

SEEDLING RECRUITMENT OF LARGE-SEEDED TROPICAL TREES PLANTED AS  
SEEDS IN THE ECUADORIAN AMAZON

By

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To my family, and all those that guide me along the way

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SEEDLING RECRUITMENT OF LARGE-SEEDED TROPICAL TREES PLANTED AS  
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Natural regeneration of large-seeded tropical forest trees in forests and pastures in landscapes fragmented by agriculture can be severely limited by lack of animal-mediated seed dispersal. Seeds that arrive by rare cases of long-distance dispersal may be critical to species persistence, provided they survive in the new sites. In addition to their value for wildlife, many tropical trees with large-seeds have fruits consumed by people. Thus, planting seeds of these species may be an inexpensive method to add economic value to the landscape.

The purpose of this study was to assess some of the factors affecting seedling recruitment of large-seeded tropical forest trees in human-modified landscapes in the Ecuadorian Amazon. In the first experiment (Chapter 2), seeds of *Pouteria caimito* (Sapotaceae), *Quararibea cordata* (Malvaceae), and *Inga densiflora* (Fabaceae) were planted in pastures and forests, and seed survival and seedling development was recorded at 2 and 14 weeks. In the second experiment (Chapter 3), I planted seeds of *Inga densiflora*, *Gustavia macarenensis* (Lecythidaceae), *Caryodendron orinocense* (Euphorbiaceae), and *Plinia* sp. (Myrtaceae) in secondary forests and survival and seedling development were monitored biweekly for 18 weeks. In both experiments,

seeds were planted on the soil surface or were buried. A caging treatment was included in the second experiment to assess seed predation levels.

Over 55% of *Inga*, *Caryodendron* and *Gustavia* (56% and 76% in the two experiments, 76%, and 64%, respectively), 17% of *Plinia*, 10% of *Quararibea*, and 2% of *Pouteria* seeds developed into seedlings and survived during the 14–18 week periods of the two experiments. Seed burial did not increase survival or seedling recruitment of any species in either experiment. In the first experiment, the location of the plots in the landscape (i.e. the indigenous community in which they were planted) affected seed removal and seedling recruitment more than did the habitat (grazed pasture, mature pasture, forest) in which the seeds were planted. Seed removal was extremely low (< 1%) in secondary forests located < 1 km from a main road.

The results of this study suggest seedlings recruit from seeds of large-seeded tropical forest species if dispersal limitations are overcome. Species differences in initial seedling recruitment can be expected, and seed predation and seedling recruitment vary among sites.

## CHAPTER 1 INTRODUCTION

Tropical forests are home to over half of the world's described species (Dirzo and Raven 2003), contain 46% of the living terrestrial carbon pool (Soepadmo 1993), and are located in countries with two-thirds of the world's human population (Wright 2005). By 2030, an additional two billion people will live in tropical countries (United Nations 2004). Economic development in these countries, combined with expanding global economies, increase the demand for forest products (FAO 2005; Fox 2000), resulting in further fragmentation and degradation of existing forests (Wade et al. 2003). The future tropical forests depends in part on the availability of restoration techniques that sustain economic values associated with forests, support local livelihoods, improve landscape-level ecological health, and catalyze natural regeneration processes (Chazdon 2008). In this thesis, I report results from experiments in which seeds of economically valuable tropical forest trees are planted in various human-modified landscapes. Survival through the early stages of seedling establishment is critical to the success of this reforestation method. In two field experiments, I tested the influence of seed burial and habitat type on the probability of seed predation, seedling recruitment, and early seedling survival.

Seed dispersal of large-seeded tropical forest trees is often severely interrupted by tropical deforestation and fragmentation. Many trees with large seeds depend on relatively large animals such as tapirs (Fragoso and Huffman 2000), primates (Nunez-Iturri and Howe 2007), and large birds (Howe and Schupp 1985; Meehan et al. 2002) for seed dispersal away from parent trees. Large bodied frugivores are highly susceptible to local extinction in fragmented landscapes because they are generally preferred by hunters (Jerozolimski and Peres 2003; Peres and Palacios 2007) and often require large, continuous tracts of forested habitat (Chiarello 1999). In

agricultural landscapes containing only remnant forest patches, the rarity of seed dispersal by large animals (White et al. 2004) frequently confines regeneration of large-seeded species to < 100 m from forest edges (Gunter et al. 2007; Wunderle 1997). Large seeds rarely persist in the soil seed bank for more than one season (Garwood 1989; Hopkins and Graham 1984), and thus are dependent on animal-mediated seed dispersal for regeneration. Without human intervention, large-seeded tropical species can be vulnerable to local extinction in fragmented and degraded landscapes (Galetti et al. 2006; Terborgh et al. 2008). Lack of large-seeded species in forests alters successional trajectories (Chazdon 2003), reducing biodiversity recovery during secondary forest succession (Turner et al. 1997).

In addition to supporting wildlife populations, fleshy fruits of many large-seeded species provide food and income for millions of people living in or near tropical forests (Chomitz 2007; FAO 2005). In the Amazon, dozens of tropical forest tree species were in the process of domestication since well before the time of European contact (Clement 1999a). Currently, numerous species previously cultivated only by small-scale farmers are currently being investigated for their economic potential as commercial crops (Akinnifesi et al. 2004; Simons and Leakey 2004). Enriching the landscape with fleshy-fruited species can generate sources of income for local people (Ricker et al. 1999), improve wildlife habitat (Bowen et al. 2007), and conserve genetic diversity of future food sources (Dawson et al. 2009).

Multiple methods of catalyzing the colonization of large-seeded species in fragmented tropical landscapes have been proposed. For example, creating forested corridors and protecting waterways promotes the movement of animals among existing forest patches (Da Silva et al. 2005; Keuroghlian and Eaton 2008). Agricultural practices that increase forest cover such as shade-grown coffee farms (Williams-Guillen et al. 2006) and planting trees to create 'living

fences' (Zahawi 2005) can also improve the habitat quality of agricultural landscapes for seed dispersing animals (Perfecto and Vandermeer 2008). The colonization of trees into pastures may be facilitated by nurse trees (Toh et al. 1999; Vieira et al. 1994) or the creation of bird and bat perches (Kelm et al. 2008; Shiels and Walker 2003). Dense planting of native trees in patches, alternatively called 'woodland islets' (Benayas et al. 2008) or 'tree islands' (Zahawi and Augspurger 2006), has also been promoted as a method to increase the colonization and survival of large-seeded species. The success of these strategies depends on the distance to seed sources, the existing seed disperser community, and the degree of site degradation (Hooper et al. 2005; Lamb et al. 2005).

When the degree of isolation from seed sources is too great or animal dispersers are too scarce to ensure the arrival of large-seeded species, forest restoration requires planting of the missing species (Wunderle 1997). In addition, people may want more control over future species composition rather than to only promote the natural colonization of large seeded species. The propagation of locally rare tree species within their native habitat is commonly called 'enrichment planting', and includes planting vegetative stakes (Zahawi 2008), seeds (Ochsner 2001), or seedlings (Raman et al. 2009). Compared to transplanting nursery-grown seedlings, planting seeds ('direct seeding') into restoration sites eliminates the costs of nurseries and decreases the labor and transportation expenses (Schmidt 2008). Furthermore, survival of direct-seeded trees can be greater than transplants due to reduced root damage during planting and better acclimation to the planting site (Kitao et al. 2006). Direct seeding also allows for the reforestation of larger and less accessible regions because seeds are smaller and easier to transport than seedlings, and seeds often cost substantially less than seedlings (Ochsner 2001).

The success of direct seeding depends on survival through early stages of seedling development in the field. If seed losses are heavy or too many seedlings die, planting of nursery-grown seedlings may be a better option. Challenges to planted seeds are similar to those of naturally dispersed seeds. Causes of seed mortality include vertebrate predation (Notman and Gorchov 2001), pathogen infection (Pringle et al. 2007), insect infestation (Camargo et al. 2002), and desiccation (Hammond 1995). Young seedlings are susceptible to pathogens (Augspurger and Kelly 1984), as well as competition with existing vegetation for light and soil resources (Dantonio and Vitousek 1992; Hooper et al. 2005). These biotic and abiotic constraints differ among habitats, and their relative importance varies among species (Dupuy and Chazdon 2008; Myster 2003).

If seeds are dispersed, large seeds of tropical forest trees may develop seedlings and survive in human-modified environments. Substantial energy and nutrient reserves allow seeds to survive partial predation (Vallejo-Marin et al. 2006) and seedlings to resprout repeatedly if the stem is damaged (Harms and Dalling 1997). Furthermore, large seeds make large seedlings (Zhang and Maun 1993) that can better emerge through thick leaf litter (Scarpa and Valio 2008), survive herbivory (Armstrong and Westoby 1993), develop large root systems (Leishman and Westoby 1994), and compete effectively with existing vegetation. Seedlings from large-seeded species also tend to survive well in the shade (Myers and Kitajima 2007) and have greater drought tolerance than seedlings from smaller seeded species (Moles and Westoby 2002).

In this thesis, I study seed and seedling survival of six species of tropical forest trees planted as seeds in pastures and forests. I investigate the relative importance of seed placement (surface planting and seed burial) and habitat (pastures and forests) on seed predation, seed survival, seedling recruitment, and early seedling survival. All research was conducted on

communally owned land in indigenous Shuar communities in the Ecuadorian Amazon. In this region, previous reforestation programs that required even moderate financial and labor investments in nursery propagation failed (Rudel 2006). Local residents were interested in low cost methods of propagating native fruit trees that would bear fruits for local consumption, market sale, and increase wildlife populations to improve subsistence hunting.

In Chapter 2, I report results from a field study comparing seedling recruitment of three species of tropical forest trees with large, recalcitrant seeds that were planted as seeds in recently grazed pastures (2-6 weeks of vegetation regrowth), mature pastures (3-6 months of vegetation regrowth), and selectively logged forests. Seed burial was hypothesized to improve seedling establishment by reducing seed predation and by mitigating harsh microclimate conditions. The species planted were *Pouteria caimito* (Sapotaceae), *Quararibea cordata* (Malvaceae), and *Inga densiflora* (Fabaceae). Seeds were planted at low densities to maximize area coverage and to mimic densities generated by rare cases of natural seed dispersal by animals. The experiment was conducted in three indigenous communities that differed in degree of forest cover. Seed removal, germination, seedling recruitment and seedling survival were recorded at 2 and 14 weeks.

In Chapter 3, I report results from a second experiment conducted the following year with a modified experimental design, using one species also planted in the first experiment (*Inga densiflora*), and three other species with large recalcitrant seeds: *Gustavia macarenensis* (Lecythidaceae), *Caryodendron orinocense* (Euphorbiaceae), and a species of *Plinia* (Myrtaceae). I added a caging treatment to isolate the effect of seed predation on seedling recruitment and checked seeds biweekly for 18 weeks to assess trends of seedling development and mortality. In this experiment I planted seeds only in secondary forests because the first

study showed no differences in seedling recruitment among field types (pastures vs. forests), and because naturally regenerating forests are extensive in the tropics and likely to be of lower value to landowners than pastures under active use.

In Chapter 4 of this thesis, I summarize my main findings and discuss broader implications of this research for conservation and restoration programs.



CHAPTER 2  
SEED AND EARLY SEEDLING SURVIVAL OF THREE LARGE-SEEDED TROPICAL  
FOREST TREES PLANTED AS SEEDS IN PASTURES AND FORESTS IN THE  
ECUADORIAN AMAZON

**Introduction**

Much of the land surface in the tropics is composed of a mosaic of large cattle ranches, industrial plantations, smaller-scale agricultural fields, and degraded and secondary forests (McNeely and Scherr 2003). Within these landscapes, many rural people depend on relatively small landholdings for subsistence farming and sale of agricultural and non-timber forest products. Propagation of locally valuable native fruit trees can provide people with food and potential market crops (Ricker et al. 1999), as well as enhance the value of the landscape for wildlife (Piotto 2007). A simple and inexpensive method of enriching degraded areas with desired species is to plant tree seeds directly in the landscape. This technique, called direct seeding, may be used in place of the more resource intensive process of nursery propagation and transplantation of seedlings (Shen and Hess 1983) if chance of seedling recruitment is sufficiently high in the field.

Seedling recruitment can be constrained by seed predation, seed desiccation, and competition with existing vegetation. Large-seeded tropical species may be suitable for direct seeding (Camargo et al. 2002; Doust et al. 2006) because they may be better able to survive early challenges to seedling establishment than smaller seeds in both pastures (Hooper et al. 2002) and degraded or secondary forests (Moles and Westoby 2004). The purpose of this study was to assess the likelihood of seedling recruitment of three species of large-seeded tropical trees that were planted as seeds in pastures and forests. I tested seed burial as a treatment for improving seedling recruitment by reducing seed predation and desiccation.

Large energy and nutrient reserves in large seeds may be advantageous for seedling recruitment. Storage carbohydrates allow for survival through partial seed predation (Vallejo-Marin et al. 2006) and longer survival of seedlings in the shade (Myers and Kitajima 2007). Rapid germination of many large-seeded species can allow for quick escape from seed predators (Daws et al. 2005). After germination, large seeds make large seedlings (Zhang and Maun 1993), which can emerge through thick leaf litter (Scarpa and Valio 2008), survive herbivory (Armstrong and Westoby 1993), resprout (Harms and Dalling 1997), and produce large root systems (Leishman and Westoby 1994).

Once seeds are planted, seed predation by vertebrates can be one of the first major barriers to seed survival. Seed removal levels of 75-100% for large-seeded species have been documented in tropical forests (Blate et al. 1998; Peña-Claros and De Boo 2002) and pastures (Holl and Lulow 1997; Vieira and Scariot 2006), though seed predation levels often vary widely among species planted in the same environment (Janzen 1969; Jones et al. 2003b). Populations of seed eating animals also vary, depending on habitat availability (Lambert et al. 2006) and hunting pressures (Carlos 2001). In landscapes devoid of large seed predators, small rodents can become important consumers and secondary dispersers of large seeds (Brewer and Rejmanek 1999). Burial of seeds can greatly reduce seed predation (Crawley 2000; Vander Wall 1990), though this effect may be less for species with large seeds that are easier for seed predators to detect by odor than smaller seeds (Thompson 1987). It should be noted that not all seeds that are removed by animals die, as some may be cached or secondarily dispersed to sites where germination is possible (Vander Wall et al. 2005).

In addition to seed predation by vertebrates, mortality of seeds can also be caused by seed desiccation (Hammond 1995), fungal infection, physical damage, insect predation (Woods and

Elliott 2004), anoxia in waterlogged soils (Fenner and Thompson 2005), and fire (Hooper et al. 2005). The thin seed coat of many tropical forest tree species makes them especially sensitive to desiccation (Daws et al. 2006). Mortality of large tropical seeds is often higher in tropical pastures (Vieira and Scariot 2006) and agricultural fallows (Notman and Gorchoy 2001) than forests, primarily due to increased air temperature, air vapor pressure deficit, and soil moisture stress in exposed environments (Benitez-Malvido et al. 2005; Holl 1999; Nepstad et al. 1996). Moisture stress can be less extreme if the seed is covered by pasture vegetation (Holl 1999). While seeds may die of desiccation in pastures, higher levels of pathogen attack of ungerminated seeds are associated with shade and forested environments (Pringle et al. 2007).

If seeds survive to germinate, mortality can still be high during germination and early seedling development in both pastures and forests. In pastures, mats of dead grass can prevent the radicle from reaching the soil, and below-ground competition with roots of pasture grasses for available soil water can limit seedling survival and growth (Dantonio and Vitousek 1992). Leaf herbivory, particularly by leaf-cutter ants, can be extensive in tropical pastures (Nepstad et al. 1991). In forests, death of seedlings can be caused by mechanical damage from falling vegetation (Scariot 2000), trampling (Beck 2006), herbivory (Lopez and Terborgh 2007) and fungal infection (Augspurger 1984b; Benitez-Malvido et al. 1999). As seed reserves are depleted, the young seedling must photosynthesize to maintain a positive carbon balance (Myers and Kitajima 2007) and although abiotic stresses may be higher in pastures, low light levels in forests results in reduced seedling growth (Augspurger 1984a).

Seed burial may improve seedling recruitment by mitigating both abiotic and biotic stresses on seeds and young seedlings. Burial of seeds can reduce moisture loss, moderate temperature extremes and provide protection from insect infestation (Forget 1990; Thompson

1987). Predation of storage cotyledons can kill young seedlings (Alvarez-Clare and Kitajima 2009), and seed burial may help protect seed reserves from post-germination predation.

The purpose of this study was to assess the likelihood of seedling recruitment of three large-seeded tropical forest tree species planted as seeds in pastures and forests. Seeds were planted at low densities in recently grazed pasture, pasture with 3-6 months of vegetation re-growth, and forests in three indigenous Shuar communities in the Ecuadorian Amazon. Seeds were planted on the soil surface and shallowly buried. At 2 and 14 weeks, seeds were checked for removal, germination, seedling recruitment and mortality. I selected the three species based on seed availability of native species with recalcitrant seeds and interests of the local indigenous landowners in propagation of trees with edible fruits.

### **Research Questions**

- How likely is seedling recruitment from seeds of large-seeded tropical forest trees planted in forests and pastures?
- How does habitat (grazed pasture, mature pasture, and forest) affect the probability of seedling recruitment?
- Does shallow seed burial increase seedling recruitment?
- Are results consistent among three indigenous communities with differences in land-use patterns of the surrounding landscape?

### **Materials and Methods**

#### **Study Site**

The study was conducted in three indigenous Shuar communities in the Morona Santiago and Pastaza provinces of the Ecuadorian Amazon. All research plots were located within 15 km of the village of Tsurakú (1 ° 48'31"S, 77°49'50'W), 51 km south of the provincial capital of Puyo on the Puyo-Macas Rd (Figure 2-1). The elevation is 850 – 950 m amsl and average monthly temperature is  $20.1 \pm 1^{\circ}\text{C}$ . The mean annual rainfall is ca 4600 mm/yr, with 265

days/yr of precipitation of at least 1 mm. Average monthly rainfall is slightly lower from December - February ( $327 \pm 23$  mm/month) and July – September ( $342 \pm 30$  mm/month), but there is no clearly defined dry season (Table A-1 and Figure A-1). A recent analysis revealed a trend of increasing temperature and evaporation/precipitation ratio over the last 30 years (Millán et al. 2008), but the climate is still wet. Soils in the region are Humic Andosols (Hydrandepts) of volcanic origin with low fertility, high susceptibility to leaching and erosion, and often low levels of aluminum toxicity (Custode 1983).

Natural vegetation in the study area is very humid premontane forest of high biodiversity (Cañadas and Estrada 1978). Prior to the 1900s, the land was inhabited by low-density mobile settlements of Shuar Amerindians (Rudel et al. 2002). Road construction and agricultural subsidies in the 1960s and 1970s led to timber extraction and larger-scale forest clearing for permanent settlements, pastures, and small-scale commercial agriculture (Rudel and Horowitz 1993). Suspension of agricultural subsidies in the 1980s led to reduction in cattle and increased cultivation of cash crops (primarily of ‘naranjilla’ - *Solanum quitoense*). Subsequent pest outbreaks on agricultural crops led to an increased reliance on revenue from selective logging in the 1980s, and migration to cities in the 1990s (Rudel and Horowitz 1993). Abandonment of agricultural lands has resulted in development of large areas of secondary forests over the last 20 years (Rudel 2006). The current landscape is a patchwork of secondary and selectively logged forests, with clearings for roads, houses, horse pastures, and home gardens.

To assess the likelihood of seedling recruitment of three large-seeded tropical forest trees, I placed seeds in pastures and forests in three indigenous communities located approximately 15 km apart (Figure 2-1). Based on my observations, the three communities (Kenkuimi, Kunkuki, and San Ramon) have approximately the same population size (~100 adults), but differ in land

uses and livelihoods of the residents. The community of Kenkuimi is surrounded by secondary and selectively logged forest, and at the time of the study the village was only accessible by foot. Most houses are located in a central clearing surrounded by secondary and selectively logged forest, and the majority of people practice a subsistence livelihood based on small home gardens (0.5 - 1 ha) located in forest clearings. In contrast, the community of Kunkuki is located on the interprovincial Puyo-Macas Road, with many single-family homes in clearings along the main road. The surrounding landscape is a mix of horse pastures and secondary forests. The nearest mature forest is approximately 10 km to the east, accessible by foot and mule trails. Many residents of Kunkuki work during the week in the provincial capital of Puyo (55 km north) or the small city of Macas (60 km south). Landowners maintain pastures larger than needed for use by their own horses, and often rent pastures to logging companies and individuals using horses for transport of supplies into roadless areas to the east. The community of San Ramon is accessible by dirt road, and the village is mostly surrounded by cattle pasture, with secondary forest and selectively logged mature forest within 0.5 km of the village center. It has more surrounding forest than Kunkuki and less than Kenkuimi.

### **Tree Species Selection**

I selected native species that were in fruit at the onset of the experiment (June 2007), that were known to have recalcitrant seeds, and that had edible fruits consumed by local people (Bennett et al. 2002). The three species chosen were *Pouteria caimito* (Ruiz and Pavon) Radlk. (Sapotaceae), *Quararibea cordata* Vischer (syn. *Matisia cordata* Humb. & Bonpl.; Malvaceae) and *Inga densiflora* Benth (Fabaceae). *Pouteria caimito* is a shade-tolerant, long-lived canopy tree (Benitez-Malvido and Kossmann-Ferraz 1999) cultivated for its fruits throughout its native range in the tropical lowlands of Ecuador, Colombia, Peru, Venezuela, and Brazil (Morton 1987a). Breeding programs for commercial fruit production began in Brazil in the 1960s

(Clement et al. 2008). *Pouteria caimito* is considered a pre-Colombian domesticate from NW Amazonia by Clement (1999). *Quararibea cordata* is a fast-growing tree also from NW Amazonia and widely cultivated for its edible fruits (Morton 1987b). It may also have been partially domesticated by pre-Colombian people in NW Amazonia (Clement 1999b). *Inga densiflora* is a medium sized tree ( $\leq 20$  m in height,  $\leq 30$  cm dbh), cultivated in Mexico, Central America, and western South America for the sweet sarcotesta surrounding its seeds (Pennington and Fernandes 1998). *Inga* is often planted as a nitrogen-fixing shade tree in coffee plantations, and it is valued for firewood production (Pennington and Revelo 1997). Due to extensive cultivation throughout Latin America, the natural distribution of this species is unknown (Pennington 1997). Hereafter, the species are referred to by generic epithets.

### **Experimental Design**

In each of the three indigenous communities (Kunkuki, Kenkuimi, San Ramon), one 0.5 ha plot was established in each of three field types: “grazed pasture” (2-6 weeks of vegetation regrowth); “mature pasture” (3 – 6 mo of vegetation regrowth); and, “forest” (mature forest selectively logged within the last 10 years). Plots within communities were separated by 100 – 500 m and communities were separated by 15-20 km. Within each plot, 50 – 100 m parallel transects were established at 3-8 m intervals, and individual seeds were sown at 1 m intervals, 1 m to the left or right of the transect (Figure 2-2).

The pasture plots consisted primarily of the American perennial pasture grass *Axonopus scoparius* (Flügge) Kuhlm, called ‘gramalote rojo’ in Spanish (Zuloaga et al. 2003) and ‘sak’ in Shuar. Due to the wet climate, fire is used to burn woody material only when the land is first cleared, and subsequent control of woody vegetation in pastures is by machete. Pasture plots had been maintained for at least 10 years, and the land was initially cleared in the 1970s - 1990s. All pasture plots contained some colonizing trees, shrubs, and large herbaceous plants (e.g.

*Miconia*, *Ochroma*, *Lonchocarpus*, *Piptocoma*, and *Heliconia*). The presence of pasture grass, woody colonizing plants and herbaceous vegetation created a heterogeneous vegetation structure in pasture plots (Figure A-2). The forest plots had been selectively logged within the last 10 years and a relatively continuous canopy cover was present at the time of the experiment (Figure A-2). Percent vegetation cover was measured with a hand-held spherical densitometer held at ground level at 20 points in each plot. Canopy cover was lowest and most variable in the grazed pasture plots ( $43 \pm 20\%$ ). Percent vegetation cover ranged from 62-88% in the mature pasture plots and 86-88% in the forest plots (Figure A-3).

In June of 2007, seeds were collected from fresh fruits of trees growing along roadsides and in home gardens in the Sucua-Macas area approximately 50-75 km south of the experimental plots (elevation 1050 m). Seeds were harvested from ripe fruits picked from trees and from freshly fallen fruits. Fruits were collected from at least three trees of each species and mixed together before planting. Fruit pulp was removed, seeds were inspected for damage, washed in freshwater, float-tested for viability, and planted within one week of harvest. Average seed sizes were 2.9 cm x 1.5 cm for *Pouteria*, 3.9 x 2.2 cm for *Quararibea*, and 4.5 cm x 2.2 cm for *Inga*. Seed and seedling characteristics, as well as common names are presented in Table A-2.

Seeds were planted in “surface” and “buried” treatments. In the “surface” treatment, seeds were placed on the ground surface, without disturbing the vegetation, litter or underlying soil. “Buried” seeds were placed in a 1-2 cm deep hole and covered with ~1 cm of soil. Seed location was marked by a 20 cm 14-gauge wire inserted into the ground beside each seed (within 1-2 cm of the planting location). Species, treatment, location along the transect, and left/right planting were completely randomized in each plot. An average of 25 replicates (range 12 – 40) of each



species x treatment combination were planted in each of the 9 plots (3 communities x 3 field types).

At each planting location, seed disappearance (only fragments of the seed coat remaining, or no seed within 30 cm of the planting site), germination (radicle emergence), seedling recruitment (survival to development of at least one true leaf  $\geq 1$  cm long), and mortality were recorded by me in early July (2 weeks) and by a trained assistant in late September (14 weeks). At 2 weeks, seeds were carefully removed to visually inspect for germination (appearance of the radicle) and returned to their original location (placed on the ground substrate or buried). At 14 weeks, all ungerminated seeds (buried and surface-planted) were cut open and inspected for damage. Seeds that were intact with solid, undamaged tissue were considered alive.

### **Data Analyses**

Treatment effects on the proportions of seeds that had disappeared by 2 weeks, died or were missing ('mortality'), and were recruited to seedling stage at 2 and 14 weeks were assessed by logistic regression using PROC GLIMMIX in SAS 9.1.3 (2005, SAS Institute, Cary, NC). Species, burial treatment (surface, buried), field (grazed pasture, mature pasture, forest), and community (Kenkuimi, Kunkuki, San Ramon) were treated as fixed effects, and fields were nested within each communities. Although environmental differences among multiple communities may vary randomly, the small sample size ( $n = 3$  communities) and variation in the factors tested precluded the treatment of community as a random effect, as the models would not converge.

I first tested full factorial models including main effects and all interactions, and subsequently reduced models by removing non-significant interactions ( $p > 0.05$ ). Reported analyses are of main effects and significant interactions. Treatment effects were further evaluated with post-hoc Bonferroni-adjusted pairwise comparisons. Strong differences among

species made models imbalanced for most analyses, and thus when species was a highly significant main effect ( $p < 0.0001$ ), individual species were analyzed separately as subsets for treatment effects. In cases of quasi-separation of the data (lack of variability in the data due to zeros in many cells), data were analyzed in subsets (Lamotte 2005), or the results reported with descriptive statistics when analysis with logistic regression was not possible.

Seed disappearance, mortality (the total of missing seeds, dead seeds, and dead seedlings combined), and seedling recruitment were analyzed at 2 weeks. I analyzed seed disappearance only at 2 weeks because it was not possible to distinguish between removal of viable seeds, decay of inviable seeds, or decay of seedlings that were recruited and died between the 2 and 14 week censuses. Seedling recruitment and mortality of all species were measured at 14 weeks. In addition, *Inga* had enough seedlings alive at 2 weeks (239) to analyze survival of the cohort of early recruiting seedlings between weeks 2 and 14.

## Results

### General Patterns of Seedling Recruitment and Survival

In the first 2 weeks, only 49 of 736 seeds disappeared from planting sites, but communities differed in the proportions of seeds missing (Figure 2-3). The majority of seedling recruitment of *Inga* occurred in the first 2 weeks, whereas seedling recruitment was slower for *Quararibea* and *Pouteria*. Seedling recruitment did not differ among field types (pastures and forests) at 14 weeks or between surface-planted and buried seeds at 2 or 14 weeks (Tables 2-1 & 2-2).

### Species Difference in Seedling Recruitment and Mortality

Species differed in seedling recruitment at 2 weeks ( $p < 0.0001$ ; Table 2-1) and at 14 weeks ( $p < 0.0001$ ; Table 2-2). At each census, there were more seedlings of *Inga* than *Quararibea*, and more seedlings of *Quararibea* than *Pouteria* ( $p < 0.01$  in all post-hoc pairwise comparisons between species). At 14 weeks, 56% (171 of 307) of *Inga*, 10% (18 of 187) of

*Quararibea*, and 2% (5 of 242) of *Pouteria* were live seedlings (Figure 2-5). When observations from the 2 and 14 week censuses were combined, 91% of *Inga*, 25% of *Quararibea* and 3% of *Pouteria* seeds had germinated (found as seedlings or seeds with a radicle emergence). Additional seeds may have germinated and decayed or been eaten between the 2 and 14 week censuses.

Species also differed in the time to seedling recruitment. Of the 171 live seedlings of *Inga* at 14 weeks, 89% were seedlings by 2 weeks. Only 18 additional *Inga* seedlings were recruited after 2 weeks. In contrast, seedling recruitment was slower for *Quararibea* and *Pouteria*. Of the 18 live *Quararibea* seedlings at 14 weeks, 11 were recruited after 2 weeks, and 4 of the 5 *Pouteria* seedlings alive at 14 weeks were recruited between weeks 2 and 14.

Mortality was calculated as the sum of all missing seeds, dead seeds, and dead seedlings divided by all seeds planted. The mortality differed among species at 2 and 14 weeks. At 2 weeks, mortality was low for all species (7-9% missing or dead in any species; Table A-3) and species differed in mortality ( $p = 0.0304$ ; Table 2-1). At 14 weeks, species differences in mortality were clear ( $p < 0.0001$ ; Table 2-2). The vast majority of *Quararibea* and *Pouteria* seeds planted were either dead or missing (93 dead and 49 missing of 187 *Quararibea* seeds, and 107 dead and 87 missing of 242 *Pouteria* seeds) whereas the majority of *Inga* seeds were alive as seedlings at 14 weeks (239 of 307; Table A-3). Of the 239 *Inga* seedlings that were alive at 2 weeks, only 28 died by week 14. Species differences in mortality at 14 weeks were nearly equivalent to species differences in seedling recruitment, because nearly all seeds were either recruited to seedlings or died, and less than 20 seeds were alive and ungerminated at 14 weeks for any species (Table A-3).

## Effects of Seed Burial

Surface-planted and buried seeds did not differ in seedling recruitment at 2 or 14 weeks, in mortality at 2 or 14 weeks, or in the proportions of seeds that were missing at 2 weeks (Tables 2-1 and 2-2).

## Community Differences in Seed and Seedling Survival

At 2 weeks, more seeds were missing and seedling recruitment was lowest in Kenkuimi than in the other two communities (Figures 2-3 & 2-4). Almost all seedlings that were recruited by 2 weeks were *Inga* (239 of 267; Table A-3), thus differences in seedling recruitment among communities at 2 weeks ( $p = 0.0115$ ; Table 2-1) are largely due to differences in recruitment of *Inga* seedlings (Figure 2-4). Lower seedling recruitment in Kenkuimi than San Ramon ( $p = 0.0085$ ) appears to be partially explained by higher levels of seed disappearance in Kenkuimi than San Ramon (Figure 2-3).

At 14 weeks, differences among communities in seedling recruitment were clearer ( $p < 0.0001$ ; Table 2-2; see Figure 2-5). More seedlings were recruited in Kunkuki than in Kenkuimi ( $p < 0.0001$ ) or San Ramon ( $p < 0.0001$ ), and more seedlings were recruited in San Ramon than Kenkuimi ( $p = 0.0060$ ; Table 2-2).

Mortality of *Inga* seedlings between weeks 2 and 14 differed among the three communities ( $p < 0.0001$ ; Table 2-2). Of 239 *Inga* seedlings alive at 2 weeks, 86 were dead at 14 weeks. More died in Kenkuimi than Kunkuki ( $p < 0.0001$ ) or San Ramon ( $p = 0.0043$ ), and more died in San Ramon than Kunkuki ( $p = 0.037$ ; Table 2-2).

Differences in mortality at 14 weeks among the three communities ( $p = 0.0174$ ) are positively correlated with differences in 14 week seedling recruitment, because the majority of live individuals were seedlings at 14 weeks and few live seeds remained (Figure 2-5). In post-hoc pairwise comparisons between communities, mortality at 14 weeks was higher in Kenkuimi

than Kunkuki ( $p = 0.0233$ ; Table 2-2). Higher mortality in Kenkuimi reflects both higher levels of seed disappearance at 2 weeks and lower survival of *Inga* seedlings between weeks 2 and 14.

### **Seedling Recruitment in Pastures and Forests**

Some differences in seed disappearance, seed survival and seedling recruitment between pastures and forests were observed at 2 weeks, but by 14 weeks seedling recruitment and mortality did not differ among field types in any community (Tables 2-1 & 2-2). At 2 weeks, more seeds were missing from the forests than the grazed plots in Kenkuimi ( $p = 0.0049$ ) and Kunkuki. In San Ramon, more seeds were missing from the pastures than the forest plot (Figure 2-5).

At 2 weeks, mortality differed among fields within communities ( $p = 0.007$ ; Table 2-1). The only significant difference in post-hoc pairwise comparisons between field types within each community was in the community of Kenkuimi, where higher mortality occurred in the forest than in the grazed pasture ( $p = 0.0057$ ; Table 2-1). This result is partially explained by higher levels of seed disappearance in the forest than pasture plots in Kenkuimi (Figure 2-3) and some differences in seedling recruitment among field types ( $p = 0.0454$ ; Table 2-1). Survival of *Inga* seedlings between weeks 2 and 14 did not differ among fields (Table 2-2).

### **Discussion**

Indigenous Amazonian cultures have a long history of enriching forested landscapes with useful species by managing naturally regenerating species (Gadgil et al. 1993; Posey 1985; Redford and Padoch 2000; Toledo and Salick 2006). Natural seed dispersal of large-seeded species in landscapes heavily used by people is often reduced due to distance from seed sources (White et al. 2004) and hunting of seed-dispersing animals (Chapman and Onderdonk 1998). When natural seed dispersal is rare, occasional natural seed dispersal or seed planting can make large differences in the regeneration of the species. If seeds grow into trees that bear fruit, they

can serve as seed sources for further population expansion by natural seed dispersal. Cultivated and naturally regenerated fruit trees also provide food and potential sources of income to rural landowners. However, a seed is not a tree, and many obstacles must be overcome, the first of which is survival of the seed to the seedling stage.

The purpose of this experiment was to assess the probability of seedling recruitment among three tropical tree species with large seeds that were planted in a variety of potential dispersal sites in three indigenous communities in a human-modified landscape. Seedling recruitment differed among the three species, as well as among the three communities. Interestingly, the community in which seeds were planted affected seed disappearance and seedling recruitment more than whether seeds were planted in pastures or forests. Contrary to my initial expectations, seed burial did not affect seed disappearance at 2 weeks or seedling recruitment at 2 or 14 weeks.

### **Landscape-Level Variation**

The indigenous community in which the seeds were planted affected the proportion of seeds that were missing at 2 weeks more than any other treatment factor. Density and species composition of seed predator communities are known to vary with changes in habitat and hunting pressures (Asquith et al. 1997), and the three communities were separated by 10-15 km and differed in surrounding forest cover and land use. Seed disappearance was highest in the community of Kenkuimi (Figure 2-3) which, at the time of the study, was not accessible by road and was surrounded by relatively continuous secondary and logged forests. Local residents informed me that there was better hunting of “guatusas” (*Dasyprocta fuliginosa*), and “guantas” (*Agouti sp.*) in Kenkuimi than in the other two communities. The “guatín” (likely *Myoprocta pratti*) was only noted as being present in Kenkuimi (Eisenberg and Redford 1999). All these animals eat seeds (Asquith et al. 1997; Beck and Terborgh 2002; Jansen et al. 2004; Silvius and

Fragoso 2003), and higher populations of these rodents may have caused higher levels of seed disappearance in Kenkuimi. The other two communities have road access and higher densities of people, and forest patches that are interspersed among larger horse and cattle pastures. Differences in seed disappearance among the three communities highlight the importance of considering small-scale, regional differences in surrounding land-use patterns on ecological processes within a landscape.

Similar to seed disappearance, seedling recruitment at 14 weeks varied among the three communities but not between pastures and forests within any community (Table 2-2). Many more seedlings of *Inga* were recruited by 14 weeks compared to the other species, thus patterns of seedling recruitment discussed henceforth are largely driven by this species (Figures 2-4 & 2-5). Initial seedling recruitment was highest in San Ramon and lowest in Kenkuimi. Survival of *Inga* seedlings that were recruited at 2 weeks differed among the three communities, with the greatest mortality in Kenkuimi and lowest mortality in Kunkuki (Table 2-2). Low mortality between the 2 and 14 week censuses resulted in greater seedling recruitment at 14 weeks in Kunkuki than the other two communities ( $p < 0.0001$ ). Pasture and forest plots did not differ in seedling recruitment within any community. These results suggest microhabitats affect early seedling survival less than larger scale, regional differences among the communities. For example, although the communities were only 10-20 km apart, rainfall patterns could have differed. Lack of rainfall would be expected to decrease seed and early seedling survival of desiccation-sensitive seeds. Other abiotic factors such as soil type and temperature extremes may also have varied among the communities, but these data were not collected. Finally, forest cover and surrounding land uses differed among the three communities and this variation could be correlated with biotic causes of early seed and seedling death such as higher population

densities of pathogens and seed predators in some communities. The order of planting (Kenkuimi, Kunkuki, and San Ramon) did not correlate with patterns of mortality or seedling recruitment, as the lowest mortality and highest seedling recruitment were both in Kunkuki.

### **Microhabitat Effects on Seed Predation**

The proportion of seeds that disappeared varied among communities, and also between field types within communities (Figure 2-3). In Kenkuimi and Kunkuki, more seeds were missing from forests than pastures, and in San Ramon, more seeds were missing from pastures than forest (Figure 2-5). Previous studies in the tropics frequently report higher levels of seed predation in earlier successional habitats than mature forests (Nepstad et al. 1996; Peña-Claros and De Boo 2002), although some report higher seed predation in forest fragments than open fields (Cole 2009) or no difference between habitat types (Holl and Lulow 1997).

Potential seed predators must be able to access seeds, while minimizing risk of exposure to their own predators (Taylor 1984). The heterogeneity of vegetation within pasture plots, as well as the location of the plots in the landscape, likely influenced patterns of seed disappearance. Forest vegetation may have provided greater protection for rodents from their predators, even if seeds were easier to find in open fields. Pasture plots with more woody vegetation or in closer proximity to forests could be expected to experience greater seed predation than open plots removed from protective cover. More seeds disappeared from pastures in Kenkuimi and San Ramon, where the pasture plots were adjacent to selectively logged forests, and almost no seeds disappeared from pastures in Kunkuki, where the two pasture plots were within larger pastures. Higher levels of seed predation by mice have been observed in temperate fields with greater woody cover (Ostfeld et al. 1997) and higher levels of seed removal were found under woody vegetation within tropical pastures in Costa Rica (Holl 2002).



Seed removal by animals does not necessarily indicate seed death (see review in Vander Wall et al. 2005), since removed seeds may be cached and later germinate (Brewer and Rejmanek 1999; Jansen and Forget 2001). This secondary seed dispersal has been reported to be relatively frequent in forest fragments and rare in pastures and secondary forests (Cole 2009). Some of the disappeared seeds may have been scatterhoarded, particularly in forest plots and in the community of Kenkuimi, which was surrounded by more forest and believed to have higher populations of scatterhoarding animals than the other two communities.

Seed predation patterns are often variable and species specific (Guariguata et al. 2000), even within apparently homogeneous environments. Similar studies in both Costa Rica (Jones et al. 2003b) and Mexico (Garcia-Orth and Martinez-Ramos 2008) observed different seed predation levels between four pasture plots located within 3-4 km of each other. Fluctuating populations of seed predators and dispersers during the year also influence seed predation levels (DeMattia et al. 2006), and results of my 2-week experiment may not apply to other times of the year.

In 2 weeks only 49 of 739 seeds were removed in this study (Table A-3), thus limited interpretation is possible regarding treatment effects on missing seeds. Although seed predators generally prefer fresh seeds (Vander Wall 1990), additional seeds may have been eaten after 2 weeks. Finally, although seed disappearance did not vary significantly among the three species tested, seed predators are known to vary in preferred foods (Brewer and Rejmanek 1999; Vieira et al. 2006), and a longer study may have revealed species differences in seed predation.

Contrary to my original expectations, seed burial did not appear to reduce the proportion of seeds removed by seed predators. Burial reduces the odor of fresh seeds and more deeply buried seeds are more difficult to detect (Vander Wall 1990), but rodents can still find buried seeds

using only olfaction (Howard et al. 1968). In a study at Barro Colorado Island, Panama, agoutis (*Dasyprocta punctata*) detected caches of 6-12 maize kernels buried 3-7 cm deep (Murie 1977). Rodents also detect seeds in moist soil more readily (Wall 2003), because as seeds imbibe water, volatile compounds are released (Duke et al. 1983). The moist conditions of fresh seeds, moist soil, and shallow burial of the seeds may have been insufficient to mask seed odors from foraging animals. Although only a small area of soil was disturbed at the planting sites, visual (but not olfactory) cues have been shown to attract agoutis to experimentally buried food caches (Murie 1977). Finally, it is possible some buried seeds were not counted simply because they are more difficult to find than surface-planted seeds, resulting in an inflated numbers of removed buried seeds.

### **Microhabitat Effects on Seedling Recruitment and Survival**

Seedling recruitment and mortality did not differ among the grazed pasture, mature pasture, or forest plots at 14 weeks (Table 2-2). Variation of vegetation cover within plots, numerous potential causes of seed and seedling death, as well as possible similarities in microsite conditions in forests and pastures may all have obscured detection of field-specific patterns of seedling recruitment (if patterns existed). Vegetation in pasture plots was a mix of woody and herbaceous species, resulting in large variation in cover at planting locations (Figure A-2). Microclimate differences at planting sites within pasture plots could have caused variability in seed and seedling survival due to fungal infection and light competition at heavily shaded planting sites and desiccation where seeds were more exposed. In addition, quick regrowth of pasture grasses at the grazed sites may have resulted in similar moisture conditions at ground level in ‘grazed’ and ‘mature’ pasture plots. At the scale of a seed, microsite conditions in pastures and forests may have been more similar than suggested by obvious larger-scale differences between the habitat types. Higher temperatures and greater moisture stress in

pastures than forests are expected (Nepstad et al. 1996), but pasture grasses can modify microclimates such that forest and pasture sites experience similar temperature and moisture conditions at ground level (Holl 1999). Surface-planted seeds in both forests and pastures were placed without disturbance of the vegetation, which resulted in some seeds lying on litter in the forest, and on mats of dead grass in the pastures. In both habitats, these seeds were at higher risk of death by desiccation, increasing the variability of survival within both pastures and forests. Overall, variability in microclimate within both forests and pastures and possible similarities between pasture and forest environments in factors affecting seed and seedling survival may have resulted in similar seedling recruitment between field types.

Seedlings were recruited equally well from surface-planted and buried seeds (Table 2-2), indicating that any potential benefit of seed burial (moisture retention, soil contact, etc.) was either unnecessary (for *Inga*) or insufficient to compensate for other mortality agents (for *Pouteria* and *Quararibea*). It is also possible that seed burial affected germination or early seedling survival of *Pouteria* or *Quararibea*, but this effect was not able to be detected due to mortality and subsequent decay of seeds between the 2 and 14 week censuses.

### **Differences Among the Three Large-seeded Species**

The three large seeded species in this study differed in time to germination and seedling recruitment as well as overall patterns of seed and seedling mortality. *Inga* germinated rapidly and seedlings developed earlier and in greater numbers than the other species. At 2 weeks, 93 % (262 of 281) of *Inga* seeds present were germinated, and 91% (239) were already plants with at least one leaf (Figure 2-4). In contrast, only 24% (41 of 173) of live seeds of *Quararibea* and 3 of 216 live seeds of *Pouteria* germinated by 2 weeks. Rapid germination and early seedling recruitment of *Inga* apparently led to greater success in total seedlings alive at 14 weeks compared to the other species. Quick seedling development reduces the duration of seed

exposure to seed predators and pathogens, and allows for quick onset of photosynthesis. For example, over 75% of seeds of *Quararibea cordata* were attacked by fungi in a three-month greenhouse trial with forest soil (Pringle et al. 2007).

Levels of germination and seedling recruitment were similar to other studies for *Inga*, but were lower than usual for *Quararibea* and *Pouteria*. Germination levels of 95-100% are common in many species of *Inga* (Pennington and Revelo 1997), and the 93% germination observed in this experiment is similar to the 99% germination level for *Inga* in the 2008 experiment (Chapter 3). Seedling recruitment of the majority of *Inga* seeds within 4 weeks was also observed in both experiments (Table A-3 and Figure 3-2). In contrast, at 14 weeks, 83% of *Quararibea* and 91% of *Pouteria* seeds had died or disappeared (Figure 2-5). In outdoor trials with forest soil, 85% of *Pouteria caimito* seeds germinated within 15 days (Sánchez et al. 2003) and most *Q. cordata* seeds germinated in 16 – 18 days (Pringle et al. 2007), suggesting germination of these species would have been occurring near the time or just after the 2 week census. The 12 week gap between the 2 and 14 week censuses in my study did not allow for accurate assessment of final germination percentages. Nevertheless, very low seedling recruitment at 14 weeks suggests lower survival of *Pouteria* and *Quararibea* than observed in other studies. Although seeds were planted within 1 week of harvest from fresh fruits it is possible that seeds of these species had low initial viability at the time of planting. Survival in the field can also be expected to be less than under more controlled conditions. Differences in seed mortality and seedling recruitment among these three species highlight the limitation of generalizing survival patterns for the group of ‘large-seeded’ species, though this issue may be resolved by including more species in future studies.

## **Recommendations for Propagation of the Study Species**

In this study, *Inga densiflora* had high survival of seeds to seedlings under all experimental conditions, and planting of this species as seeds in pastures and forests is likely to be successful. Volunteer seedlings of *Inga densiflora* were fairly common in pastures and along roadsides in the study area, suggesting seedlings can survive later stages of development in pastures with minimal management. In contrast, the vast majority of *Pouteria caimito* seeds either disappeared or died during the experiment, and very few seedlings established in the field. For *Pouteria*, transplantation of nursery-grown seedlings may be necessary to ensure seedling establishment. *Quararibea cordata* had relatively low seedling recruitment at 14 weeks (10%), but this may be acceptable for direct seeding if seed supplies are plentiful. Given that seedling recruitment did not differ between pastures and forests, additional factors may be more important when considering planting sites. For example, faster growth of seedlings would be expected in pastures than forests, and planting in open sites may be preferred to minimize time to onset of fruit production. Also to be considered is the relative value of the current land use. Within 6 months of the end of this study, landowners re-introduced horses into several of the pastures. Unless the seedlings were protected from trampling and browsing, most recruited seedlings probably died. Depending on local land use priorities, enriching forests may add greater value to the landscape than adding trees to pastures.

## **Recommendations for Future Studies**

This study would be improved by including more species and more frequent censuses of seedling development and survival. Caging of seeds would prevent the removal of viable seeds and could be used to isolate seed predation from other causes of mortality. Simultaneous greenhouse trials should be included to establish baseline seed viability data on seeds planted in the field. Including seedling transplants and a financial comparison between direct seeding and

transplant planting would give more information about planting options to land managers. Repeating the study at more sites would allow community location to be tested as a random factor to evaluate variation at the landscape level on seed mortality and seedling recruitment. Longer term studies would obviously be useful to evaluate survival of recruited seedlings in the different environments.

### **Conclusion**

Survival to the seedling stage was most strongly affected by the species planted and secondly by the indigenous community into which the seed was planted. For these three large-seeded species, microhabitat variations such as seed burial and planting in specific habitats (pastures or forests) did not affect the success of seedling development over the first 14 weeks. Seedling recruitment at 14 weeks from planted seeds was high for *Inga* (56%), low for *Quararibea* (10%), and extremely low for *Pouteria* (2%). Species are known to differ in seedling recruitment in human-impacted landscapes (Nepstad et al. 1991; Ramos and Delamo 1992), but research on the influence of the agricultural matrix surrounding tropical forest fragments has only recently gained attention in the fields of restoration ecology and conservation biology (Chazdon et al. 2009; Perfecto and Vandermeer 2008). After species selection, consideration of the landscape surrounding planting sites may be more important for early seedling recruitment than management of microsite conditions at the planting site.

Table 2-1. Results from mixed model logistic regression of seeds missing, mortality (missing or dead seeds and dead seedlings) and seedling recruitment at 2 weeks of three large-seeded tropical trees planted as seeds (surface-planted and buried) in three field types (grazed pasture, mature pasture, forest) in three indigenous communities in the Ecuadorian Amazon. Results are for reduced models that include only main effects because no interactions were significant ( $p \leq 0.05$ ).

Source	Seed disappearance at 2 wks in Kenkuimi † <sup>A</sup>				Mortality at 2 wks				Seedling recruitment at 2 wks			
	Num df	Den df	F value	P > F	Num df	Den df	F value	P > F	Num df	Den df	F value	P > F
Species	2	233	2.11	0.1239	2	707	3.51	<b>0.0304</b> † <sup>C</sup>	2	724	88.06	<b>&lt;0.0001</b> † <sup>E</sup>
Burial	1	233	0.01	0.9371	1	707	0.91	0.3397	1	724	0.96	0.3265
Field (Community)	2	233	6.31	<b>0.0021</b> † <sup>B</sup>	6	707	2.98	<b>0.0070</b> † <sup>D</sup>	6	724	2.16	<b>0.0454</b> † <sup>F</sup>
Community	...	...	...	...	2	707	0	0.9994	2	724	4.49	<b>0.0115</b> † <sup>G</sup>

†<sup>A</sup> Only Kenkuimi was analyzed because so few seeds were missing in some fields in Kunkuki and San Ramon, thus analysis by logistic regression was not possible for these communities (Figure 2-3).

†<sup>B</sup> In Kenkuimi, more seeds were missing in forest than grazed plot ( $p = 0.0049$ ) in post hoc pairwise comparisons. In Kunkuki, more seeds were missing in the forest than grazed plots, and in San Ramon, more seeds were missing from the pastures than the forest plot (Figure 2-5)

†<sup>C</sup> No pairwise comparisons significant in post-hoc tests.

†<sup>D</sup> In Kenkuimi, higher mortality in the forest plot than the grazed pasture ( $p = 0.0057$ ) in post-hoc pairwise comparisons within communities.

†<sup>E</sup> More recruitment of *Inga* seedlings than *Quararibea* ( $p < 0.0001$ ) or *Pouteria* ( $p < 0.0001$ ), and more *Quararibea* seedlings than *Pouteria* ( $p = 0.0004$ ) in post-hoc pairwise comparisons.

†<sup>F</sup> In Kunkuki, more seedlings were recruited in the forest than the mature pasture plot ( $p = 0.0171$ ) in post-hoc pairwise comparisons within communities.

†<sup>G</sup> More seedling recruitment in San Ramon than in Kenkuimi ( $p = 0.0085$ ) in post-hoc pairwise comparisons.

Table 2-2. Results from mixed model logistic regression of mortality and seedling recruitment of three large-seeded tropical trees at 14 weeks. Also shown are results of logistic regression on 14 week survival of *Inga densiflora* seedlings that were recruited at 2 weeks. Seeds were planted on the soil surface and buried in three field types (grazed pasture, mature pasture, forest) in three indigenous communities in the Ecuadorian Amazon. Results are for reduced models including only main effects and significant interactions ( $p \leq 0.05$ ).

Source	Mortality at 14 wks				14 wk seedling recruitment of all seeds planted				14 wk survival of <i>Inga</i> seedlings recruited at 2 wks <sup>†F</sup>			
	Num df	Den df	F value	P > F	Num df	Den df	F value	P > F	Num df	Den df	F value	P > F
Species	2	703	63.53	<b>0.0001</b> <sup>†A</sup>	2	724	73.05	<b>&lt;0.0001</b> <sup>†D</sup>	...	...	...	...
Burial	1	703	0.69	0.4058	1	724	0.02	0.8844	1	229	0.06	0.0869
Field (Community)	6	703	0.88	0.5118	6	724	0.99	0.4316	6	229	0.91	0.4889
Community	2	703	4.08	<b>0.0174</b> <sup>†B</sup>	2	724	22.13	<b>&lt;0.0001</b> <sup>†E</sup>	2	229	12.51	<b>&lt;0.0001</b> <sup>†G</sup>
Species*Community	4	703	4.77	<b>0.0008</b> <sup>†C</sup>	...	...	...	...	...	...	...	...

<sup>†A</sup> Higher mortality of *Pouteria* than *Inga* ( $p < 0.0001$ ) or *Quararibea* ( $p = 0.0411$ ), and higher mortality of *Quararibea* than *Inga* ( $p < 0.0001$ ) in post-hoc pairwise comparisons between species. In subsets of individual species, mortality of *Inga* differed among communities ( $p < 0.0001$ ), with higher mortality in Kenkuimi than San Ramon ( $p = 0.0029$ ) or Kunkuki ( $p < 0.0001$ ), and higher mortality in San Ramon than Kunkuki ( $p = 0.0139$ ) in post-hoc pairwise comparisons between communities.

<sup>†B</sup> Higher mortality in Kenkuimi than Kunkuki ( $p = 0.0233$ ) in post-hoc pairwise comparisons between communities.

<sup>†C</sup> In all communities, higher survival of *Inga* than *Quararibea* and *Pouteria* ( $p < 0.05$  in all pairwise comparison between species within communities in post-hoc tests). Within Kunkuki higher survival of *Quararibea* than *Pouteria* ( $p = 0.0373$ ) in post-hoc comparisons within communities.

<sup>†D</sup> More *Inga* than *Quararibea* ( $p < 0.0001$ ) or *Pouteria* ( $p < 0.0001$ ) seedlings were recruited, and more *Quararibea* than *Pouteria* ( $p = 0.0050$ ) seedlings were recruited in post-hoc pairwise comparisons between species. In subsets of individual species, seedling recruitment differed among communities for *Inga* ( $p < 0.0001$ ), with more *Inga* seedlings were recruited in Kunkuki than Kenkuimi ( $p < 0.0001$ ) or San Ramon ( $p < 0.0095$ ), and more *Inga* seedlings were recruited in San Ramon than Kenkuimi ( $p < 0.0001$ ) in post-hoc pairwise comparisons between communities.

<sup>†E</sup> More seedlings were recruited in Kunkuki than in Kenkuimi ( $p < 0.0001$ ) or San Ramon ( $p < 0.0001$ ), and more seedlings were recruited in San Ramon than Kenkuimi ( $p = 0.0060$ ) in pairwise post-hoc comparisons between communities.

<sup>†F</sup> Only mortality of *Inga* seedlings was analyzed due to low number of seedlings of *Quararibea* (27) and *Pouteria* (1) at 2 weeks.

<sup>†G</sup> Higher survival of *Inga* seedlings in Kunkuki than Kenkuimi ( $p < 0.0001$ ) or San Ramon ( $p = 0.0370$ ), and higher survival in San Ramon than Kenkuimi ( $p = 0.0043$ ) in post-hoc pairwise comparisons between communities.



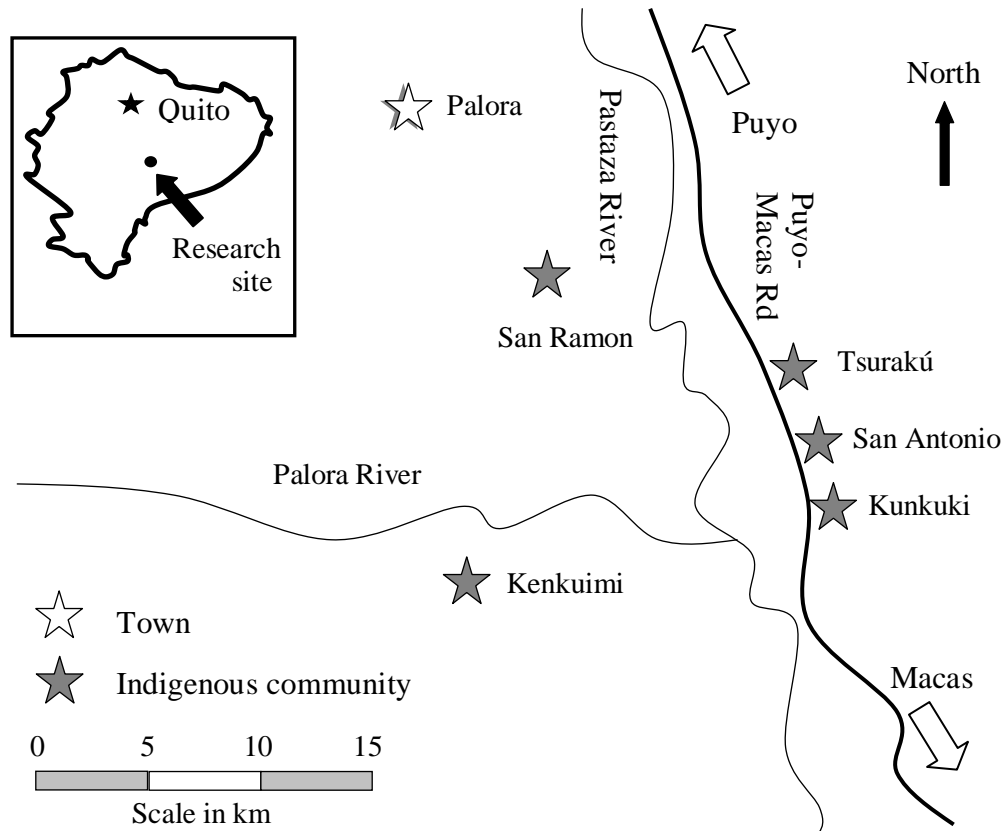


Figure 2-1. Map of the study area in Morona Santiago and Pastaza Provinces, Ecuador. Stars indicate the locations of indigenous communities and towns. The community of Tsurakú ( $1^{\circ}48'31''\text{S}$ ,  $77^{\circ}49'50''\text{W}$ ) had approximately 200 residents in 2008, and is located on the Puyo-Macac Rd, 51 km south of the provincial capital of Puyo, and 78 km north of the town of Macas. The division between the provinces in this area is the Palora River: Pastaza Province is east of the river.

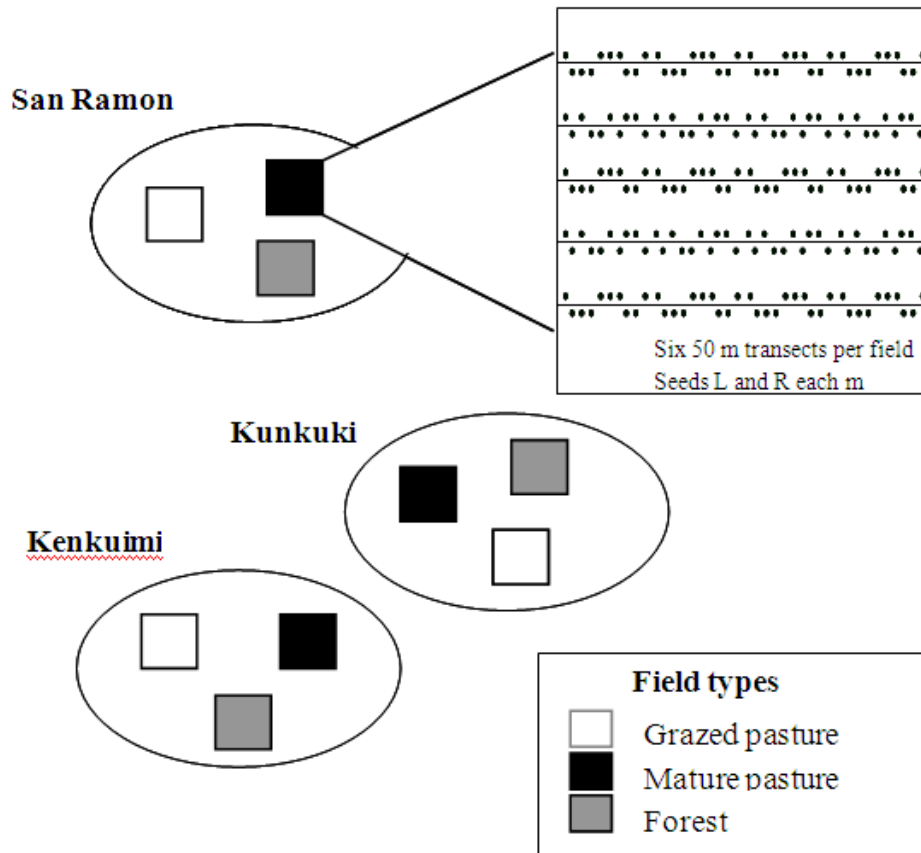


Figure 2-2. Schematic diagram of the experimental design showing nesting of field plots (grazed pasture, mature pasture, forest) in each indigenous community (Kenkuimi, Kunkuki, San Ramon). Each field plot contained six 50 m transects separated by 4-8 m. Individual seeds were planted at 1 m intervals at locations marked with a metal wire and 1 m from the transect (L/R side of transect, species, and treatment were randomized).

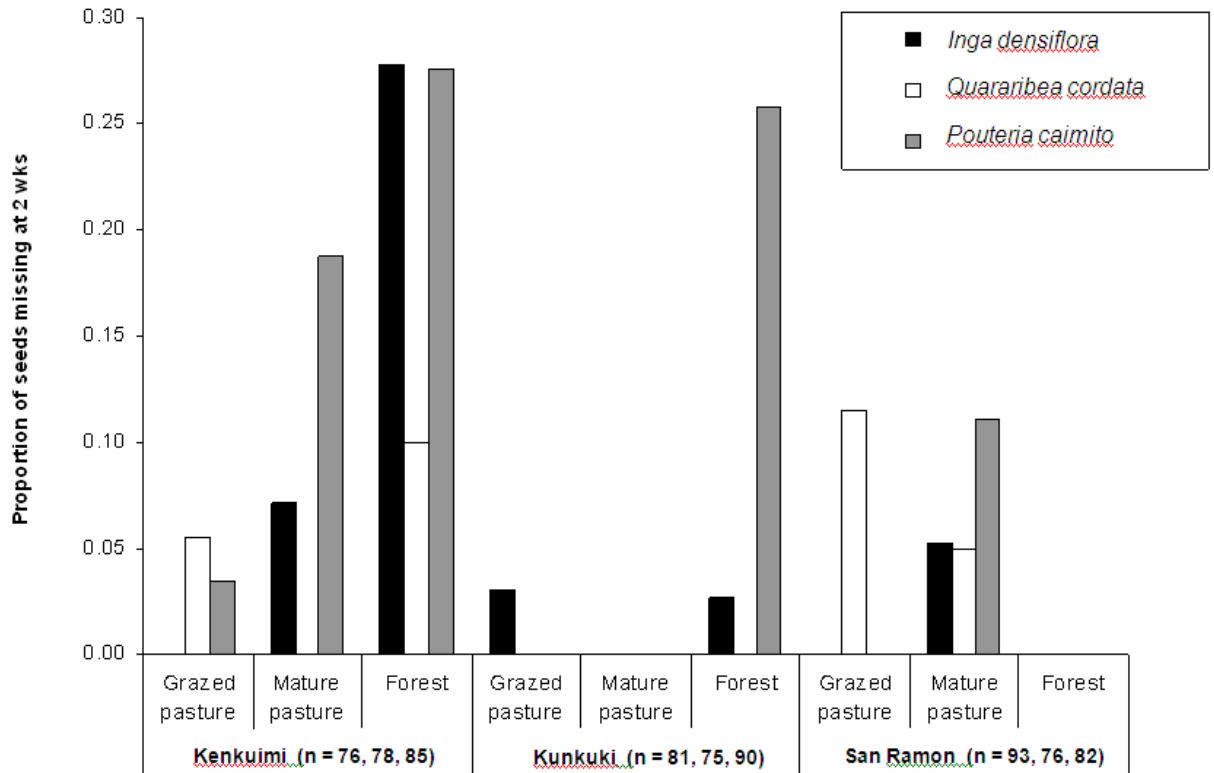


Figure 2-3. Proportion of seeds of three large-seeded tropical tree species that were missing at 2 weeks from three field types (grazed pasture, mature pasture, forest) nested in three indigenous communities (Kenkuimi, Kunkuki, San Ramon) 14-18 km apart in the Ecuadorian Amazon. More seeds disappeared from the forest than from grazed pasture in Kenkuimi ( $p = 0.0049$ ; Table 2-1). Seed disappearance in the other two communities could not be statistically analyzed due to lack of seed removal from several field types. Surface-planted and buried seeds did not differ in seed disappearance (Table 2-1), and are combined in the figure.

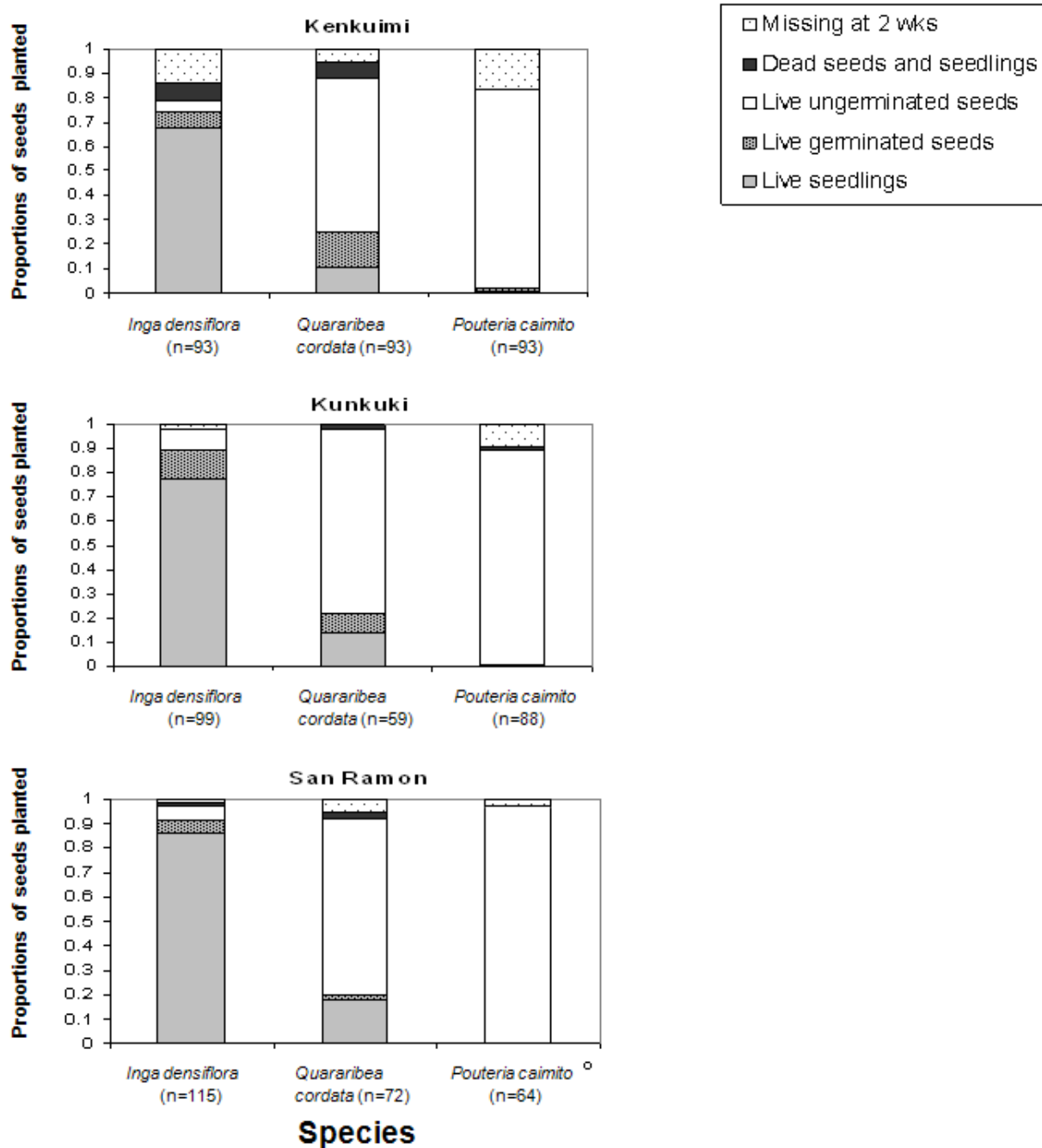


Figure 2-4. Seed fates at 2 weeks of three large-seeded tropical tree species that were planted as seeds in forests and pastures in three indigenous communities ('Kenkuimi', 'Kunkuki', 'San Ramon') 14 - 18 km apart in the Ecuadorian Amazon (Figure 2-1). Seedling recruitment differed among the species ( $p < 0.0001$ ) and communities ( $p = 0.0115$ ; Table 2-1). Surface-planted and buried seeds are combined in the figure because seed burial did not affect mortality or seedling recruitment (Table 2-1). Seed disappearance differed among field types (forest and pasture plots) and is illustrated in Figure 2-5, but field types are combined in this figure.

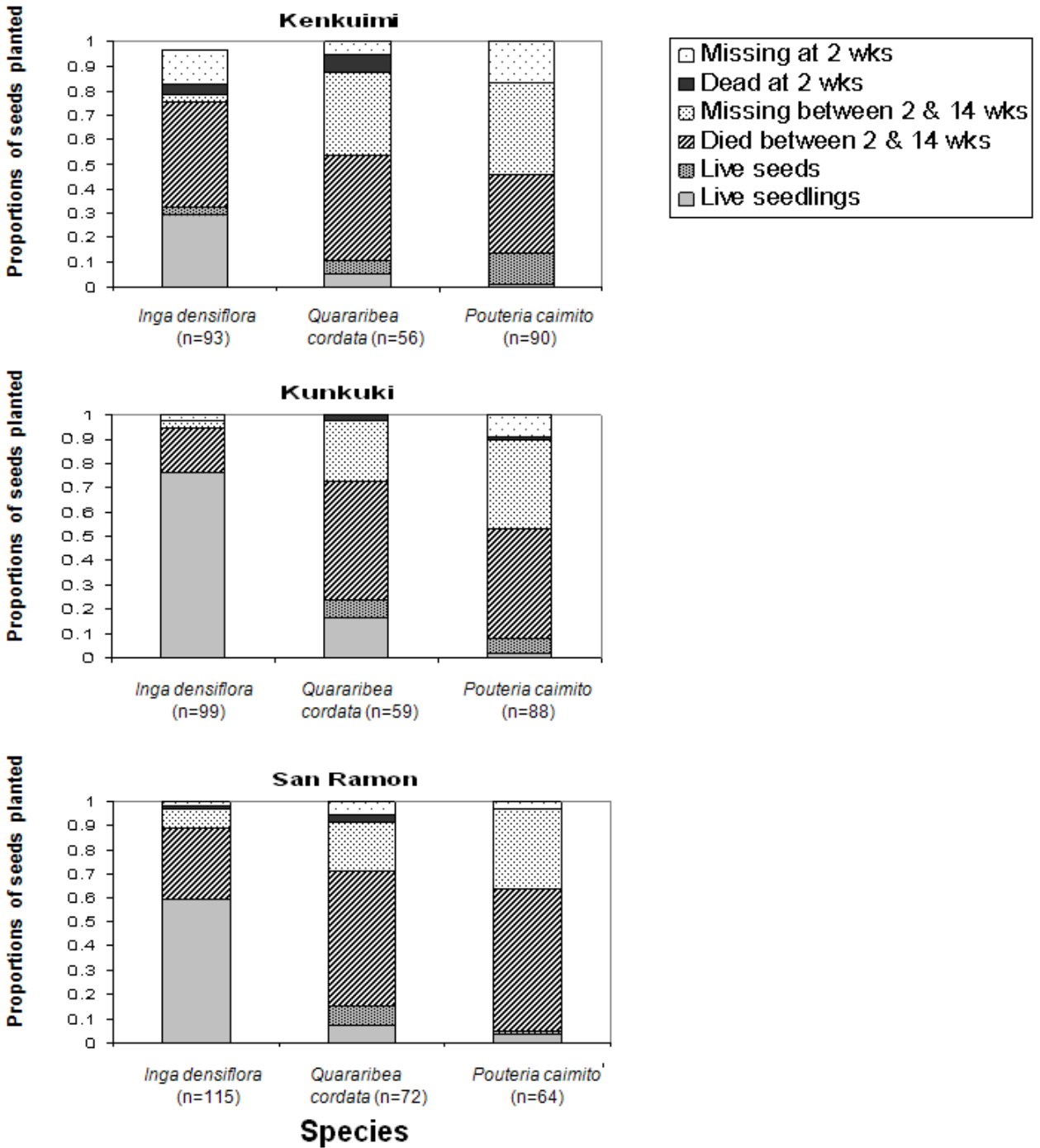


Figure 2-5. Seed fates at 14 weeks of three large-seeded tropical tree species that were planted as seeds in forests and pastures in three indigenous communities (‘Kenkuimi’, ‘Kunkuki’, ‘San Ramon’) 14 - 18 km apart in the Ecuadorian Amazon (Figure 2-1). Seedling recruitment differed among species ( $p < 0.0001$ ) and communities ( $p < 0.0001$ ; Table 2-2). Seedling recruitment did not differ among field types or surface and buried seeds (Table 2-2), and treatments are combined in the figure.

CHAPTER 3  
SEEDLING RECRUITMENT OF FOUR LARGE-SEEDED TROPICAL FOREST TREES  
PLANTED AS SEEDS IN SECONDARY FORESTS IN THE ECUADORIAN AMAZON

**Introduction**

Tropical forest management requires an ever greater understanding of secondary forests, which are expanding in area and increasingly used by people for forest products. Tropical countries are becoming more urbanized (United Nations 2004), a trend associated with abandonment of less productive agricultural land (Mather and Needle 1998) and expansion of secondary forest (Aide and Grau 2004). Local people are often dependent on these forests for timber, firewood, and nontimber forest products (e.g. fruits and medicines) for both market and subsistence uses (FAO 2005). As mature forest cover is reduced (Achard et al. 2002; Hansen et al. 2008) and increasingly fragmented by human activities (Wade et al. 2003), more management and conservation efforts are being directed toward secondary forests (Bowen et al. 2007).

The initial phases of secondary succession in tropical forests are characterized by structural recovery, a process affected by the nature of the disturbance (agricultural practices, hurricane, fire etc.; Chazdon, 2003), soil fertility (Moran et al. 2000), seed bank (Dalling and Hubbell 2002; Wijdeven and Kuzee 2000; Zahawi and Augspurger 1999), presence of resprouting trees (Zimmerman et al. 1994), and propagule input from the surrounding landscape (Cubina and Aide 2001; Galindo-Gonzalez et al. 2000); see review in (Dalling and John 2008). As succession continues, changes in species composition will largely depend on colonization of non-pioneer species (Gauriguata and Ostertag 2001; Norden et al. 2009). Lack of dispersal of later-successional species with large seeds can severely constrain species composition in subsequent phases of forest succession (Wijdeven and Kuzee 2000). In landscapes that lack animal dispersers and nearby seed sources, recovery of original forest species diversity may take centuries (Finegan 1996) or not occur at all (Turner et al. 1997). Augmenting natural seed rain

by planting large, animal-dispersed species can accelerate natural successional processes (Camargo et al. 2002; Martinez-Garza and Howe 2003).

Even in landscapes where seeds arrive to successional sites, seeds must pass through several post-dispersal filters on survival and development to reach the seedling stage. Seed predation in tropical secondary forests can be as high as 100% of dispersed seeds (Crawley 2000; Holl and Lulow 1997; Peña-Claros et al. 2002), though variability among species is common. Even if seeds are not consumed, they may be killed by desiccation, pathogens (Pringle et al. 2007), or insects (Galetti et al. 2006; Wright et al. 2000).

I investigated factors that can constrain seedling recruitment of large-seeded species in secondary forests once dispersal limitations are overcome. In the study reported in Chapter 2, I found strong species differences in post-dispersal survival but little difference among habitat types in seedling recruitment. In the study reported here, I conducted a similar experiment with a modified experimental design, using one species shared with the previous study (*Inga densiflora*), and three others with large recalcitrant seeds (*Gustavia macarenensis*, *Caryodendron orinocense* and a Myrtaceae species). Seeds were planted in secondary forests, due to the extent of this forest type in the tropics and lack of variability of early survival among habitat types (pastures and forests) found in the previous study. In Chapter 2, I discussed differences in seedling recruitment found among the three indigenous communities located 10-15 km from each other. To control for this regional variability, this study was conducted in three secondary forest plots located within 5 km of each other within the region of the first study. A caging treatment was included to test for vertebrate seed predation, which can greatly reduce the numbers of seeds available for seedling recruitment in tropical forests. The test of seed burial to reduce seed predation and increase seedling recruitment was repeated, but biweekly censuses

were made to more accurately assess mortality and trends in seedling recruitment. To better understand successional processes, I inventoried all woody species > 10 cm dbh encountered in four 50 x 2 m transects in each plot. As in the previous study, the four species planted were valued by local people for production of edible fruits.

### **Research Questions**

- How likely is seedling recruitment from seeds of large-seeded tropical forest trees planted in secondary forests?
- How does shallow seed burial affect seed removal, seedling recruitment, and mortality?
- Are results consistent among the four species of large-seeded tropical forest trees tested?
- Are results consistent among three secondary forest plots located 1-5 km apart?

### **Materials and Methods**

#### **Study Site**

This study was conducted in the Shuar indigenous communities of San Antonio and Kunkuki in the Morona Santiago Province of the Ecuadorian Amazon, about 55 km south of the provincial capital city of Puyo (1 ° 20'0"S, 78°0'10"W; Figure 2-1). Two study plots were located in secondary forests in San Antonio, and one plot was in Kunkuki. The climate, soils, and vegetation type of the region are described in Chapter 2.

#### **Tree Species**

Species were selected from native trees with large, recalcitrant seeds that were in fruit at the onset of the experiment (January 2008). The four species were *Inga densiflora* Benth (Fabaceae), *Gustavia macarenensis* Philipson (Lecythidaceae), *Caryodendron orinocense* Karst (Euphorbiaceae), and a Myrtaceae identified as a species of *Plinia* by Bruce K. Holst (Selby Botanical Gardens). All species will be referred to by their generic name after description in the next paragraph. Average fresh weight of seeds ranged from 2.3 grams to 19 grams (Table A-2).



Voucher specimens of the four species were deposited in the National Herbarium of Ecuador, Quito (QCNE) in July of 2008, and duplicates were packed for shipment to the University of Florida Herbarium (FLAS) via the Missouri Botanical Gardens.

All species have edible fruits that are consumed locally and occasionally sold at small markets in nearby towns (Palora and Puyo). Fruit collection is usually from ostensibly wild trees, but the species are all occasionally planted, and naturally regenerating seedlings are sometimes transplanted to forest gardens (Byg and Balslev 2006). *Inga densiflora* was used in the previous experiment, and is described in detail in Chapter 2. *Gustavia macarenensis* is a medium sized (10-20 m height) forest tree found in Ecuador, Peru and Venezuela (Prance and Mori 1979). It has pink -red indehiscent globose fruits of 5 – 15 cm containing 3-7 large polygonal seeds. The pulpy orange mesocarp surrounding the seeds is eaten raw by the Shuar (Bennett et al. 2002). *Caryodendron orinocense* is a slow-growing tree, native to the eastern foothills of the Andes in Venezuela, Ecuador, and Colombia (Neito and Rodriguez 2002). The fruits are capsules that open when the fruit falls to release (typically) 3 seeds. The seeds are high in protein and oil (Padilla et al. 1998), and are eaten both toasted and raw by people (Schnee 1973). The ground seeds have been studied as a potential substitute for commercial soybean protein meal (Padilla et al. 1996). The specimens of *Plinia* sp. used in the experiment had ovoid berry fruits (1 seed per fruit) that were approximately 10 x 15 cm with thin yellow to orange skin and a flesh, white slightly aromatic mesocarp that is consumed raw (Figure A-4). The species is cultivated on a small scale around Palora, Ecuador and is known locally as ‘shawi’. It is similar to a fruit called ‘mulchi’, cultivated in the Napo Province (Ecuador), about 80 km NW of Palora. Prior to this study, no herbarium specimens of this species were in the National Herbarium of Ecuador (QCNE).

Seeds were collected from fresh fruits of  $\geq 3$  trees of *Gustavia* and *Caryodendron* trees growing in mature forest approximately 15 km west of the experimental plots. *Inga* seeds were collected from five roadside trees in Kunkuki, and *Plinia* seeds were collected from two trees growing in pastures near the town of Palora (see Figure 2-1 for location of towns). Fruit pulp was removed, seeds were inspected for insect holes and damage, washed in freshwater, float-tested for viability, and planted within one week of harvest. Due to lack of seed availability at the start of the experiment (February 2008), *Caryodendron* seeds were planted 2 weeks after the other three species. All data are reported as weeks since planting. Thirty seeds of each species were also planted 1 cm deep in outdoor raised planting beds of forest soil in full sunlight.

### **Secondary Forest Plots**

Three 0.5 ha study plots were established in 10-15 yr old secondary forests in February 2008. Two plots ('Hartensia' and 'Cascada') were located in the Shuar indigenous community of Kunkuki and one ('Centro Semillas') in San Antonio (Figure 2-1). All plots were within 0.5 km of the Puyo-Macas Road, and separated by 1–5 km. The secondary forests were located within larger tracts of secondary and selectively logged forest. The landscape surrounding Kunkuki is described in Chapter 2. The secondary forests were all natural regrowth from either horse pasture ("Cascada" plot in Kunkuki) or abandoned home gardens of maize, yucca and plátano ("Hartensia" plot in Kunkuki and "Centro Semillas" plot in San Antonio).

Vegetation in the secondary forest plots was characterized by percent canopy cover measured with a spherical densitometer held at 1 m above ground level at 20 points per plot, and by height and dbh measurements of woody stems measured in four 50 m x 2 m transects per 0.5 ha plot (modified Gentry transects; Phillips *et al.* 2000). Canopy cover ranged from  $77 \pm 8\%$  (Cascada) to  $83 \pm 4\%$  (Centro Semillas), and differed among the three plots ( $p = 0.0011$ ; Figure A-5). Woody stem density of trees  $> 10$  cm dbh was 425-875 stems/ha and average height of

trees encountered was  $12 \pm 6$  m. Woody tree density of stems  $\geq 2.5$  cm dbh was estimated to be between 3225–3625 stems/ha (Table A-4).

### **Experimental Design**

A 2 x 2 factorial design was used to test seedling recruitment and mortality of buried vs. unburied and caged vs. uncaged seeds, resulting in four treatment combinations (surface & caged, surface & uncaged, buried & caged, buried & uncaged). In the “surface” treatment, seeds were placed on the ground surface after removal of woody debris. “Buried” seeds were placed in a 1-2 cm deep hole and covered with ~1 cm of soil. Cylindrical cages were made of 24 gauge galvanized 0.5 mm wire mesh, and measured approximately 15 cm diameter x 30 cm tall. Cages were open on the bottom and closed on the top. Cages were inserted 1 cm into the ground and anchored in place by three 20 cm hook-shaped 14-gauge wires. Locations of uncaged seeds were marked by 20 cm 14-gauge wires inserted into the ground beside each seed. In each of the three secondary forest plots, 50-100 m long parallel transects were established at 3-8 m intervals as described in Chapter 2 (See Figure 2-2). Species, burial treatment, caging, and left/right planting were randomized along transects, with an average of 20 replicates of each species x treatment combination planted in each of the three plots.

Seed disappearance (defined as no seed found within 30 cm of the wire that marked the planting location), germination, seedling recruitment and mortality were recorded at 2, 4, 6, 8, 10, 16, and 18 weeks after planting for *Caryodendron*, and at weeks 2, 4, 6, 8, 10, and 18 for the other three species. Germination (emergence of radicle or epicotyl from the seed) was recorded at each census without disturbing seeds. In most cases, germination of buried seeds could not be detected until the stem emerged above the ground surface. Seedling recruitment was defined as development of at least one true leaf  $\geq 1$  cm long (or photosynthetic cotyledon, in the case of *Caryodendron*; see Table A-2 for cotyledon and seedling types). At 18 weeks, remaining seeds,

both buried and non-buried, were cut open and visually inspected to determine germination and viability. Seeds with solid, intact, and undamaged endosperm were considered alive.

To determine if any seed-eating animals were present at the study site, 9 kernels of maize were placed on the soil surface at 20 locations in each plot in early May, and the numbers of kernels remaining were recorded 14 days later.

## **Data Analyses**

Effects of species, seed burial, and plot location on seedling recruitment and mortality were assessed by logistic regression using PROC GLIMMIX in SAS 9.1.3 (2003, SAS Institute, Cary, NC). I first tested full factorial models including main effects and all interactions, and subsequently reduced models by removing non-significant interactions ( $p > 0.05$ ). I report analyses of main effects and significant interactions. Significant ( $p \leq 0.05$ ) interactions were further evaluated in post-hoc Bonferroni-adjusted pairwise comparisons. When species was a highly significant main effect ( $p < 0.0001$ ), treatments were tested separately for each species in mixed models. Data were discarded if the wire marking the planting location was not found in the final census.

## **Results**

### **General Patterns of Seeding Recruitment and Survival**

Over the first 2 weeks, only 5 of 410 uncaged seeds disappeared from their planting sites. None of the 421 caged seeds and no additional uncaged seeds disappeared by 18 weeks. Survival of seeds and seedlings to 18 weeks differed among species ( $p < 0.0001$ ; Table 3-1), and ranged from 73% (*Plinia*) to 94% (*Gustavia*; Figure 3-1). At 18 weeks, seedling recruitment also differed among the four species ( $p < 0.0001$ ; Table 3-1), and ranged from 17% (*Plinia*) to 76% (*Inga* and *Caryodendron*; Figure 3-2). Very few (16 of 498) seedlings died during the experiment (Figure 3-2).

## Species Differences

Seedling recruitment at 18 weeks differed among species ( $p < 0.0001$ ; Table 3-1) and was lowest for *Plinia* ( $p < 0.0001$  in post-hoc pairwise comparisons with each of the other species; no other pairwise comparisons between species were significant; Table 3-1). At 18 weeks, 76% (174 of 228) of *Caryodendron*, 64% (128 of 198) of *Gustavia*, 76% (144 of 189) of *Inga*, and 17% (36 of 216) of *Plinia* seeds planted were present as live seedlings (Figure 3-1). Seedling recruitment at 18 weeks was positively correlated with early germination. At 2 weeks, germination was observed in  $\geq 90\%$  of surface-planted *Caryodendron*, *Gustavia*, and *Inga* seeds, and only 19% of surface-planted *Plinia* seeds (only germination of unburied seeds could be assessed at 2 wks without disturbing developing seedlings). Most *Caryodendron* and *Inga* seeds developed to seedlings by week 6, with few additional seeds becoming seedlings after 10 weeks. In contrast, seedling development was still continuing for *Gustavia* and *Plinia* at 18 weeks (Figure 3-2).

Species differed in mortality (dead seeds and seedlings and missing seeds) at 18 wks ( $p < 0.0001$ , Table 3-1; Figure 3-1). *Gustavia* had higher survival than *Caryodendron*, *Inga* or *Plinia* ( $p = 0.0002$ ,  $p = 0.0003$ ,  $p < 0.0001$ , respectively) and *Inga* had greater survival than *Plinia* ( $p = 0.0003$ ; Table 3-1). Mortality of seeds that had not become seedlings in 18 weeks also differed among species ( $p < 0.0001$ ; Table 3-1). Almost all (38 of 44) of *Caryodendron* seeds that did not become seedlings were dead, whereas 84% (58 of 69) of *Gustavia*, 63% (25 of 40) of *Inga*, and 67% (121 of 180) of *Plinia* seeds that had not been recruited to seedlings were alive at 18 weeks (Figure 3-1).

## Seed Burial

At 18 weeks, seedling recruitment was higher for seeds planted on the soil surface than for buried seeds ( $p < 0.0001$ ; Table 3-1, Figure 3-1). This effect was primarily due to lower seedling

recruitment of *Gustavia* and *Inga* from buried seeds ( $p < 0.0001$  and  $p = 0.0015$ , respectively, in individual species subsets; Table 3-1). Of seeds that had not developed to the seedling stage by 18 weeks, more buried than non-buried seeds were dead ( $p = 0.04$ ; Table 3-1). This finding was almost entirely due to higher mortality of buried *Plinia* seeds ( $p = 0.0203$ ; no other species showed effect of burial treatment; Table 3-1; see Figure 3-1).

### **Plots**

The three secondary forest plots did not differ in seedling recruitment, total mortality, or mortality of seeds that did not become seedlings (Table 3-1).

### **Caging**

Caged and uncaged seeds did not differ in seedling recruitment, total mortality, or mortality of seeds that did not become seedlings (Table 3-1, Table A-6).

### **Species Inventory**

A total of 129 species of trees  $> 2.5$  cm dbh representing 69 genera and 34 families were recorded in twelve 50 x 2 m transects (4 transects x 3 plots). The most frequently encountered species  $> 10$  cm dbh in all plots was *Piptocoma discolor* ('pigüé', Asteraceae; Table A-5). Common understory species (2.5-10 cm dbh) were *Calliandra trinervia* (Fabaceae), *Casearia* spp. (Flacourtiaceae), *Hedyosmum racemosum* (Chloranthaceae), *Inga* spp. (Fabaceae), *Miconia* spp. and *Ossaea* spp. (Melastomataceae), *Palicourea* spp. (Rubiaceae), *Piper obliquum* (Piperaceae), *Saurauia* spp. (Actinidiaceae), *Schefflera morototonia* (Araliaceae) and *Tournefortia* sp. (Boraginaceae). Large-seeded species encountered in transects included *Caryodendron orinocense* (one of the study species), multiple *Inga* species, *Socretea*, *Ocotea*, *Guarea*, *Brosimum*, and *Virola* (Table A-2).

## Discussion

The majority of forests in the tropics are degraded by human activities or in a state of secondary succession (I.T.T.O. 2002). Mature tropical forests continue to be fragmented and reduced by logging, new plantations, agricultural expansion (Wassenaar et al. 2007) and increased frequency and intensity of fires (Mayaux et al. 2005). At the same time, secondary forests in the tropics are expanding, reclaiming former agricultural land (Aide and Grau 2004) and as much as 10% of forest cover claimed by logging in the last two decades (Wright 2005). Future species composition of these forests will depend on natural successional trajectories based on prior land use and ecology of the surrounding landscape, combined with management interventions to increase the growth and survival of desired species.

The purpose of this experiment was to assess the likelihood of seedling recruitment of four late-successional species that were experimentally dispersed into 10-15 yr old secondary forests. High levels (> 60%) of seedling recruitment of three of the four species resulted from extremely low levels of seed removal (5 of 410 uncaged seeds), high germination (> 90% of non-buried seeds), and low mortality of newly recruited seedlings (16 of 482 seedlings). Seed burial did not increase seedling recruitment and was associated with increased seed mortality of *Plinia*, the species with the lowest seedling recruitment at 18 weeks (17%).

### Low Seed Removal

Seed predation can dramatically reduce the number of seeds available for seedling recruitment (Notman and Gorchoy 2001; Peña-Claros and De Boo 2002). However, in my experiment, very few seeds disappeared from planting sites, and thus seed predation presented virtually no obstacle to seedling recruitment. The near complete lack of seed removal probably reflects the lack of large mammalian seed predators (and secondary dispersers) in the study area. All plots were < 0.5 km from houses along the Puyo-Macas road, and I was told by local

residents that large animals such as peccaries and monkeys were uncommon in the area. I also observed that medium to large wild animals were nearly always hunted when encountered (agoutis, peccaries, birds, etc.). Populations of large animals that consume large seeds can be dramatically decreased by hunters (Jerozolimski and Peres 2003), and resulting low levels of seed predation of large-seeded species have been documented in other defaunated tropical rainforests (Dirzo et al. 2007). Some evidence for lower seed removal in this area was also found in the experiment described in Chapter 2 where the lowest level of seed removal among three communities was in Kunkuki (Figure 2-3), the village closest to the study plots in this experiment (Figure 2-1).

The observed infrequency of seed removal could also indicate that seeds were unpalatable to seed predators. Small rodents are often common in disturbed habitats where large mammals are extirpated (Dirzo et al. 2007), but tend to prefer smaller seeds than those used in this experiment (Mendoza and Dirzo 2007; Vieira et al. 2006). Granivores that consume small seeds were present since 68% ( $\pm 23.8\%$ ) of maize kernels were removed in two weeks. These were likely small rodents, although birds could also have removed seeds. Another explanation for lack of seed predation of the planted seeds is that secondary compounds in the seeds could also have deterred predation. For example, the *Plinia* seeds smelled of volatile oils, and other Myrtaceae species (*Eucalyptus*, *Melaleuca* etc.) are known to produce aromatic compounds that are unpalatable to most mammals (Jones et al. 2003a).

Seed predation may also have been reduced by quick germination of three of the four study species, which minimized the time the seeds were exposed to potential seed consumers. At least 90% of *Inga*, *Gustavia*, and *Caryodendron* seeds placed on the soil surface germinated in the first 2 weeks. Within days of germination, all seed resources in *Caryodendron* seeds were



converted into the young plant (only the seed coat remained). Although the chemical composition of seed tissue changes during germination (Bewley and Black 1994) in ways that generally may make them less attractive to seed predators (Forget 1990), germination itself does not provide complete escape from seed predators for all large seeds because storage cotyledons may still be consumed after the seedling has developed (Alvarez-Clare and Kitajima 2009). *Inga*, *Gustavia* and *Plinia* all had large storage cotyledons that were still attached to recruited seedlings at 18 weeks, although none were damaged by rodents.

### **High Germination**

By 18 weeks, over 90% of *Inga*, *Gustavia*, and *Caryodendron* seeds and at least 79% of *Plinia* seeds had germinated. These levels are similar to those found in previous studies. Many *Inga* species regularly exhibit germination levels of 95-100%, often within days of removal from the fruit (Pennington and Revelo 1997). Likewise, 100% germination has been observed for *Caryodendron* seeds within 12-15 days of planting (Jimenez and Bernal 1989; Neito and Rodriguez 2002). In Panama, 463 of 500 (93%) seeds of another *Gustavia* species, (*G. superba*) germinated during an 8-week study (Dalling and Harms 1999). At 12 months, germination of morphologically similar Brazilian species of *Plinia* (also cultivated for fruit production) was 81% in one study (Danner et al. 2007), and 70-85% in another (Andrade and Martins 2003).

### **Seed Burial**

As was also found in the study presented in Chapter 2, seed burial did not result in higher germination or seedling recruitment for any species. Seed burial can reduce the probability of detection by seed predators, but seed removal of study species was minimal and did not present an obstacle to seedling recruitment. Seed burial prevents moisture loss (Fenner and Thompson 2005), which can be a major cause of post-dispersal mortality for desiccation-sensitive seeds in disturbed or exposed sites (Vieira and Scariot 2006), but desiccation of seeds was rarely

observed during this experiment. Moisture loss can be avoided by rapid germination (Daws et al. 2005), and at 2 weeks, over 90% of surface-planted *Caryodendron*, *Gustavia* and *Inga* seeds were germinated. The combination of rapid germination and an overall wet climate (average of ~400 mm of rain in March; Table A-1) may have minimized any moisture-retention benefit of seed burial. Rather, it appears buried seeds were more susceptible to pathogens since more seed death was observed in buried seeds. At 18 wks, all 26 dead *Plinia* seeds and nearly all 58 live *Plinia* seeds that were removed from the soil showed signs of decay in the form of discolored tissue. In contrast, 29 of 30 seeds buried in outdoor raised planting beds of forest soil that were exposed to full sunlight were live seedlings by 12 weeks after planting (Table A-2). Moist and shaded conditions under forest cover are associated with increased pathogen attack (Augspurger 1984b), and this is probably why seed survival and seedling recruitment were higher in planting beds than in the forest.

### **Secondary Forests**

The results of this study indicate that young seedlings will recruit from large-seeded tropical forest trees if the seeds are dispersed into secondary forests. Many large-seeded species (including two of the study species) were found in the surveys of the plots (e.g. *Caryodendron orinocense*, multiple *Inga* species, *Socotrea*, *Ocotea*, *Guarea*, *Brosimum*, *Virola*). This indicates that seeds of large-seeded species were naturally dispersed into these forests and survived to establish as young trees during the 10 – 15 years since abandonment of agricultural use. Natural regeneration of common large-seeded species in young secondary forests was also found by Norden et. al. (2009) in Costa Rica in an agricultural landscape that included fragments of mature forest and an intact animal disperser community. Although larger-bodied animals were hunted in the region of my study, the presence of large-seeded trees in 10-15 yr old secondary forests indicates at least some large-seeded species are being dispersed from nearby remnant

trees or patches of selectively logged forest, and possibly from the mature forest located approximately 10 km to the east. In addition, some species may have regenerated by sprouting (Mwavu and Witkowski 2008), but evidence of this was not noted in the surveys.

### **Recommendations for Propagation of the Study Species**

Higher initial mortality of seedlings can be expected when species are planted in secondary forests rather than in nurseries, but this may be worth the tradeoff in avoiding extra expenses associated with nursery propagation. At 18 weeks, seedling recruitment of *Inga*, *Caryodendron* and *Gustavia* ranged from 65-76% and seed losses were relatively minimal (15%, 5%, and 8%, respectively; Table A-6). These species may be suitable for direct-seeding. The fourth species, *Plinia*, had the lowest (17%) and slowest recruitment to seedlings (Figure 3-2), and seeds were subject to pathogen infection when planted in secondary forests. For this species nursery planting may be advantageous if seed sources are scarce. For all species, seedling recruitment levels were high (87-100%) when seeds were planted below the soil surface in raised outdoor planting beds of forest soil in full sunlight (Table A-2). Seed burial was detrimental to seed and seedling survival in secondary forests, and is not recommended for any species if seeds are being planted in forests. After seedlings have established in the forest, removal of some overstory trees is generally recommended in enrichment planting to promote growth of desired species (Peña-Claros et al. 2002; Romell et al. 2008).

### **Recommendations for Future Studies**

Results of this study suggest that regeneration of large-seeded species in secondary forests in this region is not severely constrained by mortality during seedling recruitment. To better understand constraints on establishment of large-seeded species beyond the stage of seeding development the experimental plantings would need to be monitored over a longer time period (1 yr). Seed trap studies and more extensive vegetation surveys of the seedling and sapling

understory could be combined with the experimental plantings to better assess the relative impact of experimental seed augmentation on successional processes and forest diversity.

### **Conclusion**

Results of this research have implications for understanding of successional processes in young tropical secondary forests. The majority (> 60%) of seeds of three out of four large-seeded, later successional tree species (*Inga*, *Gustavia* and *Caryodendron*) became seedlings by 18 weeks. Seedling development was slower for *Plinia*, but still over 15% of seeds planted were live seedlings at 18 weeks. Seed predation was extremely low (< 1% of seeds), and seed burial did not improve survival or seedling recruitment for any species. Large-seeded species that overcome dispersal barriers to reach secondary forests near human settlements appear to have a high chance of seedling establishment. Hunting reduces populations of animal dispersers, but may foster succession by reducing seed predation pressure on occasionally dispersed (or planted) seeds. Recovery of large-seeded species in secondary forests can be augmented by planting seeds, improving the value of the landscape for both wildlife and humans.

Table 3-1. Results from mixed model logistic regression of seedling recruitment, total mortality (missing seeds, dead seeds and seedlings), and mortality of remaining seeds at 18 wks of four large-seeded tropical tree species planted as seeds in three secondary forest plots in the Ecuadorian Amazon. Seeds that disappeared (n = 5) are counted as dead in the analysis of total mortality and are excluded from the analysis of mortality of the remaining seeds. Results are for reduced models of only main effects and significant interactions ( $p \leq 0.05$ ).

Source	18-week seedling recruitment of all seeds planted				18-week mortality of all seeds planted				18-week mortality of remaining seeds that had not developed into seedlings			
	Num df	Den df	F value	P > F	Num df	Den df	F value	P > F	Num df	Den df	F value	P > F
Species	3	817	21.66	< <b>0.0001</b> <sup>†A</sup>	3	823	12.84	< <b>0.0001</b> <sup>†E</sup>	3	325	13.72	< <b>0.0001</b> <sup>†G</sup>
Plot	2	817	0.1	0.9076	2	823	1.92	0.3381	2	325	2.72	0.1089
Cage	1	817	0.01	0.033	1	823	0.69	0.7546	1	325	2.4	0.2029
Buried	1	817	19.57	< <b>0.0001</b> <sup>†B</sup>	1	823	9.04	<b>0.0126</b> <sup>†F</sup>	1	325	5.97	<b>0.0400</b> <sup>†H</sup>
Species*buried	3	817	3.77	<b>0.0105</b> <sup>†C</sup>	...	...	...	...	...	...	...	...
Cage*species	3	817	2.85	<b>0.0364</b> <sup>†D</sup>	...	...	...	...	...	...	...	...

<sup>†A</sup> Fewer *Plinia* seedlings were recruited than the other three species ( $p < 0.0001$  in all post-hoc tests).

<sup>†B</sup> Fewer seedlings from buried seeds.

<sup>†C</sup> In individual species subsets, fewer seedlings were recruited from buried than surface-planted seeds for *Gustavia* ( $p < 0.0001$ ) and *Inga* ( $p = 0.0015$ ).

<sup>†D</sup> In individual species subsets, fewer *Plinia* seedlings were recruited from caged than uncaged seeds ( $p = 0.0166$ ).

<sup>†E</sup> Higher mortality of *Plinia* than *Gustavia* ( $p < 0.0001$ ) or *Inga* ( $p = 0.0003$ ), and higher mortality of *Caryodendron* than *Gustavia* ( $p = 0.0002$ ) or *Inga* ( $p = 0.038$ ) in post-hoc pairwise comparisons between species. In individual species subsets, an interaction between caging and burial was observed only for *Plinia* ( $p = 0.0348$ ), with higher mortality of caged ( $p = 0.0169$ ) and buried ( $p = 0.0004$ ) *Plinia* seeds.

<sup>†F</sup> More buried than surface-planted seeds died.

<sup>†G</sup> More *Caryodendron* than *Gustavia*, *Inga* or *Plinia* seeds died ( $p \leq 0.0001$  in each post-hoc pairwise comparison). More *Plinia* than *Gustavia* seeds died ( $p = 0.0203$ ). In individual species subsets, more buried than surface-planted *Plinia* seeds died ( $p = 0.0203$ ).

<sup>†H</sup> More buried than surface-planted seeds died.

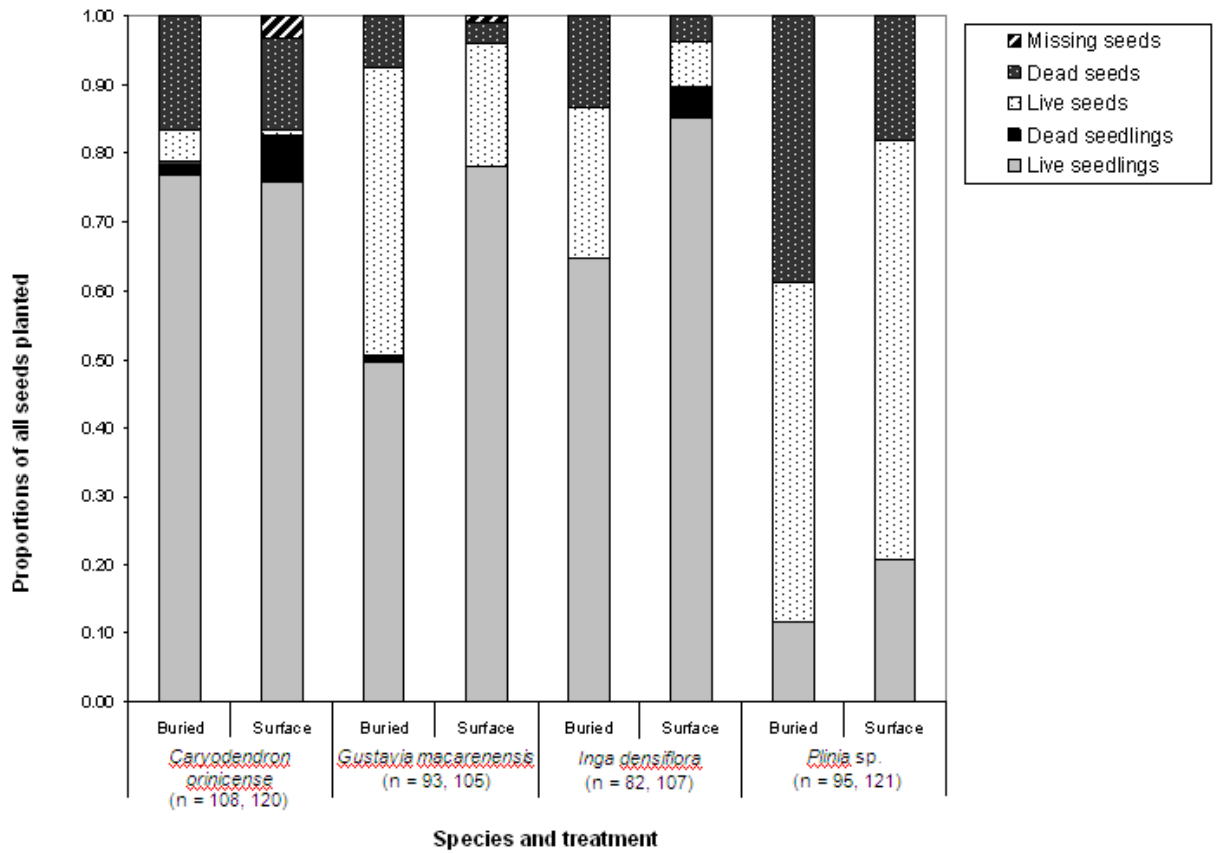


Figure 3-1. Seed fates at 18 weeks of four species of large-seeded tropical trees that were planted on the soil surface and buried in three secondary forests plots in the Ecuadorian Amazon. Live seedlings and dead seedlings, live and dead seeds, and seeds that disappeared are indicated (see key). Fewer seedlings were recruited from buried seeds ( $p < 0.0001$ ; Table 3-1). Cages and uncaged seeds did not differ in seedling recruitment or survival (Table 3-1) and are combined in the figure.

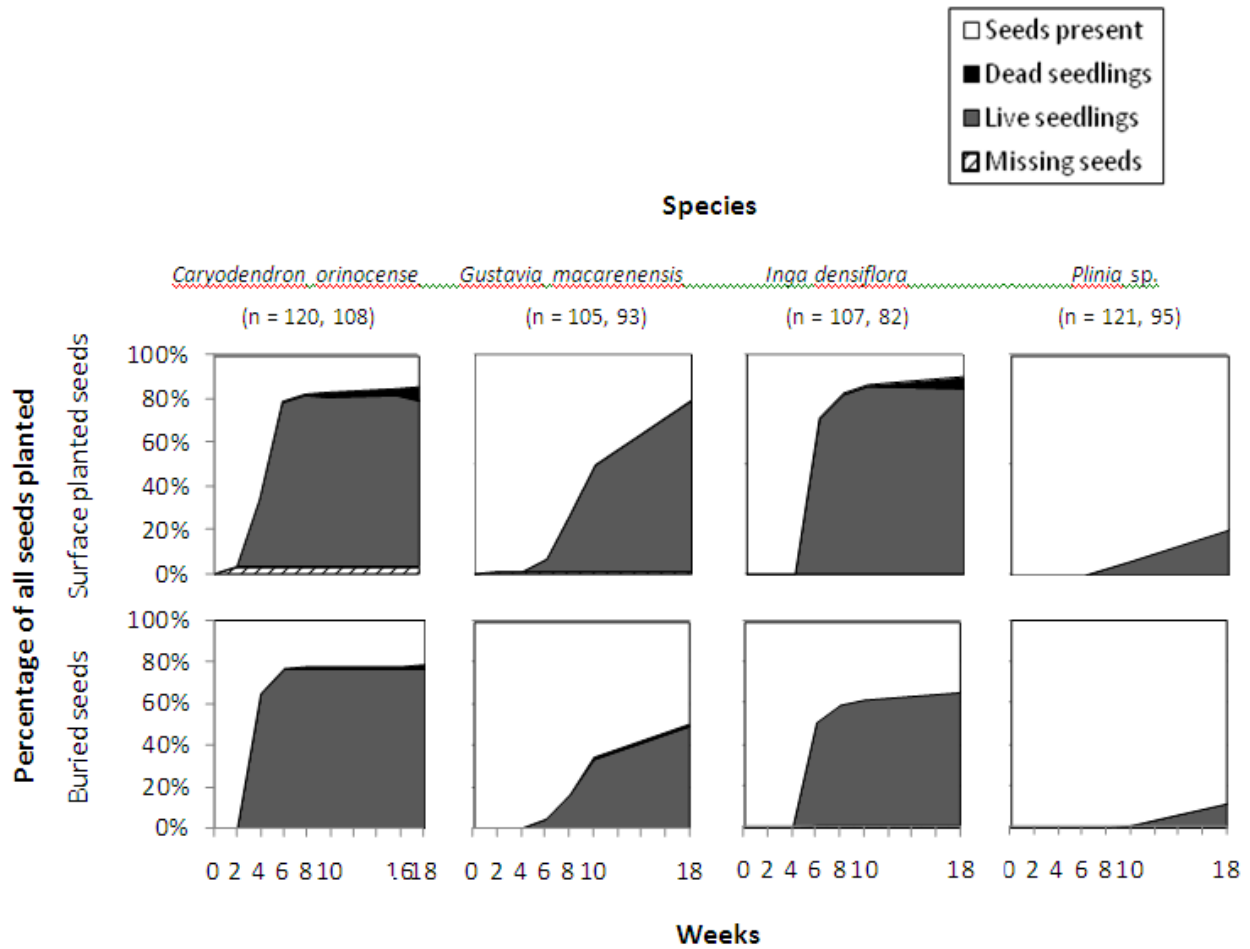


Figure 3-2. Seedling development of four species of large-seeded tropical trees that were planted as seeds on the soil surface and buried in secondary forests in the Ecuadorian Amazon. Live seedlings are indicated in grey, dead seedlings in black, and seeds that disappeared from planting sites by the hashed shading. The white areas are seeds that did not become seedlings during the 18 week experiment (see Figure 3-1 for 18-week mortality of seeds). Data are presented for weeks 2, 4, 6, 8, 10, 16 and 18 for *Caryodendron*, and weeks 2, 4, 6, 8, 10, and 18 for the other three species. Caged and uncaged seeds did not differ in seedling recruitment or survivorship (Table 3-1) and are combined in the figure.

## CHAPTER 4 CONCLUSION

Natural regeneration of large-seeded tropical forest trees in degraded forests and agricultural landscapes is often severely limited by lack of animal-mediated seed dispersal. The substantial energy and nutrient reserves in large seeds may allow for relatively high levels of seedling recruitment when dispersal limitation is overcome. In fragmented tropical forests near human settlements, arrival of mature forest seeds by rare cases of long-distance dispersal may be critical to species persistence, providing seeds survive at the new sites. In addition to being of value to wildlife, many tropical fruit trees with large-seeds have fruits consumed by people, and if successful, planting seeds of these species into the landscape ('direct seedling') is an inexpensive method to propagate large-seeded species.

The goal of this thesis was to assess the chance of seedling recruitment of large-seeded tropical forest trees in human-modified landscapes in the Ecuadorian Amazon. Seeds of six species of native large-seeded tropical trees with recalcitrant seeds were planted in a variety of habitats, and seedling recruitment and survival were assessed for 3-5 months. Species selection reflected the interest of local indigenous landowners in propagating fruit-bearing trees. Seed burial was hypothesized to increase seedling recruitment by reducing seed predation and desiccation.

Over 55% of *Inga*, *Caryodendron* and *Gustavia* (56 & 76% in the two experiments, 76%, and 64%, respectively), 17% of *Plinia*, 10% of *Quararibea*, and 2% of *Pouteria* seeds developed into seedlings and survived during the 14–18 week periods of the two experiments. Seed burial did not increase survival or seedling recruitment of any species. The location of the plots in the landscape (the indigenous community in which seeds were planted) affected seed removal and seedling recruitment more than the habitat in which seeds were planted ("grazed



pasture” (2-6 weeks vegetative regrowth at time of planting), “mature pasture” (3-6 months of vegetative regrowth), and selectively logged forest; Chapter 2). In both studies, seed removal was rare (0-10%) and was not reduced by seed burial. Large-seeded species were present in surveys of 10-15 yr old secondary forest, confirming that large-seeded species were able to recruit from naturally dispersed seeds (Chapter 3).

Direct seeding of large-seeded species may be a useful technique for large-scale restoration projects. Planting seeds instead of transplanting seedlings allows for the reforestation of larger and less accessible regions because seeds are smaller and easier to transport than seedlings, and the cost of seeds is often substantially less than the cost of seedlings. Large-seeded tropical species often have fleshy fruits which provide food for larger-bodied animals, which can help catalyze further seed dispersal of mature forest species from remaining forest patches. Ironically, the chances of establishment of large-seeded species from seeds may be higher in regions most disturbed by human activities because hunting and habitat loss also reduce populations of seed predators of large seeds.

Direct-seeding can be an advantageous strategy when the long-term investment in forest restoration is not possible due to logistical, financial or political limitations. For example, if an NGO only has funding for a 6-month project, direct seedling allows for immediate tree planting at the project outset when outside resources as well as local interest in new projects are often highest. During the 2 years of this research, at least two forest restoration projects using seedling nurseries were started and abandoned by internationally-funded NGO groups operating in the study area. Many more seedlings died nurseries than were planted in the field. Finally, forest restoration is a long-term endeavor and predicting future land use in the tropics is often difficult. The simplicity of direct seeding reduces the costs of planting at many sites, thus allowing

landowners and managers to account for the inevitable conversion of some sites to agriculture or other uses and still accomplish forest restoration at other sites.

The results of this research suggest human-modified landscapes can be managed to help recover tropical forest biodiversity. Large-seeded tree species reestablished within a decade of agricultural abandonment, and seed planting of five of six species was largely successful in early seedling recruitment and survival. Long-term studies will be useful to evaluate later constraints on seedling survival and provide further management suggestions for the propagation of large-seeded species.

APPENDIX  
CHARACTERIZATION OF RESEARCH SITES AND SPECIES USED IN THE  
EXPERIMENTS

Table A-1. Average monthly precipitation and air temperatures (1974-2007) and number of days with rainfall (1961-1990) from the Puyo weather station M008 of the Instituto Nacional de Meteorología en Hidrológica (INAHMI), Pastaza Province, Ecuador (S 1°30'27", W 77°56'38", 960 m). The station is 30-45 km northwest of the experimental plots.

Month	Air temperature (°C)			Days with at least 1 mm rainfall	Precipitation (mm)		
	Max	Min	Average		Max	Min	Average
January	22.3	19.8	21.2	21.1	476.3	88.2	306.7
February	22.4	19.1	21.0	20.0	570.8	88.6	322.2
March	22.8	20.2	21.2	23.0	584.5	71.5	396.8
April	22.2	20.5	21.2	23.0	761.7	254.1	493.8
May	22.1	20.3	21.0	24.0	782.3	227.0	459.3
June	21.3	19.4	20.4	24.0	835.7	275.8	472.4
July	20.8	14.0	19.8	22.0	634.8	210.4	367.4
August	24.9	19.4	20.6	21.0	436.8	114.8	309.1
September	29.9	20.0	21.2	21.0	489.4	115.0	349.4
October	31.8	20.4	21.7	22.0	607.5	171.9	394.5
November	22.0	20.6	21.4	22.0	693.5	271.3	392.6
December	22.8	20.4	21.2	22.0	599.7	87.6	351.5
Average monthly	23.8 ± 3.5	19.5 ± 1.8	20.1 ± 1.0	22.1 ± 1.2	622.8 ± 125.8	164.7 ± 79.2	384.7 ± 63.1
Total				265.1			4615.8

Table A-2. Common names, seedling types, cotyledon characteristics, seed sizes, and seedling recruitment of six large-seeded tropical forest species from the Ecuadorian Amazon used in the two studies. Superscripts of 1 are species used in the 2007 study (Chapter 2), and 2 in the 2008 study (Chapter 3).

Species	Family	Spanish name (in Ecuador)	Shuar name	Seedling type (Garwood, 1996)	Cotyledon functional type			Seedling recruitment in planting bed (n=30)			Seed size (n=20)		Seed fresh wt (g) (n=25)
					cotyledon enclosure by seed coat after germination	Cotyledon position	cotyledon morphology	planted 3/9/08	seedling 5/28/08	% recruited	Length (cm)	Width (cm)	
					phanerocotylar (free of seed coat) or cryptocotylar (enveloped by seed coat)	epigeal or hypogeal	foliaceous or reserve						
<i>Caryodendron ornicense</i> <sup>2</sup>	Euphorbiaceae	maní del árbol <sup>†C</sup>	nampi <sup>†B</sup>	PEF	phanerocotylar	epigeal	foliaceous	30	29	97	...	...	2.3±0.7
<i>Gustavia macarenensis</i> <sup>2</sup>	Lecythidaceae	sachi avocate	iniák <sup>†A</sup>	PHR	phanerocotylar	hypogeal	reserve	30	26	87	...	...	19.4±4.9
<i>Inga densiflora</i> <sup>1,2</sup>	Fabaceae	guaba machetona	sampi <sup>†A</sup>	PHR	phanerocotylar	hypogeal	reserve	30	30	100	4.5±1.0	2.2±0.4	7.2±1.4
<i>Plinia</i> sp. <sup>2</sup>	Myrtaceae	shawi	shawi <sup>†D</sup>	CHR	cryptocotylar	hypogeal	reserve	30	29	97	...	...	14.2±4.0
<i>Pouteria caimito</i> <sup>1</sup>	Sapotaceae	caimito	yáas <sup>†B</sup>	CHR	cryptocotylar	hypogeal	reserve	...	...	...	2.9±1.6	1.5±0.2	...
<i>Quararibea cordata</i> <sup>1</sup>	Malvaceae	sapote	saput <sup>†B</sup>	CHR	cryptocotylar	hypogeal	reserve (huastorial)	...	...	...	3.9±0.7	2.2±0.3	...

<sup>†A</sup> Van den Eynden, V., E. Cueva, et al. (2003)

<sup>†B</sup> Bennett, B. C., M. A. Baker, et al. (2002)

<sup>†C</sup> Jimenez, L. C. & H. Y. Bernal (1989)

<sup>†D</sup> Local name near Palora, Ecuador. Species was undescribed in Ecuador at time of the study (2008).

Table A-3. Number of seeds that were planted, missing, dead as seeds and seedlings, and alive as seeds and seedlings at 2 and 14 weeks after planting of three large-seeded tropical forest trees that were planted as seeds (buried and surface-planted) in three field types (grazed pasture, mature pasture and forest) nested in three indigenous communities (Kenkuimi, Kunkuki, San Ramon) in the Ecuadorian Amazon.

<i>Inga densiflora</i>														
Community	Field	Treatment	Planted	Missing at 2 wks	Dead seed at 2 wks	Dead seedling at 2 wks	Live ungerminated seed at 2 wks	Live germinated seeds at 2 wks	Live seedling at 2 wks	Missing between wks 2 and 14	Died between wks 2 and 14 (seed or seedling)	Live but not seedling at 14 wks	Live seedling at 14 wks	
Kenkuimi	Forest	Surface	17	4	0	0	1	0	12	1	7	0	5	
		Buried	19	6	0	0	1	0	12	1	6	0	6	
	Forest Total			36	10	0	0	2	0	24	2	13	0	11
	Grazed	Surface	17	0	1	5	0	0	11	0	7	0	4	
		Buried	12	1	0	0	1	2	8	0	6	2	3	
	Grazed Total			29	1	1	5	1	2	19	0	13	2	7
	Mature pasture	Surface	11	1	0	1	0	0	9	0	5	0	4	
		Buried	17	1	0	0	1	4	11	1	9	1	5	
Mature pasture Total			28	2	0	1	1	4	20	1	14	1	9	
Kenkuimi Total			93	13	1	6	4	6	63	3	40	3	27	
Kunkuki	Forest	Surface	20	1	0	0	4	2	13	0	3	0	16	
		Buried	17	0	0	0	3	4	10	0	5	0	12	
	Forest Total			37	1	0	0	7	6	23	0	8	0	28
	Mature pasture	Surface	18	0	0	0	2	1	15	2	4	0	12	
		Buried	15	1	0	0	0	3	11	1	4	0	9	
	Grazed Total			33	1	0	0	2	4	26	3	8	0	21
	Mature pasture	Surface	16	0	0	0	0	1	15	0	2	0	14	
		Buried	13	0	0	0	0	0	13	0	0	0	13	
Mature pasture Total			29	0	0	0	0	1	28	0	2	0	27	
Kunkuki Total			99	2	0	0	9	11	77	3	18	0	76	
SanRamon	Forest	Surface	20	0	0	0	2	0	18	1	4	0	15	
		Buried	16	0	0	0	0	1	15	1	8	0	7	
	Forest Total			36	0	0	0	2	1	33	2	12	0	22
	Grazed	Surface	20	0	0	0	0	2	18	1	9	0	10	
		Buried	21	0	1	0	0	2	18	2	2	0	16	
	Grazed Total			41	0	1	0	0	4	36	3	11	0	26
	Mature pasture	Surface	20	0	0	0	3	1	16	3	5	0	12	
		Buried	18	2	0	1	1	0	14	1	6	0	8	
Mature pasture Total			38	2	0	1	4	1	30	4	11	0	20	
SanRamon Total			115	2	1	1	6	6	99	9	34	0	68	
Surface Total			159	6	1	6	12	7	127	8	46	0	92	
Buried Total			148	11	1	1	7	16	112	7	46	3	79	
Grand Total			307	17	2	7	19	23	239	15	92	3	171	

Table A-3. Continued.

*Quararibea cordata*

Community	Field	Treatment	Planted	Missing at 2 wks	Dead seed at 2 wks	Dead seedling at 2 wks	Live ungermin ated seed at 2 wks	Live germinat ed seeds at 2 wks	Live seedling at 2 wks	Missing between wks 2 and 14	Died between wks 2 and 14 (seed or seedling)	Live but not seedling at 14 wks	Live seedling at 14 wks	
Kenkuimi	Forest	Surface	11	1	1	0	7	2	0	6	2	0	1	
		Buried	9	1	0	0	5	3	0	1	5	1	1	
	Forest Total			20	2	1	0	12	5	0	7	7	1	2
	Grazed	Surface	9	1	0	0	5	1	2	5	3	0	0	
		Buried	9	0	0	0	6	0	3	1	7	1	0	
	Grazed Total			18	1	0	0	11	1	5	6	10	1	0
	Mature pasture	Surface	9	0	2	0	4	2	1	5	1	0	1	
		Buried	9	0	1	0	8	0	0	1	6	1	0	
Mature pasture Total			18	0	3	0	12	2	1	6	7	1	1	
Kenkuimi Total			56	3	4	0	35	8	6	19	24	3	3	
Kunkuki	Forest	Surface	12	0	0	0	9	2	1	2	9	0	1	
		Buried	10	0	1	0	8	0	1	0	4	3	2	
	Forest Total			22	0	1	0	17	2	2	13	3	3	
	Mature pasture	Surface	9	0	0	0	6	0	3	2	4	1	2	
		Buried	8	0	0	0	7	0	1	5	2	0	1	
	Grazed Total			17	0	0	0	13	0	4	7	6	1	3
	Mature pasture	Surface	11	0	0	0	8	1	2	3	7	0	1	
		Buried	9	0	0	0	7	2	0	3	3	0	3	
Mature pasture Total			20	0	0	0	15	3	2	6	10	0	4	
Kunkuki Total			59	0	1	0	45	5	8	15	29	4	10	
SanRamon	Forest	Surface	17	0	0	0	13	0	4	6	9	0	2	
		Buried	9	0	1	0	7	0	1	1	6	0	1	
	Forest Total			26	0	1	0	20	0	5	7	15	0	3
	Grazed	Surface	13	1	0	0	9	1	2	1	9	1	1	
		Buried	13	2	1	0	6	0	4	3	7	0	0	
	Grazed Total			26	3	1	0	15	1	6	4	16	1	1
	Mature pasture	Surface	12	0	0	0	11	0	1	4	6	2	0	
		Buried	8	1	0	0	6	0	1	0	3	3	1	
Mature pasture Total			20	1	0	0	17	0	2	4	9	5	1	
SanRamon Total			72	4	2	0	52	1	13	15	40	6	5	
Surface Total			103	3	3	0	72	9	16	34	50	4	9	
Buried Total			84	4	4	0	60	5	11	15	43	9	9	
Grand Total			187	7	7	0	132	14	27	49	93	13	18	

Table A-3. Continued.

<i>Pouteria caimito</i>														
Community	Field	Treatment	Planted	Missing at 2 wks	Dead seed at 2 wks	Dead seedling at 2 wks	Live ungerminated seed at 2 wks	Live germinated seeds at 2 wks	Live seedling at 2 wks	Missing between wks 2 and 14	Died between wks 2 and 14 (seed or seedling)	Live but not seedling at 14 wks	Live seedling at 14 wks	
Kenkuimi	Forest	Surface	17	7	0	0	10	0	0	5	2	3	0	
		Buried	12	1	0	0	10	1	0	5	6	0	0	
	Forest Total			29	8	0	0	20	1	0	10	8	3	0
	Grazed	Surface	17	1	0	0	16	0	0	12	3	1	0	
		Buried	12	0	0	0	12	0	0	3	8	1	0	
	Grazed Total			29	1	0	0	28	0	0	15	11	2	0
	Mature pasture	Surface	17	1	0	0	15	0	1	8	4	3	1	
		Buried	15	5	0	0	10	0	0	1	6	3	0	
Mature pasture Total			32	6	0	0	25	0	1	9	10	6	1	
Kenkuimi Total			90	15	0	0	73	1	1	34	29	11	1	
Kunkuki	Forest	Surface	17	5	0	0	12	0	0	3	7	2	0	
		Buried	14	3	1	0	10	0	0	2	6	2	0	
	Forest Total			31	8	1	0	22	0	0	5	13	4	0
	Mature pasture	Surface	17	0	0	0	17	0	0	12	4	0	1	
		Buried	14	0	0	0	14	0	0	4	9	0	1	
	Grazed Total			31	0	0	0	31	0	0	16	13	0	2
	Mature pasture	Surface	17	0	0	0	16	1	0	6	11	0	0	
		Buried	9	0	0	0	9	0	0	5	3	1	0	
Mature pasture Total			26	0	0	0	25	1	0	11	14	1	0	
Kunkuki Total			88	8	1	0	78	1	0	32	40	5	2	
SanRamon	Forest	Surface	8	0	0	0	8	0	0	2	6	0	0	
		Buried	12	0	0	0	12	0	0	3	9	0	0	
	Forest Total			20	0	0	0	20	0	0	5	15	0	0
	Grazed	Surface	13	0	0	0	13	0	0	4	9	0	0	
		Buried	13	0	0	0	13	0	0	6	6	0	1	
	Grazed Total			26	0	0	0	26	0	0	10	15	0	1
	Mature pasture	Surface	10	0	0	0	10	0	0	5	5	0	0	
		Buried	8	2	0	0	6	0	0	1	3	1	1	
Mature pasture Total			18	2	0	0	16	0	0	6	8	1	1	
SanRamon Total			64	2	0	0	62	0	0	21	38	1	2	
Surface Total			133	14	0	0	117	1	1	57	51	9	2	
Buried Total			109	11	1	0	96	1	0	30	56	8	3	
Grand Total			242	25	1	0	213	2	1	87	107	17	5	

Table A-4. Vegetation characteristics of three secondary forest plots in the Ecuadorian Amazon from four 50 x 2 m modified Gentry transects (Phillips et al. 2002) established in each of three plots. The average dbh and heights ( $\pm 1$  S.D.) of woody stems of two size classes (2.5-10 cm, >10 cm), number of dead trees, vines and palms are presented for each plot. Individuals between 1-2.5 cm dbh were surveyed in one of the 50 x 2 m transects per plot. Heights were estimated in the field.

Plot name	woody stems 2.5 cm - 10 cm dbh			woody stems >10 cm dbh			# stems $\geq$ 1 and < 2.5 cm dbh / 100 m <sup>2</sup>	# palms $\geq$ 2.5 cm dbh / 400 m <sup>2</sup>	# dead stems $\geq$ 2.5 cm dbh / 400 m <sup>2</sup>	# vines $\geq$ 2.5 cm dbh / 400 m <sup>2</sup>
	# stems / 400 m <sup>2</sup>	dbh (cm)	height (m)	# stems / 400 m <sup>2</sup>	dbh (cm)	height (m)				
Hartensia	106	4.5 $\pm$ 1.8	4.2 $\pm$ 1.9	17	20 $\pm$ 6	14 $\pm$ 4.7	1	2	11	3
Cascada	111	4.6 $\pm$ 1.8	5.1 $\pm$ 2.5	19	17 $\pm$ 7.2	12 $\pm$ 4.1	12	0	28	3
Centro Semillas	93	4.4 $\pm$ 1.7	3.7 $\pm$ 1.4	35	20 $\pm$ 7.5	12 $\pm$ 7.3	1	1	17	3
Average	103	4.5 $\pm$ 1.8	4.4 $\pm$ 2.1	71	19 $\pm$ 7.1	12 $\pm$ 6	4.7	1	18.7	3



Table A-5. Numbers of woody species with  $\geq 2.5$  cm dbh encountered in four 50 x 2 m transects (400 m<sup>2</sup>) established in each of three secondary forest plots in Pastaza Province in the Ecuadorian Amazon. Identifications were made at the Herbario Nacional del Ecuador in Quito (QCNE). Unidentified species were classified to morphospecies.

Family	Genus	Species	Plot name			Total	
			Hartensia	Cascada	Centro Semillas		
Actinidiaceae	<i>Saurauia</i>	sp #1	1	6	1	8	
Anacardiaceae	<i>Tapirira</i>	<i>guianensis</i>	3	2	1	6	
Annonaceae	<i>Annona</i>	<i>duckei</i>			1	1	
		<i>edulis?</i>			1	1	
	<i>Porcelia</i>	<i>mediocris</i>			1	1	
	<i>Rollinia</i>	<i>dolichopetala</i>		1		1	
		<i>mucosa</i>		3		3	
		<i>pittieri</i>		2		2	
Araliaceae	<i>Schefflera</i>	<i>morotonia</i>	2	1	6	9	
	<i>Iretea</i>	<i>deltoides</i>	1			1	
Arecaceae	<i>Socratea</i>	<i>exorrhiza</i>	1			1	
	<i>Wettinia</i>	sp #1			1	1	
Asteraceae	<i>Mikania</i>	sp #1			1	1	
	<i>Piptocoma</i>	<i>discolor</i>	6	14	18	38	
Bignoniaceae	<i>Jacaranda</i>	<i>copaia</i>	2			2	
Boraginaceae	<i>Cordia</i>	<i>nodosa</i>	1			1	
		<i>ucayaliensis</i>			1	1	
	<i>Tournefortia</i>	sp #1	3	1	3	7	
Caryocaraceae	<i>Caryocar</i>	<i>glabrum</i>			1	1	
Cecropiaceae	<i>Cecropia</i>	sp #1			3	3	
		sp #2	1			1	
		sp #3			1	1	
		<i>sciadophylla</i>	2			2	
		<i>Pourouma</i>	<i>minor</i>	1			1
Chloranthaceae	<i>Hedyosmum</i>	<i>racemosum</i>	9			9	
	<i>Chrysochlamys</i>	<i>membranacea</i>		1		1	
Clusiaceae	<i>Tovomita</i>	sp #1			1	1	
		<i>Vismia</i>	<i>baccifera</i>	1			1
		sp #1	1		2	3	
		sp #2	2		1	3	
Erythroxylaceae	<i>Erythroxylum</i>	<i>macrophyllum</i>			1	1	

Table A-5. Continued.

Family	Genus	Species	Plot name			Total	
			Hartensia	Cascada	Centro Semillas		
Euphorbiaceae	<i>Caryodendron</i>	<i>orinocense</i>			5	5	
	<i>Croton</i>	<i>matourensis</i>			1	1	
	<i>Hyeronima</i>	<i>alchorneoides</i>	1			1	
		sp #1		1		1	
		<i>oblonga</i>	1			1	
		<i>Mabea</i>	<i>standleyi</i>			1	1
		<i>Margaritaria</i>	<i>nobilis</i>		1		1
		<i>Sapium</i>	sp #1			1	1
		<i>Tetrorchidium</i>	sp #1		2		2
Fabaceae	<i>Calliandra</i>	<i>trinervia</i>	19		1	20	
	<i>Dalbergia</i>	<i>frutescens</i>		3		3	
	<i>Dussia</i>	<i>tessmannii</i>		1		1	
	<i>Inga</i>	sp #1		2		2	
		sp #2		2		2	
		sp #3	1			1	
		sp #4			1	1	
		sp #5		1		1	
		sp #6	1			1	
		sp #7	1			1	
		sp #8		1		1	
		<i>nobilis</i>	1	1		2	
		<i>vismifolia</i>		1		1	
		<i>Senna</i>	<i>bacillaris</i>	3	5		8
	Flacourtiaceae	<i>Banara</i>	sp #1	1		2	3
		<i>guianensis</i>		1		1	
		<i>guianensis?</i>			1	1	
		<i>nitida</i>	1			1	
		<i>Casearia</i>	sp #1	2	1	5	8
			sp #2	1			1
			sp #3			1	1
			<i>sylvestris</i>	1		2	3
		<i>Hasseltia</i>	<i>floribunda</i>	1	6		7
		<i>Neosprucea</i>	sp #1	2	3		5
Lauraceae	<i>Tetrathylacium</i>	<i>macrophyllum</i>		1		1	
	<i>Ocotea</i>	sp #1	1			1	
	Genus #1	sp #1			1	1	
Lecythydaceae	<i>Eschweilera</i>	sp #1					

Table A-5. Continued.

Family	Genus	Species	Plot name			Total	
			Hartensia	Cascada	Centro Semillas		
Melastomataceae	<i>Clidemia</i>	sp #1	1			1	
	<i>Miconia</i>	<i>cercophora</i>			2	2	
		sp #1	1	1		2	
		sp #2	1		2	3	
		sp #3	1	4		5	
		sp #4			2	2	
		sp #5	1	2		3	
		sp #6	1			1	
		sp #7			1	1	
		sp #8			1	1	
		sp #9			1	1	
		sp #10			1	1	
		<i>punctata?</i>		1		1	
		<i>Ossaea</i>	sp #1	1		1	
			sp #2			1	
		sp #3		7	7		
Meliaceae	<i>Cabralea</i>	<i>canjerana</i>			1	1	
	<i>Guarea</i>	<i>kunthiana</i>	1			1	
Mimosaceae	<i>Abarema</i>	<i>jupunba</i>		1		1	
Monimiaceae	<i>Siparuna</i>	<i>decipiens</i>	2			2	
		<i>schimpffii</i>			2	2	
		<i>schimpffii</i>	2			2	
		sp #1			4	4	
Moraceae	<i>Brosimum</i>	sp #1	2			2	
	<i>Ficus</i>	<i>c.f. tonduzii</i>	1			1	
		sp #1			1	1	
		sp #2		1		1	
		<i>Perebea</i>	<i>guianensis</i>	1		1	2
		<i>Pseudolmedia</i>	<i>rigida</i>			1	1
	<i>Trymatococcus</i>	<i>amazonicus</i>	2			2	
Myristicaceae	<i>Virola</i>	<i>sebifera</i>	2	2		4	
		sp #1	1			1	
Myrsinaceae	<i>Parathesis</i>	sp #1			1	1	
Myrtaceae	<i>Myrcia</i>	sp #1	1			1	
		sp #2		1		1	
	Genus #1	sp #1			1	1	
Nyctaginaceae	<i>Neaa</i>	<i>divaricata</i>	1			1	
		sp #1		1		1	
		sp #2		2		2	
		sp #3			2	2	
Piperaceae	<i>Piper</i>	<i>obliquum</i>	5	7	2	14	
		sp #1	2			2	

Table A-5. Continued.

Family	Genus	Species	Plot name			Total
			Hartensia	Cascada	Centro Semillas	
Rubiaceae	<i>Agouticarpa</i>	sp #1			2	2
	<i>Chimarrhis</i>	<i>glabriflora</i> or <i>hookeri</i>			2	2
	<i>Palicourea</i>	sp #1	3		1	4
		<i>subalatoides</i>	1	1	4	6
		<i>Pentagonia amazonica</i>	2	2	1	5
		<i>Psychotria</i>	sp #1		1	1
		Genus #1	sp #1		1	1
Rutaceae	<i>Zanthoxylum</i>	sp #1		1		1
		sp #2		1		1
Sapindaceae	<i>Allophylus</i>	sp #1			1	1
		sp #2			1	1
Solanaceae	<i>Cestrum</i>	<i>megalophyllum</i>		1	2	3
		<i>silvaticum</i>		3		3
	<i>Solanum</i>	<i>grandiflorum</i>	1			1
		sp #1	1			1
		sp #2	1			1
		Genus #1	sp #1		1	1
Sterculiaceae	<i>Herrania</i>	sp #1	1			1
Verbenaceae	<i>Vitex</i>	sp #1				
Total Families			24	22	26	34
Total Genera			33	35	34	69
Total species			40	84	70	129

Table A-6. Numbers of seeds of four tropical tree species that were planted, died as seeds, were alive (sum of live seeds and seedlings), and were live seedlings at 18 weeks under two treatments (surface-planted and buried) in three secondary forest plots in the Ecuadorian Amazon. The five seeds disappeared from planting sites (4 surface-planted *Caryodendron* seeds and one surface-planted *Gustavia* seed), and are included in the total 'Planted'.

Plot name	Treatment	<i>Caryodendron orinocense</i>				<i>Gustavia macarenensis</i>				<i>Inga densiflora</i>				<i>Plinia</i> sp.			
		Planted	Died as seed	Live	Live seedling	Planted	Died as seed	Live	Live seedling	Planted	Died as seed	Live	Live seedling	Planted	Died as seed	Live	Live seedling
Hartensia	Surface, uncaged	16	3	10	10	16	1	14	10	18	1	15	12	20	1	19	6
	Surface, caged	21	2	18	18	17	0	17	13	18	2	16	15	21	4	17	4
	Surface Total	37	5	28	28	33	1	31	23	36	3	31	27	41	5	36	10
	Buried, uncaged	18	5	13	12	14	1	12	7	13	1	12	9	19	5	14	3
	Buried, caged	19	1	18	15	17	0	17	6	15	1	14	14	15	4	11	3
	Buried Total	37	6	31	27	31	1	29	13	28	2	26	23	34	9	25	6
Hartensia total		74	11	59	55	64	2	60	36	64	5	57	50	75	14	61	16
Cascada	Surface, uncaged	18	0	16	15	22	1	21	16	22	1	20	19	24	4	20	8
	Surface, caged	24	3	20	20	21	1	20	20	18	0	17	16	21	6	15	1
	Surface Total	42	3	36	35	43	2	41	36	40	1	37	35	45	10	35	9
	Buried, uncaged	15	0	15	14	15	1	14	7	17	3	14	9	16	9	7	1
	Buried, caged	19	3	14	14	18	3	15	7	16	2	14	9	13	6	7	0
	Buried Total	34	3	29	28	33	4	29	14	33	5	28	18	29	15	14	1
Cascada total		76	6	65	63	76	6	70	50	73	6	65	53	74	25	49	10
Centro Semillas	Surface, uncaged	20	6	11	11	16	0	16	14	16	0	16	16	18	0	18	4
	Surface, caged	21	2	17	17	13	0	13	9	15	0	14	13	17	7	10	2
	Surface Total	41	8	28	28	29	0	29	23	31	0	30	29	35	7	28	6
	Buried, uncaged	20	5	11	15	14	1	13	7	10	1	9	7	13	4	9	3
	Buried, caged	17	4	17	13	15	1	14	12	11	3	8	5	19	9	10	1
	Buried Total	37	9	28	28	29	2	27	19	21	4	17	12	32	13	19	4
Centro Semillas Total		78	17	56	56	58	2	56	42	52	4	47	41	67	20	47	10
Uncaged total		107	19	76	77	97	5	90	61	96	7	86	72	110	23	87	25
Caged total		121	15	104	97	101	5	96	67	93	8	83	72	106	36	70	11
Surface total		120	16	92	91	105	3	101	82	107	4	98	91	121	22	99	25
Buried total		108	18	88	83	93	7	85	46	82	11	71	53	95	37	58	11
Total		228	34	180	174	198	10	186	128	189	15	169	144	216	59	157	36

Table A-7. Comparison between the two seed planting experiments presented in Chapter 2 (2007) and Chapter 3 (2008) of this thesis, in which species of large-seeded tropical forest trees were planted in a variety of human modified landscapes in the Ecuadorian Amazon.

	2007	2008
Species	<i>Inga densiflora</i> , <i>Quararibea cordata</i> , <i>Pouteria caimito</i>	<i>Inga densiflora</i> , <i>Gustavia macarenensis</i> , <i>Caryodendron orinocense</i> , <i>Plinia</i> sp.
Field type	grazed pasture (2 – 6 wks regrowth), mature pasture (3 – 6 mo regrowth), selectively logged forest	10 – 15 yr old secondary forest
Treatments	Surface-planted vs. buried	2x2 factorial, Surface-planted vs. buried, caged vs. uncaged
Indigenous community	3 communities, 14-18 km apart (Kenkuimi, Kunkuki, San Ramon)	2 communities, 5 km apart on Puyo-Macas Rd. (Kunkuki, San Antonio)
Number of plots	9 (3 field types x 3 communities)	3 plots
Distance between plots	14-18 km between communities, 50-500 m between plots	1-5 km between plots
Planting site pre-treatment	Seed planted without removal of surface debris	Surface debris cleared
Planting dates	mid-June 2007	late Feb/early March 2008
Data collected	Seed disappearance, germination, seed/seedling death	Seed disappearance, germination seed/seedling death
Data collection schedule	At 2 & 14 wks (14 wk check by trained assistant)	Biweekly to 18 weeks
Duration of experiment	14 weeks	18 weeks

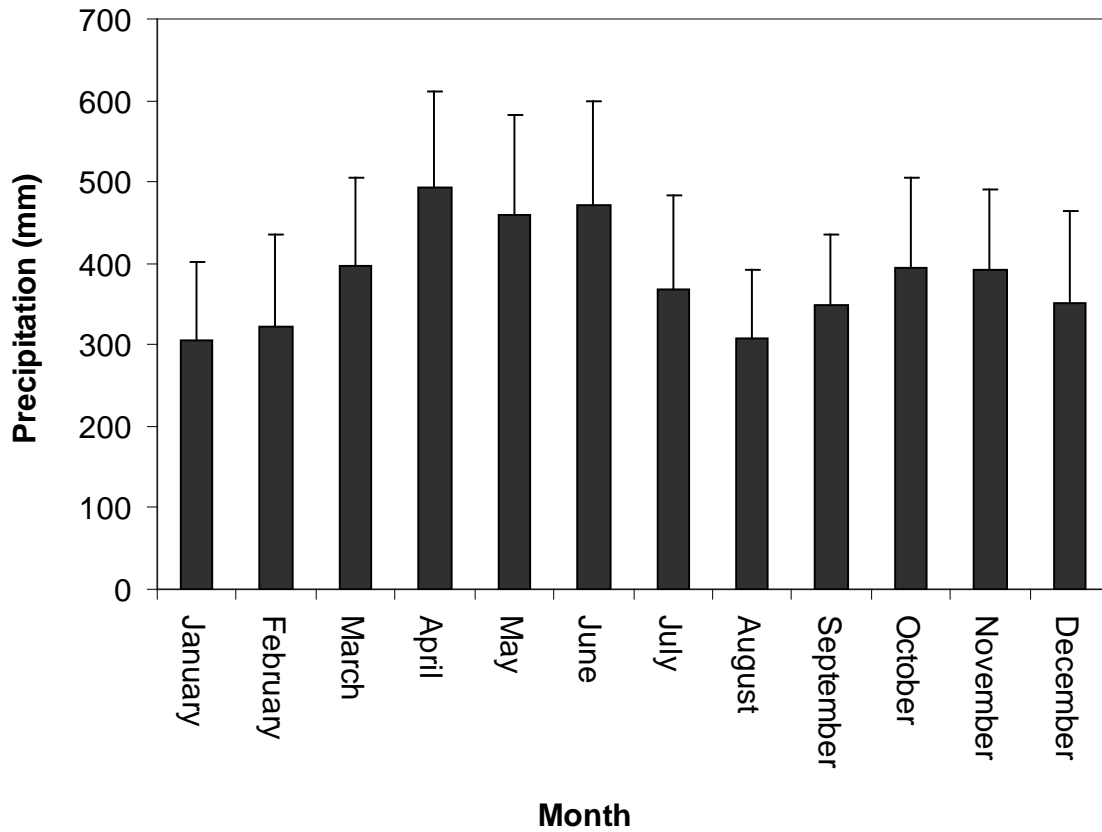


Figure A-1. Average monthly rainfall and precipitation (1974-2007) from the Puyo weather station M008 of the Instituto Nacional de Meteorología en Hidrológica (INAHMI), Pastaza Province, Ecuador (S 1°30'27", W 77°56'38", 960 m). The station is 30-45 km northwest of the experimental plots. Error bars represent 1 S.D.



Figure A-2. Photos of the vegetation in the field plots in three indigenous communities described in Chapter 2 (Figures 2-1 & 2-2). Pictured are “grazed pasture” plots in Kenkuimi (A), San Ramon (B) and Kunkuki (C), “mature pasture” plots in Kunkuki (D) and Kenkuimi (E), a pasture abutting forest in Kunkuimi (F), and “forest” plots in Kunkuimi (G) and Kunkuki (H). The “grazed pasture” plots had 2-6 weeks of vegetation regrowth and the “mature pasture” plots had 3-6 months of regrowth at the time the experiment was established (June 2007).



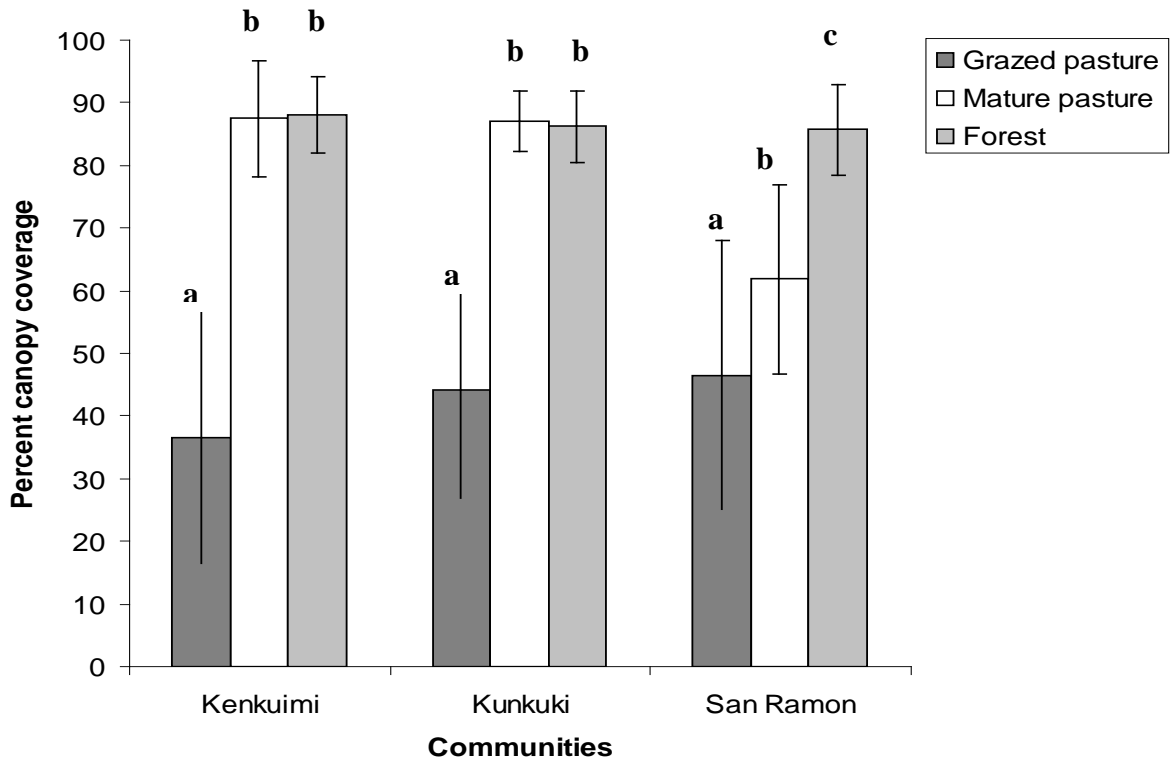


Figure A-3. Average percent canopy cover of three types of field plots (grazed pasture, mature pasture, and forest) in three indigenous communities (Kenkuimi, Kunkuki, San Ramon) in the Ecuadorian Amazon. Percent canopy cover was measured with a handheld spherical densitometer (Robert E. Lemmon Forest Densitometer, Model C) held at ground level at 20 points per plot. Error bars represent 1 S.D. Fields were nested within communities, and letters represent differences between fields ( $n = 3$ ) within each community in pair-wise Bonferroni-adjusted t-test comparisons assuming unequal variances on untransformed data.

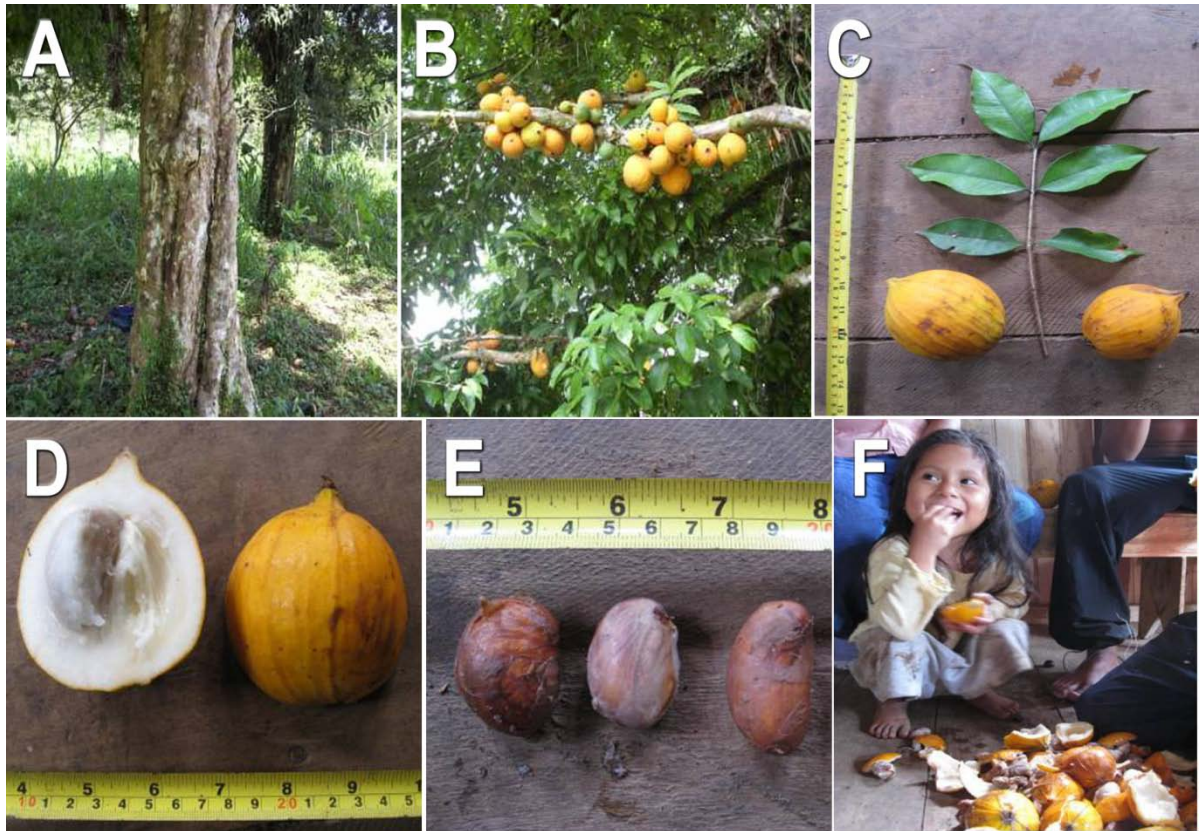


Figure A-4. Photos of the Myrtaceae species planted in the experiment described in Chapter 3. Pictures are photos of the tree trunk (A), branch with fruit (B), leaves and mature fruits (C), longitudinal cut through fruit (D), fresh seeds (E), and consumption of fresh fruits (F). The species was identified (from photos and description) to be in the genus *Plinia* by Bruce K. Holst, Collections Manager of the Marie Selby Botanical Gardens in Sarasota, Florida. Herbarium specimens were deposited in the Herbario Nacional del Ecuador in Quito.

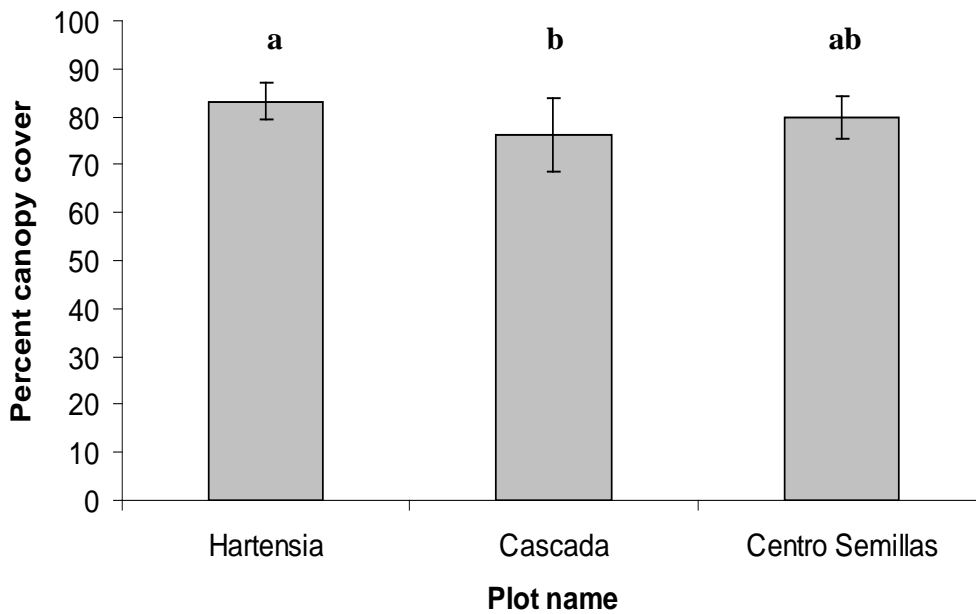


Figure A-5. Average percent canopy cover of three secondary forests measured with a handheld spherical densitometer (Robert E. Lemmon Forest Densitometer, Model C) held at 1 m above ground level at 20 points per plot. Error bars represent one S.D. Percent canopy cover differed among the three plots ( $p = 0.0011$ , ANOVA on arcsine transformed data), and letters in graph show results from Tukey's test.

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## BIOGRAPHICAL SKETCH

Erica Van Etten was born in Ithaca, New York in 1971. She attended Newfield public schools until she left her small hometown to begin college at the University of California at Santa Cruz in 1989. She transferred to Cornell University in 1990 and also attended the S.U.N.Y. Environmental Science and Forestry Ranger School before graduating in 1993 from Cornell with a B.S. in Natural Resource Management.

After graduation, she pursued her interests in forestry and land management in a series of jobs with the National Park Service and National Forest Service in California and Oregon. A visit to Ithaca in the fall and a purchase of lumber at a farm auction led to a move back to upstate NY, where she built a house and continued her work in natural resource management with the County Soil and Water Conservation District.

Passionate about teaching and hands-on learning, Erica then worked for five years at schools and outdoor education programs located on farms in Massachusetts and Vermont. In this work she combined her training in biology and land management with carpentry and farming skills to help students understand how human activities interact with natural ecosystems.

A desire for an international perspective on environmental issues led her to begin travelling and working in Central and South America in 2005. After working 6 months on a restoration project at a biological station in the rainforests of coastal Ecuador, she decided to invest her time in restoration project that worked directly with local landowners. In 2006, she began a reforestation project with indigenous Shuar communities in the Ecuadorian Amazon. After constructing several seedling nurseries, she decided to focus her Masters research on direct seeding, a potentially cheaper and easier method of planting trees than using nursery-grown seedlings. Erica turned over the management of the reforestation project to her Ecuadorian collaborators in 2008.

After completing her master's degree, Erica plans to continue her work in the field of international conservation and management of projects that combine her interests in teaching, research, ecological restoration, and mentorship