten. Seeds that were removed from their line and flagging were also considered moved if no evidence (*e.g.*, shell fragments) could be found that they were eaten within 1 m of their original location. In this model, forest type and species were the main effects and plot was included as a random effect nested within forest type. All statistical analyses



FIGURE 2. Average percent seed mortality by morality source in young and mature forest and in open or caged treatment. Black bars represent mortality due to vertebrate predation. Light gray bars denote mortality due to invertebrate predation. Dark gray bars indicate other sources of mortality, including fungal pathogens, desiccation, and unknown. Error bars show standard error of the means.

were performed using SAS statistical software (SAS Institute Inc. 1990, Cary, North Carolina, USA).

RESULTS

SOURCE OF MORTALITY .--- In general, predation from the open treatment was by vertebrate predators and predation within the cage treatment was by invertebrates (Fig. 2); less than 1 percent of seeds in the open treatment were preyed on by invertebrates. Although the fate of seeds within the cages could not always be determined, there were only two cases in which vertebrates appeared to have dug under the cages and ate seeds. Other sources of mortality included desiccation, infection by fungal pathogens, and unknown (perhaps nonviable seeds; Fig. 2). It is possible that some seeds that died due to insect attack were scored in the "other" category because evidence of insect predation was not clear. This type of error, however, should have been consistent among treatments and forest types, and thus should not have had a major impact on the analysis. It is also possible that some seeds in the open treatment that were scored as eaten by vertebrates were eaten by insects. This probably did not happen frequently, however, since comparison of eaten seeds in the open treatment and the caged treatment showed that the remaining bits of seeds left behind in these two treatments were clearly distinguishable. Leaf-cutter ants (Atta sp.) may have removed some of the smaller seeds; however, leafcutter ants appeared to be uncommon in both of



FIGURE 3. Mean percent seed mortality due to vertebrate and invertebrate seed predation. In (A) seeds in open treatment and young forest; (B) seeds in open treatment and mature forest; (C) seeds in cage treatment and young forest; (D) seeds in cage treatment and mature forest. Gray bars represent seed predation, black bars represent combined seed and seedling predation. Error bars show standard error of the means (N = 16 replicates for all species). The species name corresponding to each species number is given in Table 1. Species are organized in ascending order according to level of seed predation.

these forest types and their trails were never observed within any of the experimental plots. It is also possible that a number of seeds scored as eaten by vertebrates were in fact removed from their line and subsequently cached. Survival of known cached seeds, however, was very low and almost all cached seeds were eventually eaten.

SEED PREDATION.—Total average seed predation for all species was over eight times higher for unprotected seeds (82.0%) than for caged seeds (9.6%). Mean seed predation of unprotected seeds ranged from a low of 38.7 (*Protium* sp.) to a high of 98.8 percent (*Ocotea* sp.) (Fig. 3a, b). For seeds protected from vertebrate predators, mean seed predation ranged from a low of 0 percent (*Licania urceatoris*, *Wettinia augusta, and Tapirira* sp.) to a high of 35.8 percent (*Pouteria* sp.).

Seed predation was significantly different among the main effects of species and exclosure treatment, but not between forest types (Table 2a; Figs. 3 and 4a). There were also significant differences in seed predation among plots nested within forest type (Fig. 4a). Interpretation of the differences in seed predation between these main effects is complicated, however, because all two-way interactions were significant (Table 2a). The three-way interaction between these treatments was also significant.

The rank order of seed predation among species was correlated between young and mature forest for both unprotected and protected seeds (df = 26, Kendall's Tau-b = 0.42, P = 0.003, and df = 26, Kendall's Tau-b = 0.58, P = 0.0001, respectively) but not between protection treatment in either young or mature forest (df = 26, Kendall's Tau-b = 0.22, P = 0.13 and df = 26, Kendall's Tau-b = 0.13, P = 0.36, respectively).

TOTAL PREDATION.—Patterns of total predation were similar to those of seed predation. General patterns between the two forests and between ex-

TABLE 2. Analysis of variance for the effect of forest type (young vs. mature), exclosure treatment (open vs. cage), species of seed, and plot (nested within forest) on percent seed predation (arcsine transformed); (a) pre-germination and (b) total. Plot and species were treated as random effects; all other terms were fixed effects. Degrees of freedom are for the source of variation followed by the error term.

Source of variation	df	SS	MS	F	Р
(a) Dependent variable: arcsine	(% pre-germination	seed predation)			
forest	1,6	0.0764	0.0764	0.23	0.6519
exclosure treatment	1, 1404	280.21	280.21	4553.8	0.0001
species	25, 1404	21.803	0.8721	14.17	0.0001
plot (forest)	6, 1404	2.0356	0.3393	5.51	0.0001
forest*treatment	1, 1404	3.6842	3.6842	59.87	0.0001
forest*species	25, 1404	4.8829	0.1953	3.17	0.0001
treatment*species	25, 1404	16.085	0.6434	10.46	0.0001
species*plot (forest)	150, 1404	14.883	0.0992	1.61	0.0001
forest*treatment*species	25, 1404	2.4125	0.0965	1.57	0.0370
error	1404	101.28	0.0652		
(b) Dependent variable: arcsine	(% total seed predat	ion)			
forest	1, 6	1.8101	1.8101	9.22	0.0229
exclosure treatment	1, 1404	309.07	309.07	5954.0	0.0001
species	25, 1404	13.988	0.5600	10.79	0.0001
plot (forest)	6, 1404	1.1780	0.1963	3.78	0.0010
forest*treatment	1, 1404	3.7843	3.7843	72.90	0.0001
forest*species	25, 1404	3.2592	0.1304	2.51	0.0001
treatment*species	25, 1404	13.808	0.5523	10.64	0.0001
species*plot (forest)	150, 1404	11.426	0.0762	1.47	0.0004
forest*treatment*species	25, 1404	2.3549	0.0941	1.81	0.0083
error	1404	84.309	0.0543		_



FIGURE 4. Mean percent seed mortality due to vertebrate and invertebrate predation for 26 species in young forest plots (gray bars) and mature forest plots (black bars) for seeds exposed to all predators (treatment = open) or protected from vertebrate predators (treatment = cage). Each bar represents mean percent mortality in one plot; error bars show standard error of means (N = 104 replicates). Seed predation is either pre-germination (Fig. 4A) or total predation (Fig. 4B).

closure treatments did not change after early seedling predation was also included. The importance of seedling predation, however, did differ between species. Some species that had relatively low levels of seed predation had much higher levels of seedling predation (Fig. 3). Seeds in the open treatment that escaped high levels of seed predation but had high seedling predation tended to germinate rapidly (e.g., Leonia glycycarpa, Sclerolobium sp., and Protium sp.). Seedling predation was generally more important for caged seeds than for seeds exposed to predation by vertebrates. While an average of 88 percent of seeds were removed from the open treatment by vertebrates before germination, only 58 percent of seeds attacked by insects in the exclosures were attacked before germination. Predation by insects may have increased after germination because protective tissue such as a seed coat or endocarp must open for the seed to germinate.

Overall levels of seed and seedling predation by vertebrates was extremely high, with all species having over 75 percent of their seeds or seedlings eaten. Insects were less important predators with only 10 of the 29 species having over 25 percent of their seeds or seedlings eaten or killed by insects. Average total predation for all species was over five times higher for unprotected seeds (92.0%) than for caged seeds (16.2%). Mean total predation of un-

TABLE 3. Analysis of variance for the effect of forest (young vs. mature), exclosure treatment (open vs. cage), species of seed, and plot (nested within forest) on percent total seed mortality (arcsine transformed); (a) pre-germination and (b) total. Plot and species were treated as random effects; all other terms were fixed effects. Degrees of freedom are for the source of variation followed by the error term.

Source of variation	df	SS	MS	F	Р			
(a) Dependent variable: are	a) Dependent variable: arcsine(% pre-germination seed mortality)							
forest	Ĩ, 6	0.1166	0.1166	0.23	0.6478			
exclosure treatment	1, 1404	223.29	223.29	3102.0	0.0001			
species	25, 1404	21.918	0.8767	12.18	0.0001			
plot (forest)	6, 1404	3.0301	0.5050	7.02	0.0001			
forest*treatment	1, 1404	1.6420	1.6420	22.81	0.0001			
forest*species	25, 1404	4.3422	0.1737	2.41	0.0001			
treatment*species	25, 1404	20.795	0.8318	11.55	0.0001			
species*plot (forest)	150, 1404	16.259	0.1084	1.51	0.0002			
error	1554	116.93	0.0752	_				
(b) Dependent variable; ar	csine(% total seed m	ortality)						
forest	1, 6	0.4115	0.4115	1.68	0.2429			
exclosure treatment	1, 1404	234.19	234.19	3973.0	0.0001			
species	25, 1404	25.227	1.0091	17.12	0.0001			
plot (forest)	6, 1404	1.4723	0.2454	4.16	0.0004			
forest*treatment	1, 1404	1.3222	1.3222	22.43	0.0001			
forest*species	25, 1404	2.9569	0.1183	2.01	0.0023			
treatment*species	25, 1404	17.962	0.7185	12.19	0.0001			
species*plot (forest)	150, 1404	12.122	0.0808	1.37	0.0030			
error	1404	94.370	0.0607					

protected seeds in both forest types ranged from a low of 77.5 percent (*L.glycycarpa*) to a high of 100 percent (*Bactris gasipes*). For seeds protected from vertebrate predators, mean total predation ranged from a low of 0 percent (*L. urceatoris*) to a high of 51.6 percent (*Pouteria* sp.).

Total predation was significantly different among species, exclosure treatment, and forest types (Table 2b; Figs. 3 and 4). Predation was also significantly different among plots nested within forest (Fig. 4). As with seed predation, interpretation is similarly complicated for total predation because the two-way interactions between all the main terms were significant, as was the three-way interaction. The majority of species, however, had higher or equal levels of total predation by vertebrates in the young forest with only 6 of the 26 species having higher total predation by vertebrates in mature forest (Fig. 3a, b). Conversely, 19 of the 26 species had higher total predation by insects in the primary forest (Fig 3c, d). Although mean total predation for all species in the open treatment was not significantly different between young and mature forest (pairwise comparison of least squares means: df = 6, t = 1.82, P > 0.1), mean total predation for all species in the caged treatment was significantly higher in mature forest than young forest (pairwise comparison of least squares means: df = 6, t = 9.99, P < 0.0001).

The rank order of total predation among species was correlated between young and mature forest for both unprotected and protected seeds (df = 26, Kendall's Tau-b = 0.41, P = 0.047 and df = 26, Kendall's Tau-b = 0.71, P = 0.0001, respectively) but not between protection treatments in either young or mature forest (df = 26, Kendall's Tau-b = -0.04, P = 0.77 and df = 26, Kendall's Tau-b = 0.04, P = 0.74, respectively).

PRE-GERMINATION AND TOTAL MORTALITY.—Patterns of average percent mortality were similar to those of predation alone. Average seed mortality in both forests was 82.5 percent for seeds in the open treatment and 16.9 percent for seeds in the caged treatment. Average total mortality was 93.4 percent in the open treatment and 26.2 percent in the caged treatment. For both pre-germination mortality and total mortality, the main effects of species and exclosure treatment were both significant, as was plot nested in forest and all two-way interactions. The effect of forest, however, was not significant for either pre-germination or total mortality. The threeway interaction among forest, species, and exclosure treatment was also not significant (Table 3a, b).

Average mortality in the combined vertebrate and invertebrate exclosures in young forest (14.4%) was not significantly different than in mature forest

TABLE 4.	Analysis of variance for the effect of forest (young vs. mature), species of seed, and plot (nested within forest
	type) on percent seeds moved (arcsine transformed). Plot and species were treated as random effects; all other
	terms were fixed effects. Degrees of freedom are for the source of variation followed by the error term.

Source of variation	df	SS	MS	F	Р
Dependent variable: arcsi	ine(% seed moved)			
forest	1, 6	0.0049	0.0049	0.015	0.9052
species	26, 804	1.9235	0.3206	20.00	0.0001
plot (forest)	6, 804	47.593	1.8305	3.503	0.0020
forest*species	26, 804	3.2352	0.1244	1.360	0.1093
error	804	73.578	0.0915		_

(9.8%; ANOVA: df = 1, 6.01, F = 0.878, P < 0.38), but mortality was different among species (df = 13, 468, F = 3.94, P < 0.001) and plots nested within forest (df = 2, 468, F = 5.54, P < 0.001).

SEED MOVEMENT.—The percentage of seeds moved differed significantly among different species, as well as between different plots nested within forest. The percentage of seeds moved was not different between forest types and there was no significant interaction between forest type and species (Table 4). The percentage of seeds moved ranged from a low of 11.3 percent for *Virola elongata* to a high of 92.5 percent for *B. gasipes* (Fig. 6). Few moved seeds were found cached (<5%), and of those that were, almost all were eventually eaten during the course of the study.



FIGURE 5. Mean percent survival for seeds of 26 species in abandoned agricultural sites (gray) and primary forest (black) for (A) seeds exposed to all predators and (B) seeds protected from vertebrate predators. Error bars show standard error of means (N = 80 for all species except species 1, for which N = 48). The species name corresponding to each species number is given in Table 1.

DISCUSSION

Results of this study showed that there are clear differences in the levels of seed predation by vertebrates and invertebrates, and that vertebrate seed predators were the most important mortality source for these large-seeded species. Levels of seed predation also differed depending on the species of seed, and variation among species was greater for seed predation by insects than for predation by vertebrates. There were not, however, clear differences in the overall level of seed predation between young and mature forests. Nor were there differences in the handling of seeds (measured as movement of seeds) between young and mature forest.

SPECIES IDENTITY.—Levels of percent seed and seedling predation, seed and seedling mortality, and seeds moved were all significantly different among the species of seeds studied. The effect of species identity was not, however, consistent between forest types or exclosure treatments for most of these



FIGURE 6. Mean proportion of seeds moved from the open treatment by species in (A) mature and (B) young forest. Error bars show standard error of the means (N = 16 replicates for all species). The species name corresponding to each number is given in Table 1.

analyses. Species with the highest levels of seed predation by vertebrates did not have the highest levels of insect seed predation (Fig. 3). These differences were reflected in the lack of a significant correlation between species ranks in these two treatments. Species ranking for seeds in the same treatment were fairly similar between forest types and were significantly correlated.

These results indicate that insects and vertebrates responded to the same seeds differently. Given the large potential difference in foraging behavior and food selection between these predator types, these findings are not very surprising. Characteristics that make a seed attractive to a vertebrate predator such as a rodent do not necessarily make this seed attractive to an insect such as an ant or cricket (Notman 2000).

Many studies in a wide range of habitats in both tropical and temperate ecosystems have found significant variation in levels of seed predation depending on the seed species (Samper 1992, Terborgh et al. 1993, Hammond 1995, Nepstad et al. 1996, Silman 1996, Asquith et al. 1997, Holl & Lulow 1997, Adler & Kestell 1998, Blate et al. 1998, Sanchez-Cordero & Martinez-Gallardo 1998). These species-specific differences in seed survival may in part be responsible for patterns of species distributions, as well as community diversity (Janzen 1969, 1971; Connell 1971, 1978; Clark & Clark 1984) and composition (Brown & Heske 1990, Leigh et al. 1993, Guo et al. 1995, Asquith et al. 1997). The importance of species identity to seed predation, however, makes generalizations about patterns of seed predation difficult and highlights the need to find patterns based on species characteristics.

Because not all seeds were put out at the same time, it is possible that differences in seed predation were due at least in part to conditions related to time of seed placement, such as weather, population of seed predators, or abundance of other resources for predators. Although this possibility cannot be completely ruled out, regressions of the effect of time of placement on levels of seed predation showed no clear relationship.

The significant difference among species in the percentage of seeds moved suggests that either different predators were eating different species of seeds or that the same predator treated different species differently. The probability of a seed having been moved was likely to be in part due to different handling time of seeds. Seeds that require longer handling time may have been more likely to be taken to a more protected area before being consumed. Two of the largest-seeded species (*L. urceatoris*, and *Sacoglottis* sp.) appeared to have been moved and cached more frequently than other species. Almost all of these cached seeds were eventually eaten, but it is possible that the very small percentage that were left buried and uneaten had a significantly increased chance of survival (Forget 1992, 1996). A few species may have been moved less frequently than reported in this study because aspects of their morphology reduced the chance of finding evidence that they were eaten. Seeds with a very thin seed coat may have been consumed on the spot but if no evidence had remained, they would have been scored as removed.

FOREST AGE.—There was no consistent difference in seed or seedling predation between young and mature forest. Although there was a significant main effect of forest type on total predation, this effect depended on species and predator identity. Total insect predation was significantly greater in mature forest but total predation by vertebrates was not different between young and mature forest. The greater insect predation in mature forest may have been due to abiotic conditions that affected insect community composition (Didham 1997) or foraging, or greater abundance of specialist insect predators in mature forest where adults of their host species occurred.

Despite greater insect predation in mature forest, total mortality was not different between the two forests types, because of higher mortality due to other causes in the young forest (Fig. 2). Although it was not always possible to determine the cause of mortality for these seeds, many of them appeared to have died due to desiccation. The floor of the young forest was considerably more heterogeneous than that of the mature forest because it included areas of direct sun. Mortality rates of seeds protected from both vertebrates and invertebrates were also slightly higher in the young forest than in the mature forest, further suggesting that abiotic conditions of the young forest were less favorable for some species.

Conditions within the young forest, however, appeared to have been more favorable to later seedling survival than those within mature forest. When mortality after the production of the first leaf was included, total survival was higher for most species in the young forest (Fig. 5). Interpretation of this data must be done with caution, however, since for many species only a small fraction of their seeds made it to the seedling stage before the experiment was terminated.

The significant differences among plots within the same forest type suggests that although different areas in the forest are structurally similar, other factors may have influenced the probability of seed survival. It is possible that these plots encompassed the home range of only a few individuals of the most important vertebrate predator species, and differences in seed preferences of those species or individuals played an important role in the probability of survival. Similar differences in spatial patterns of insect predator abundance may have influenced probability of survival for protected seeds. Large variation in seed predation within a single habitat also has been found in other studies (Silman 1996, Holl & Lulow 1997, Meiners & Stiles 1997).

Previous studies have reported higher seed predation in young forest (abandoned agriculture) than other forest types (Uhl 1987, Hammond 1995). These studies are not directly comparable, however, since Hammond (1995) studied a dry forest in Mexico and Uhl (1987) compared predation in young tropical wet forest to that in forest gaps. For two genera used in both Uhl's (1987) study and this one, Ormosia and Licania, levels of predation reported by Uhl (1987) were slightly lower but similar to levels of predation observed in young forest in this study. Interestingly, several studies have found that seed predation in gaps also tended to be lower than that in surrounding forest (Samper 1992, Nepstad et al. 1996, Silman 1996; cf. Schupp 1988). This suggests that small natural forest disturbances may affect probability of survival in an opposite manner than larger human disturbances. Nepstad et al. (1996) also found that seed removal rate was greatest in abandoned pasture, intermediate in the forest understory, and lowest in forest gaps.

EXCLOSURE TREATMENT—PREDATOR IDENTITY.—The consistently greater predation in the open treatment, regardless of forest type or species identity, suggests that predation of dispersed seeds by vertebrates was the major cause of seed mortality for large-seeded species in this area. Mean seed predation by insects was similar to that of vertebrate predation for only one species, *L. glycycarpa* (Fig. 3). Mortality due to sources other than predation was much lower in the open treatment than in the caged treatment, probably because seeds in the open treatment were removed rapidly and were thus exposed for shorter periods to other mortality sources such as fungus or desiccation.

Based on evidence such as teeth marks found

on partially eaten shells, as well as by trapping (Notman 2000), vertebrate seed predation appeared to be mostly due to small or medium-sized rodents, principally Proechimys spp. Granivorous birds also can be major seed predators in some habitats (Brown et al. 1979) and may have also been responsible for some of the seed predation observed in this study, particularly in the young forest where birds such as the Undulated Tinamou (Crypturellus undulatus) were seen and infrequently captured with seed bait (Notman 2000). Predation by birds may have been underestimated because seeds are typically swallowed whole, thus leaving no evidence. Birds also may have been discouraged from eating seeds by the attached line if they were less able to manipulate seeds and remove the line before consumption.

It was more difficult to determine the identity of insect seed predators because they did not leave characteristic marks on seed remains. The insect most frequently observed eating seeds was an unidentified species of cricket, which buried the seeds under ca 1 cm of soil and ate them while buried. Several small, unidentified species of ants were also observed eating seeds. Ants were seen eating thickshelled seeds only after they were first damaged by rodents. Seeds of several species also were killed by unobserved insects that cut, but did not eat, the developing hypocotyl and/or epicotyl.

This study has clearly shown the importance of small vertebrates to plant reproduction and the processes of forest regeneration. Although rodents are not likely to have as large an impact on survival of later life history stages of trees and lianas, they are still likely responsible for the majority of the post-dispersal mortality of large-seeded trees and lianas. The high levels of predation found in this study are particularly important; seeds in this experiment were dispersed at low densities and away from any conspecific adults, conditions that generally have been found to favor higher survival (Janzen 1970, Clark & Clark 1984). It is possible that seeds at high density under the parent tree experienced greater mortality from sources other than rodents.

Direct comparison of the results of this study with other studies are complicated due to the use of different methods; however, examination of general trends is still possible. Mammals, particularly rodents, have been found to be important seed predators in most studies of tropical forest and associated human-disturbed habitats. Studies by Adler and Kestell (1998), Asquith *et al.* (1997), Blate *et al.* (1998), Hammond (1995), Holl & Lulow (1997), Nepstad et al. (1996), Samper (1992), Sanchez-Cordero & Martinez-Gallardo (1998), Silman (1996), and Terborgh et al. (1993) all found that rodents were the major source of seed removal for medium to large seeds. In addition, although seed removal varied depending on species, overall removal levels of unprotected seeds were frequently greater than 50 percent. The particularly high rates of predation for all species in this study may have been due to the long period that seeds were exposed to predation. Many other studies followed the fate of seeds over shorter time periods and did not include mortality at the young seedling stage. Predation rates however, are still high, when compared to other studies, even when predation on seedlings is excluded. Predation rates may have been slightly underestimated in this study because all seeds were placed under a layer of leaf litter (seeds under leaf litter are more likely to escape predation; Samper 1992, Hammond 1995).

SEED VERSUS SEEDLING SURVIVAL.-Predation continued to be the major source of mortality for seeds in the open treatment, even after germination; the period directly after germination may have been a particularly vulnerable period, as many species in the caged treatment that had escaped significant insect predation were attacked after germination. The importance of predation appeared to decrease, however, once seedlings had produced their first true leaves. For several species that had large, persistent storage cotyledons (e.g., Hevea sp., L. urceatoris, and Virola spp.), the cotyledons were frequently removed by animals but the seedling was left intact. The high light conditions of the young secondary forest may have been advantageous for plants that escaped seed and early seedling predation.

SEED MOVEMENT.—Although the secondary dispersal observed in this study did not appear to increase survival, rare scatter-hoarding events may be important to seed survival for some species. The fact that seed movement was frequent and was not different between young and mature forest suggests that the potential for successful secondary dispersal exists in both young and mature forest. Secondary dispersal also may be important for bringing seeds from the boundary of young and mature forests into the young forest, but the observation of such movements was precluded by the experimental design used in this study.

MANAGEMENT IMPLICATIONS .- Swidden agriculture is generally a low impact form of disturbance when local population levels and land availability allow for sufficient fallow time between reuse. The use of large areas of land and the use of mature undisturbed forest, however, may have a large impact on species populations and regional diversity. There has been increasing interest in exploring the possibilities for encouraging the growth of economically important trees in sites of abandoned agriculture (Uhl 1987, Smith et al. 1999). Understanding the factors that may influence regeneration in these areas is therefore very important. Recent reforestation efforts in the Peruvian Amazon around the Iquitos area have focused on planting seedlings in areas of abandoned agriculture. Planting of seedlings is time and energy consuming, and frequently there is a high percentage of mortality due to seedling damage or desiccation during transport or replanting. Methods that encourage natural regeneration or enhance survival of regeneration from seeds may be more efficient. Based on the high survival of seeds protected from vertebrate predators to the seedling stage, regeneration techniques that use inexpensive protection of planted seeds or other methods such as seed burial (Andresen 1999, Asquith et al. 1999) may result in higher survival at lower costs than methods that use seedling planting techniques. Protecting the important predators of small mammals (e.g., felids) also may reduce predation by rodents.

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