AN ABSTRACT OF THE DISSERTATION OF

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Title: Limitations to Seedling Regeneration on Tropical Forest Restoration Plantations in Northern Thailand.

Abstract approved:

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This dissertation investigated potential ecological limitations to seedling regeneration in young, seasonally dry, evergreen forest restoration plantations in northern Thailand. We explored whether recruitment of colonizing tree species in the restoration plantations can be attributed to seed dispersal mode (i.e. abiotic or animal dispersal) and seed size. We did this by determining the distribution of these traits among colonizing seedlings in the understory of 4- to 8-year-old restoration plantation plots and comparing it to the distribution of traits among trees in two reference forests. We found that while the distribution of dispersal modes among colonizing seedlings in the restoration plantations was similar to the distribution of trees in an intact reference forest, there were fewer larger-seeded species among animal-dispersed colonizers than might be expected from the proportion of large- and very large-seeded trees in the reference forest. This supported the hypothesis that seed size limits dispersal and recruitment of large-seeded species in tropical forest restoration. We also conducted a seed sowing experiment that explicitly tested seed and microsite limitations for five large-seeded tree species that were present in nearby forest but had not naturally recolonized the restoration plantations. We sowed seeds belonging to the five species in 13-year-old restoration plantations using four microsite seedbed treatments to simulate some of the conditions that naturally-dispersed seeds may encounter. The treatments included sowing seeds above pre-existing leaf litter and on top of bare

mineral soil, as well as burying seeds below leaf litter and bare mineral soil. We found that seedbed microsite treatments did not limit the germination or establishment of any of the five species. This supported the hypothesis that seedlings of large-seeded species are absent due to inadequate seed availability, rather than inadequate microsite conditions. Finally, we investigated the relationships between microsite variations in environmental conditions (i.e. understory light availability and dry-season soil moisture) and the survival and growth of naturally-recruited seedlings belonging to 13 tree species in 11 – 14-year-old restoration plantations. We found that although most monitored pioneer species had poor growth and survival in the plantation understories, seedlings of intermediate- and late-successional species had high two-year survival and slow but continuous growth. Neither microsite light availability nor dry-season soil moisture were significantly correlated to seedling survival; however, light availability was strongly positively correlated to seedling height and diameter growth. Despite this correlation, statistical models incorporating microsite light availability explained only about a third of the variance in seedling growth. This suggests that additional factors, such as microsite variations in soil nutrients, may also be influential.

This dissertation has several implications for management of tropical forest restoration. Our study of seed dispersal traits among colonizing seedlings underscores the potential importance of dispersal limitations in filtering large-seeded, animal-dispersed tree species from restored forests. Our seed sowing experiment suggests that direct-seed enrichment planting in the understory of restoration plantations may facilitate the recruitment of some large-seeded species. The results of the experiment also suggest that seedbed treatments may be unnecessary for their seedling establishment. High survival of intermediate- and late-successional species in the plantation understories suggests additional management interventions to increase light availability are unnecessary to promote seedling survival, although thinning to increase light may hasten seedling development. Finally, we found that the seedlings of several plantation species (i.e. species planted to establish the restoration plots) regenerate well in the understory and were abundant due to the presence of seed sources on the plots. In order to provide enrichment planted species with a competitive head start over plantation species, the best time to conduct enrichment efforts may be while the plantations are young, before plantation trees have become reproductively mature. This would also allow enrichment planted species to take advantage of high light availability to maximize growth.

Limitations to Seedling Regeneration on Tropical Forest Restoration Plantations in Northern Thailand

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Hathai A. Sangsupan, Author

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Chapter 1 – Introduction to the Dissertation Project

Hathai A. Sangsupan

1. Background

Tropical forests are ecosystems of unparalleled species diversity. Although they cover less than 10% of the Earth's surface, they are home to an estimated half to two-thirds of its species (Raven 1988). Of these there are at least 40,000 tropical tree species (Slik et al. 2015). Over the last half century, however, rampant deforestation has led to the destruction and degradation of hundreds of millions of hectares of tropical forests worldwide (ITTO 2002). The loss of tropical forest habitat has resulted in unprecedented rates of extinctions, with tropical forest species diversity estimated to be declining at a rate of 14,000 – 40,000 species per year (Hughes et al. 1997). Furthermore, tropical forest destruction has created potential extinction debts - pools of species that are likely to become extinct in the near future if habitats are not increased (Tilman et al. 1994).

Habitat loss is especially acute in seasonally dry tropical forests (SDTFs). SDTFs occur in all of the world's tropical regions and originally accounted for approximately 42% of all tropical forest area (Miles et al. 2006). However, due to deforestation and degradation by humans, SDTFs are now considered the Earth's most threatened tropical forest type (Janzen 1988, Miles et al. 2006). These forests are considered distinct from aseasonal tropical moist and rainforest because they experience at least one prolonged season (5 – 6 months) of severe to absolute drought. Seasonal water stress has a profound influence on SDTF dynamics, shaping patterns of growth and mortality, nutrient and water cycling, and the timing of flower, fruit, and leaf phenology (Murphy and Lugo 1986b, Singh and Singh 1992, Dirzo et al. 2011, McShea and Davies 2011). Although species richness in SDTFs is less than in aseasonal tropical rainforest, they contain some of the world's highest diversity of plant functional groups, are home to high concentrations of endemic species, and exhibit the highest beta diversity (i.e. spatial species turnover) of any terrestrial ecosystem (Dirzo et al. 2011).

The worldwide decline of SDTFs is due primarily to agricultural conversion (Murphy and Lugo 1986a, Miles et al. 2006). Today, however, millions of hectares of former tropical forest have been degraded and subsequently abandoned (Murphy and Lugo 1986a, ITTO 2002, Chazdon 2003). These lands represent an opportunity for forest recovery and a safety net for species that might otherwise become extinct (Wright and Muller-Landau 2006). In many instances, natural succession has led to regeneration of forests on abandoned land. Consequently, secondary forests make up approximately half the world's remaining tropical forests (ITTO

2002). In some situations, however, the frequency, scope, and magnitude of anthropogenic disturbance may have pushed former forest systems over an ecological threshold into an alternative stable state (ITTO 2002, Lamb et al. 2005, Chazdon 2014). On these sites soil deterioration, harsh climatic conditions, competition with herbaceous weeds, and the absence of tree seed sources (i.e. nearby remnant forest) may delay or completely prevent natural forest succession (Parrotta et al. 1997, Chapman and Chapman 1999, Elliott et al. 2003).

Under these circumstances, active intervention in the form of ecological restoration may be necessary to overcome barriers to succession and accelerate the recovery of tropical forest structure and function. Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed (SER 2004). Although practitioners may interpret the objectives of ecological restoration in different ways, the primary goal of this approach is to recover as much species composition and structure as possible and to develop a functionally effective, self-sustaining, and natural system (Goosem and Tucker 1995, Lamb 2011). Strategies for accomplishing ecological restoration can take many forms and efforts to develop rapid, low-cost, low-tech tropical forest restoration techniques for abandoned agricultural fields and similarly degraded lands are being independently undertaken in several tropical nations (Lamb et al. 2005, de Souza 2004, Elliott, 2003).

Ecological tropical forest restoration is still a relatively young field, but thus far the most promising results have been achieved by the direct planting of a variety of indigenous tree species at high densities on the effected land (See review in Lamb 2011). When conducted in conjunction with fire prevention, this strategy has been shown to rapidly re-establish forest cover in both former tropical rainforest and SDTF (Tucker and Murphy 1997, Parrotta and Knowles 2001, Elliott et al. 2003, Elliott et al. 2013). By quickly establishing a closed canopy, the plantings shade out weeds, improve soil conditions, and ameliorate the understory microclimate (Goosem and Tucker 1995, Elliott et al. 2003, Lamb et al. 2005). This in turn facilitates the establishment of tree seedlings. Restoration plantations are then dependent on recruitment and establishment of naturally-dispersed seeds from remnant forests and trees to continue the recovery of species composition as most tropical tree species lack soil seed banks (Skoglund 1992, Vazquez-Yanes and Orozco-Segovia 1993) and those with seed banks tend to be weed and pioneer species (Garwood 1989, Chen et al. 2013).

Seedling surveys from young (4 – 22 years old) restoration plantations in Brazil, Australia, and Thailand have documented the development of seedling communities in the understory (Tucker and Murphy 1997, Parrotta and Knowles 2001, Sinhaseni 2008, Lamb 2011). These communities demonstrate that conditions for seedling recruitment improve rapidly following canopy closure. Consequently the identification of unplanted tree seedlings belonging to intermediate and late-successional stages within the communities provides evidence that some tree species are successfully being dispersed into the plantations from outside (Tucker and Murphy 1997, Sinhaseni 2008, Lamb 2011, Bertacchi et al. 2016). Taken together, these findings are an encouraging indication that restoration plantings catalyze the initial stages of natural forest regeneration.

Beyond this, though, little is known about the characteristics and dynamics of tree regeneration in restoration plantations. However, natural succession in tropical forests following intense disturbance indicates that while recovery of the ecosystem is restricted in part by physical and abiotic factors, ecological filters play a critical role in regulating which species colonize and the order of colonization. These filters include constraints on the arrival of seeds in the system as well as environmental factors that might prevent the establishment and maturation of seedlings that reach the forest. They may have profound effects on the trajectory of forest development. Their impact is demonstrated in the apparent development of alternative states in some secondary tropical forests. These forests retain distinctly different floristic assemblies from their corresponding primary forests decades after the initial disturbances have ceased (Aide et al. 2000, Chazdon 2003, Brearley et al. 2004, Chua et al. 2013).

2. Dissertation Project

To develop strategies that avoid or minimize the development of alternative pathways of succession in restored tropical forest, practitioners require an understanding of how ecological filters may impede community assemblage in the restoration setting. This dissertation addresses this need by investigating potential ecological filters to seedling regeneration in young Thai seasonally dry evergreen forest (SDTF) restoration plantations. Here I provide an overview of the investigations described in the following three chapters followed by a description of the study site.

2.1 Dispersal Traits of Colonizing Tree Seedlings

Restoration plantations rely primarily on natural seed dispersal to re-assemble the forest's original tree composition; however, distance from the intact forest and the loss of large frugivores may favor recruitment of abiotically-dispersed species and smaller-seeded, animal-dispersed species over animal-dispersed species with larger seeds. Reduced recruitment of larger-seeded, animal-dispersed trees may have consequences, both for regeneration of these species and for the composition, structure and ecological functioning of the restored forest. In Chapter 2 we investigate whether recruitment of colonizing tree species in recently restored tropical forest can be attributed to dispersal mode (i.e. abiotic or animal dispersal) or seed size. We also determine the distribution of these traits among colonizing seedlings in 4- and 8-year-old restored forest plots, in Northern Thailand and compare them to the distribution of traits among species and trees in two intact reference forests. Finally, we investigate the potential impact of early seedling composition on future stand composition, by using the distribution of dispersal traits among seedlings in the restored forest to project the future distribution of dispersal traits among large trees (≥ 10 cm diameter at breast height).

2.2 Recruitment Microsite Limitations of Large-seeded Trees

Delayed recovery of floristic composition in many secondary forests is due in part to slow recolonization by large-seeded, animal-dispersed tree species (Aide et al. 2000, Chazdon 2003, Brearley et al. 2004, Chua et al. 2013). Limited seed-dispersal is the likely cause of delayed recolonization of large-seeded trees in both actively-restored and naturally-regenerating tropical forest (Lamb 2011, Chazdon 2014, Reid et al. 2015). However, dispersal of seeds into deforested areas alone does not guarantee recruitment. Establishment (i.e. germination and seedling survival) may also be limited by the availability of microsites with suitable abiotic conditions (Guariguata and Ostertag 2001). In Chapter 3 we describe the results of an experiment that explicitly tested seed and microsite limitations for large-seeded tree species that have failed to naturally recolonize young restoration plantations, despite being present in nearby forest. We also explore the relationship of light availability and soil water content with seedling survival during the first dry season. Finally, we discuss the implications of the results of this investigation for future management of restored tropical forests.

2.3 Seedling Dynamics in Response to Limiting Environmental Factors

Recruitment of a diverse seedling community, though necessary, is only the first step in the re-assembly of the tropical forest ecosystem. During the seedling stage, habitat filtering, the non-random survival of individuals as a result of variations in habitat characteristics, is strongest (Baldeck et al. 2013). In addition to survival, variations in habitat characteristics may also limit seedling growth and maturation, resulting in long-term understory repression. Over time, species filtering and seedling repression may be as consequential to the trajectory of forest development as initial seedling recruitment. In Chapter 4 we describe a two-year observational study that characterizes seedling dynamics (i.e. the survival and growth) for thirteen naturally-recruited seedlings in 11 – 14 year restoration plantations and investigates the effect of microsite variations in light and dry season soil moisture on seedling dynamics. Since the monitored species spanned a range of functional groups and included species recruited from both inside and outside of the plantations, this study also looked for patterns that might increase our understanding of regeneration strategies used by these groups. Finally, we discuss the potential management implications suggested by our results and observations.

3. Study Site

The field portion of this study was conducted on 11 – 14 year old experimental forest restoration planting plots in Doi Suthep-Pui National Park (DSNP), Northern Thailand. The study site was originally covered with seasonally dry, evergreen forest (EGF). This forest type is sometimes also referred to as lower montane forest (Bunyavejchewin et al. 2011) or hill evergreen forest (Gardner et al. 2007). As the name suggests, the majority of EGF trees are evergreen (73% in DSNP). Many SDTFs in Southeast Asia are evergreen which contrasts with the primarily deciduous SDTFs in other regions (Champion and Seth 1968, Murphy and Lugo 1986a). Seasonal evergreen forests throughout Southeast Asia are characterized by high species richness (Bunyavejchewin et al. 2011), and of DSNP's six forest types, EGF supports the most tree species (≥ 250) and contains the largest number of rare and endangered plant species restricted to a single forest type (Maxwell and Elliott 2001). EGF also has the tallest (≥ 30 m) and densest canopy. Although no single species or genus dominates this forest type, many of the characteristic canopy trees belong to the Lauraceae, Moraceae, and Fagaceae families.

Throughout Southeast Asia, deforestation and degradation of EGF has been widespread due in part to its relatively fertile soils (Bunyavejchewin et al. 2011). Much of DSNP's EGF has also been cleared for cultivation; making it the park's most endangered forest type. The restoration plantation plots under consideration were cleared for farming over two decades prior to restoration planting. The land was later abandoned due to declining fertility and became dominated by herbaceous weeds (Elliott et al. 2000).

The forest restoration plantation plots are located along or immediately below the ridge of a watershed (1,207 – 1,310 m above mean sea level). At the time of this investigation, most of the slopes below the plots were still being cultivated to provide income and subsistence for the residents of Ban Mae Sa Mai, a Hmong village community (population of about 1,700) within park boundaries (Neef et al. 2004), approximately 2 km south of the experimental blocks (18º52´N, 98º51´E). The nearest extensive patch of intact, primary EGF is approximately 1 – 2 km east of the plots.

Average annual precipitation at the elevation of the forest restoration plots is 2,095 mm (as recorded by the Kog-Ma Watershed Research Station, the weather station nearest to the plots) and virtually all rainfall occurs during the six-month wet season that extends from May through October. Precipitation averages less than 100 mm per month during the dry season from November to April (Elliott 2003). While the overall volume of rainfall places the study site at the moist end of the precipitation spectrum for seasonally dry tropical forests as defined by several authors (Miles et al. 2006, Dirzo et al. 2011); this paper adopts the broader definition of SDTF used by Bunyavejchewin et al. (2011) which includes all forests that exhibit dynamics (e.g. flower, fruit, and leaf phenology as well as growth and mortality) synchronized with seasonal drought.

In 1997, Chiang Mai University's Forest Restoration and Research Unit (FORRU) began establishing experimental forest restoration plots at the research site to test and refine the Framework Species Method (FSM) for EGF restoration. Since that time, FORRU has added new plots annually. The FSM employs mixed plantings of 25 – 30 species of hardy, fast-growing native trees planted at a density of approximately 3,125 trees ha^{-1}. Canopy closure in the plantations is usually complete within four years of planting (Anusarnsunthorn and Elliott 2004, FORRU 2005). At the start of this investigation, the oldest plantation plots had begun to develop a dense two-layered canopy (Wydhayagarn et al. 2009). Additional details regarding the planting, maintenance, and monitoring of the plots can be found in Elliot et al. (2003).

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Chapter 2 – Dispersal Traits of Colonizing Tree Seedlings in Northern Thai Tropical Forest Restoration Plantations

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ABSTRACT

Distance from intact forest and the loss of large frugivores may favor recruitment of abiotically-dispersed and smaller-seeded, animal-dispersed species over large-seeded animal-dispersed species in tropical forest restoration plantations. We investigated whether colonization of tree species on 4- and 8-year-old restoration plantation plots in northern Thailand can be attributed to dispersal mode (i.e., abiotic or animal dispersal) and seed size. We compared the distribution of dispersal traits among colonizing seedlings to the distribution of dispersal traits among trees in two intact reference forests. We also explored the potential impact of seedling species composition on future stand composition, by using the distribution of dispersal traits among seedlings in the restoration plantations to project the future distribution of dispersal traits among mature trees (≥ 10 cm diameter at breast height). Most colonizing seedlings in the restoration plantations were animal-dispersed, and the percentages of species and seedlings that were animal-dispersed were similar to the percentages of animal-dispersed species and trees in the reference forests. This contrasts with previous studies that report increasing abiotic (i.e. wind or mechanical) seed dispersal with increasing separation and distance from intact forest. However, only 4% of colonizing, animal-dispersed seedlings in the plantations grew from seeds > 10 mm in length, while more than half of the overall population of trees in a reference forest had seeds > 10 mm. This supports the hypothesis that dispersal limitations due to large seed size are an ecological species filter in restored forest plantations. We projected that the future forest will have a similar number of animal-dispersed trees as the reference forest, but almost 80% fewer medium- and large-seeded (10 – 25 mm long) trees. Trees with very large seeds (> 25 mm long) will be almost entirely composed of the offspring of three very large-seeded plantation species (i.e. species planted to establish the plantations). By our projection, colonizing trees with very large seeds will be very rare (< 1 tree ha^{-1}).

1. Introduction

Over the last half century, rampant deforestation has led to the destruction and degradation of hundreds of millions of hectares of tropical forests worldwide (ITTO 2002). Much of this deforestation has been for agricultural conversion (Murphy and Lugo 1986, Miles et al. 2006). The loss of tropical forest habitat has resulted in unprecedented rates of extinctions, with tropical forest species diversity estimated to be declining at a rate of 14,000 – 40,000 species per year (Hughes et al. 1997). Yet millions of hectares of agricultural land are also being abandoned due to declining soil productivity (Murphy and Lugo 1986, ITTO 2002, Chazdon 2003). These lands could provide opportunities for tropical forest recovery; a safety net that prevents extinction of some of the forest-dependent species that are currently threatened by habitat loss (Martínez-Garza and Howe 2003, Chazdon et al. 2009). However, succession on abandoned lands may proceed along different trajectories, depending on local and landscape-level environmental conditions and the scale, duration, and intensity of previous land use (Chazdon 2003).

In some cases, advanced soil deterioration, harsh climatic conditions, competition from herbaceous weeds, and the absence of tree seed sources delay or completely prevent re-establishment of forest trees (Parrotta et al. 1997, Chapman and Chapman 1999, Elliott et al. 2003). In 2002 The International Tropical Timber Organization (2002) estimated that there were over 350 million hectares of formerly forested tropical land that could no longer support the spontaneous regeneration of forest. On these lands, active intervention may be required to overcome barriers to succession and prevent conversion of abandoned land into less desirable stable states, such as open forest or savanna (Khurana and Singh 2001). Rapid, low cost, low technology reforestation techniques are being developed in several tropical countries (Lamb et al. 2005, de Souza 2004, Elliott, 2003). The most commonly employed strategy involves planting native tree species that have been selected for high survival and growth rates under harsh conditions. As the trees mature, their crowns rapidly shade out competing herbaceous species and gradually improve soil conditions, thus ameliorating the understory microclimate and facilitating the establishment of shade tolerant tree species. After canopy closure, recovery of the species composition of the tree community and increases in species richness depends on seed dispersal from nearby remnant forest into the restoration site. At this stage, barriers that hinder seed dispersal and seedling establishment often determine floristic community assembly.

While there is some evidence that natural seed dispersal is responsible for increases in species richness and diversity in the understory seedling community (Sinhaseni 2008, Lamb 2011, Bertacchi et al. 2016), little is known about the extent to which the species composition of the community may be influenced by limitations due to seed-dispersal traits. The majority of tropical tree species rely on birds and mammals for seed dispersal (Howe and Smallwood 1982) and are therefore negatively affected by long distances and disconnection from intact forest, which inhibit dispersal by forest animals (Cordeiro and Howe 2001). Furthermore, dispersal opportunities decline with increasing seed size (Wheelwright 1985, Kitamura et al. 2002). Whereas frugivores of all body sizes can swallow small seeds, only the larger species can swallow and disperse larger seeds. Worldwide, large frugivorous species (e.g. elephants, rhinos, wild cattle, bears, hornbills, large fruit bats etc.) are declining, due to hunting, habitat loss and forest fragmentation (Corlett 2007, Peres and Palacios 2007, Effiom et al. 2013). In human-dominated landscapes where abandoned agricultural fields are most common, large frugivores have been largely extirpated (Sodhi et al. 2004, Harrison 2011). In such areas, larger-seeded trees have reduced dispersal distances and poor recruitment relative to areas where large frugivore populations persist (Chapman and Onderdonk 1998, Wright and Duber 2001, Brodie et al. 2009, Terborgh et al. 2011, Wotton and Kelly 2011), while tree species with abiotically-dispersed (i.e., wind- or mechanically-dispersed) seeds or small animal-dispersed seeds appear to proliferate (Wright et al. 2007, Terborgh et al. 2008). This suggests that dispersal limitations reduce representation of large-seeded trees in tropical forests. This may have consequences for future forest structure since large-seeded, animal-dispersed trees are more likely to be long-lived, late-successional, shade tolerant species that are able to regenerate in the forest understory (see review in Leishman et al. 2000). The ecological function of the forest may also be affected since large-seeded trees tend to grow larger and develop denser wood than small-seeded species, resulting in higher CO_2 fixation and storage (Osuri and Sankaran 2016). Ultimately, the failure of large-seed tree species to regenerate will increase their likelihood of extinction (Brodie et al. 2009, Wotton and Kelly 2011, Caughlin et al. 2014).

Abiotically-dispersed tree species may have fewer dispersal limitations than animal-dispersed species. Thus wind-dispersed species are often over-represented in the early stages of succession on abandoned fields (Aide et al. 1996, Holl 1999, Muñiz-Castro et al. 2012). However, high dispersal does not always result in high recruitment. In some abandoned fields and early successional forests the proportion of wind-dispersed species among seedlings and saplings is far lower than the proportion of wind-dispersed seeds in seed rain (Ingle 2002, Teegalapalli et al. 2010). This suggests effective seed dispersal may be far lower than actual dispersal. In these cases, the greater success of animal-dispersed species, compared with abiotically-dispersed species, may be due to remaining animal dispersers disproportionately depositing animal-dispersed seeds on sites favorable to survival.

Cole (2010b) reported that most seeds arriving at a 1.5 – 4 year-old restored forest were wind-dispersed, but five years later Reid (2015) found a much greater proportion of animal-dispersed seeds in the same forest. This suggests that dispersal-limitations decline over time; however, not for all species. Large seeds were still poorly represented in the restoration site compared with the reference forest (Reid et al. 2015). Even if dispersal limitations for all animal-dispersed species, small and large, were to decrease as the restored forest matured, the order of species arrival may also determine the long-term trajectory of forest development. Small-seeded animal-dispersed and abiotically-dispersed species recruited from early seed rain may inhibit the recruitment and maturation of late-arriving species until the initial colonizers senesce and gap dynamics permit late-arriving species in the understory to mature (Finegan 1996, Chazdon 2008). The impact of initial limits on dispersal may remain evident in the restored forest ecosystem for decades to come.

To date no studies have determined whether dispersal mechanism or seed size affects tree species recruitment in recently restored tropical forest. In this paper, we addressed this gap by investigating whether recruitment of unplanted, colonizing tree species in recently restored tropical forest can be attributed to dispersal mode (i.e. abiotic or animal dispersal) or seed size. We determine the distribution of these traits among colonizing seedlings in 4- and 8-year-old forest restoration plantation plots, in Northern Thailand, compared with the distribution of these traits among trees in two intact reference forests. We also investigated the potential impact of early seedling composition on future stand composition, by using the distribution of dispersal traits among seedlings in the restored forest to project the future distribution of dispersal traits among large trees with diameter at breast height (dbh) ≥ 10 cm.

2. Study Site

This investigation focuses on the distribution of dispersal traits among naturally-recruited seedlings on six 0.16 ha experimental forest restoration plantation plots located along or immediately below the ridge of a watershed (1,207 – 1,310 meters above sea level (mamsl)) in Doi Suthep-Pui National Park National Park (DSNP), Northern Thailand. Covering an area of 261 km^2, the DSNP encompasses one north-south aligned granitic mountain, rising to 1,685 m elevation (Maxwell and Elliott 2001). The plantation plots were located along or immediately below the upper ridges of a degraded watershed (1,207 – 1,310 m elevation), within the Mae Sa Valley at the northern end of the park.

The site of the restoration pots was originally covered with seasonal evergreen forest (EGF). EGF is the most diverse of DSNP's six forest types. EGF supports over 250 tree species (~75% of which are evergreen) and contains the largest number of rare and endangered plant species restricted to a single DSNP forest type (Maxwell and Elliott 2001). However, much of the DSNP's EGF has been cleared for cultivation making EGF also the park's most endangered forest type.

The original forest at the study site had been cleared at least 30 years prior to this investigation (Elliott et al. 2003). After clearance the area went through several cycles of burning, cultivation, and fallow before being abandoned. When the restoration plantation plots were established in 1998 and 2000 (8 and 4 years prior to this investigation) the site was dominated by weedy herbs, including ubiquitous grasses (e.g. *Phragmites vallatoria* (Pluk. ex L.) Veldk., *Imperata cylindrica* (L.) P. Beauv. var. *major* (Nees) C.E. Hubb. ex Hubb. & Vaugh. and *Thysanolaena latifolia* (Roxb. ex Horn.) Honda (Gramineae)), Compositae herbs (e.g. *Ageratina adenophora* (Spreng.) R.M.King & H.Rob., *Chromolaena odorata* (L.) R.M.King & H.Rob. and *Bidens pilosa* L. var. *minor* (Bl.) Sherf,) and bracken fern (*Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae).

The Forest Restoration and Research Unit (FORRU) of Chiang Mai University established the 8- and 4-year-old restoration plantation plots as two groups (one group for each year) of three replicate plots. The plots were planted to test and refine the Framework Species Method (FSM) of forest restoration for EGF forest (sensu Goosem and Tucker 1995). The FSM seeks to accelerate the process of forest succession on degraded land by using mixed plantings of 25–30 species of hardy, fast-growing, indigenous trees to create a canopy that shades out competing grasses and herbaceous weeds and moderates the understory climate for colonizing tree seedlings (Goosem and Tucker 1995, Elliott et al. 2003, Lamb et al. 2005). After canopy closure, the FSM relies on natural seed dispersal from outside of the plantations to increase tree species diversity within the plantations as most tropical tree species lack soil seed banks (Skoglund 1992, Vazquez-Yanes and Orozco-Segovia 1993) and those with seed banks tend to be weed and pioneer species (Garwood 1989, Chen et al. 2013).

FORRU established the 8-year-old restoration plots with a mixture of 29 tree species and the 4-year-old restoration plots with a mixture of 30 tree species. Due to differences in seedling availability between the different planting years, the species compositions of the planting mixtures varied somewhat between the different aged plots, but 13 species were planted in both mixtures. All plots were planted at a density of 3,125 trees ha^{-1}. Canopy closure was mostly complete within four years after tree planting (Anusarnsunthorn and Elliott 2004, FORRU 2005) and a dense two-layered canopy was present in the 8-year-old plots at the start of this study (Wydhayagarn et al. 2009).

Each of the three 8-year-old plots was separated from its nearest neighboring replicate plot by at least 0.7 km. The land between the plots included older and younger restoration plantations, small secondary forest patches, and agricultural land. The three 4-year-old plots, however, were planted in a continuous row. This row was separated from the nearest 8-year-old plot by about 0.2 km. Additional details regarding the planting, maintenance and monitoring of the plots can be found in Elliot et al. (2003).

At the time of this investigation in 2006, most of the slopes below the plots were still being cultivated for corn, cabbages and litchi by the residents of Ban Mae Sa Mai, a Hmong village community, 2 – 3 km northeast of the plots (18º52´N, 98º51´E). The nearest large patch (>100 ha) of less disturbed EGF was the community’s sacred forest, Pah Dong Saeng, situated 1 – 3 km to the east for the forest restoration plots, although some much smaller remnants of secondary forest were sparsely scattered throughout the area, particularly on the steeper ridges. These provided potential seed sources for natural forest regeneration. Fruit bats and birds, especially bulbuls (Chanthorn, 1999), were the most likely vectors of very small to medium-sized seeds (≤ 15 mm in length) from forest into the plots, although remnant populations of larger animals (e.g. Common Barking Deer, Common Wild Pig, Hog Badger and civets) may also play a role in long-distance seed dispersal. Animal dispersers of the largest seeds (> 25 mm in length) such as hornbills, Asian elephants, wild cattle, and rhinoceroses were extirpated from the national park in the 1960s. Natural recruitment of some wind-dispersed trees (e.g. *Schima wallichii* Choisy and *Dipterocarpus costatus* C.F. Gaertn.) (pers. obs.) into the plots suggests that wind also disperses seeds from nearby forest remnants into the plots over distances of as much as several kilometers.

Average annual precipitation at the elevation of the plots is 2,095 mm (as recorded by the Kog-Ma Watershed Research Station, the weather station nearest to the plots){Elliott, 2003 #5}, with virtually all rainfall occurring during the six-month wet season that extends from May through October. During the dry season (from November to April) precipitation averages less than 100 mm per month (Elliott 2003).

This investigation compared the distribution of seed dispersal traits among seedlings in the forest restoration plantation plots with the distribution of seed dispersal traits among trees in intact Doi Suthep EGF (hereafter, DS-EGF) and a 50-ha forest dynamics plot in Huai Kha Khaeng Wildlife Sanctuary, located in west-central Thailand (15°40’ N, 99°10’ E), approximately 500 km south of DSNP. The Huai Kha Khaeng (HKK) forest dynamics plot (hereafter, HKK-FDP) is part of a global network of large-scale demographic forest plots, established by the Center for Tropical Forest Science (CTFS). It is situated in seasonal evergreen forest (Bunyavejchewin et al. 2001). Like DSNP, the climate of HKK is seasonal, with a six-month dry season November to April; however, the elevation of the HKK (549 – 638 mamsl) is lower than that of the restoration plots and the area receives less precipitation (1,500 mm per year). Also in contrast to DSNP, HKK is home to many large seed-dispersers, including hornbills, wild cattle, bears, and elephants (Chimchome et al. 1998, Bunyavejchewin et al. 2001).

3. Methods

3.1 Seedling Survey

Between 2006 and 2007, Sinhaseni (2008) surveyed tree seedling abundance and diversity within the six restoration plots. The plots were initially chosen to compare differences in seedling recruitment across different aged plantations; however, the abundances of colonizing EGF species in the 8- and 4-year-old plots was similar (388 seedlings/942.5 m^2 and 402 seedlings/942.5 m^2, respectively). For this investigation we chose to combine the seedlings in both sets of plots to maximize the number of sampled seedlings for the creation of dispersal trait distributions.

Four 10 m diameter circular sampling subplots were established in each restoration plot, one circular subplot in approximately the center of each plot quarter (78.54 m^2/subplot, totaling 24 subplots, covering approximately 0.19 ha). The survey was carried out three times: i) during the 2006 monsoon season (May-September), ii) during the 2006 dry season and iii) during the 2007 monsoon season (Sinhaseni 2008). Seedlings of all woody plant species (defined as juveniles shorter than 100 cm) were tagged, counted, and identified to species to monitor recruitment and mortality. However, our analysis, as reported here, is limited to seedlings or saplings of trees or treelets (as in "Vegetation and Vascular Flora of Doi Sutep-Pui National Park, Northern Thailand," (Maxwell and Elliott 2001); the most complete record of DSNP's flora, enumerating 2,247 vascular plant species collected and identified from DSNP from 1987 to 2000). We define the number of seedlings recruited of each species as the sum of the seedlings identified over the three survey sampling events ignoring mortality.

We categorized surveyed species as EGF or non-EGF based on whether or not the range of forest habitats for each species listed in Maxwell and Elliott (2001) included EGF. Furthermore, we assumed that all seedlings belonging to species that were planted to establish a restoration plantation plot were the offspring of the plantation trees (hereafter, "plantation seedlings") rather than colonizing species from outside of the restoration plots.

We also derived a complete list of tree and treelet species for DS-EGF across the entire national park from Maxwell and Elliott (2001). The HKK-FDP tree and treelet species and abundance data for trees ≥ 10 cm dbh are from a 1999 survey of the entire 50 ha plot, conducted by the CTFS (Bunyavejchewin et al. 2009)

We used information from academic literature, field guides, online botanical databases and FORRU's research database to categorize tree and treelet species by dispersal mode and to obtain seed sizes for animal-dispersed species. Animal-dispersed species were categorized as those with fleshy and/or colorful fruits, mimetic seeds, or edible nuts. Abiotically-dispersed species were categorized as those that rely on gravity or ballistic dehiscence for dispersal, as well as species with winged seeds/fruits indicative of wind dispersal. When the dispersal mode was in doubt, we searched for literature documenting the dispersal mode for either the species in question or closely related species within the same genus.

We further categorized animal-dispersed species by seed size according to the ranges in Table 2.1. We assigned size categories using the measurement of the largest available dimension, usually length. Comparing seed length alone may be justified as length is closely related to width for tropical tree species (Peres and van Roomalen 2002).

Table 2.1 Seed dispersal mode and seed size categories, abbreviations for dispersal modes and seed sizes, and measurement ranges for animal-dispersed size categories.

Dispersal and size category	Abbreviation	Largest seed dimension (mm)
Abiotically-dispersed	Abiotic	n/a
Animal-dispersed	Animal	n/a
Very small	VS	≤5.0
Small	S	5.1 to ≤10.0
Medium	M	10.1 to ≤15.0
Large	L	15.1 to ≤ 25.0
Very large	VL	>25.0

Information on seed measurements was unavailable for roughly 30% of the animal-dispersed tree species. In many instances we were able to infer seed size category from available fruit size information. For example, we assumed that species with fruit measuring less than 5 mm in width and length must also have seeds smaller than 5 mm in both of those dimension. We therefore categorized these species as VS-seeded. Furthermore, seed sizes across species for some genera are very similar (e.g. *Ficus* spp. generally have seeds with length < 2 mm). Thus we assumed that all species within those genera fell into the same seed size categories. For a few species, we estimated seed size from photographs and illustrations of seeds that featured scale bars. Finally, in a few instances where scale bars were absent, we used fruit size measurements to provide scale for estimating seed sizes in photographs juxtaposing fruit and seed. A complete listing of all tree species and their seed size categories is provided in Appendix A of this dissertation.

3.2 Analysis

3.2.1 Comparing Dispersal Trait Distributions

In this investigation, we compared the percent frequency distributions of dispersal modes and seed sizes among colonizing tree and treelet species on restoration plots with the that of trees in DS-EGF and HKK-FDP (for trees ≥ 10 cm dbh). We also compared the percent abundance of dispersal traits among colonizing tree and treelet seedlings on the restoration plot, irrespective of species, to that of trees ≥ 10 cm dbh in the HKK-FDP. DS-EGF was not included in this comparison, as species abundance data for DS-EGF were unavailable**.**

Direct comparisons between colonizing seedlings in the restoration plots and seedlings in the reference forests were not possible because corresponding seedling survey data for the reference forests did not exist. The availability of tree species lists for DS-EGF and HKK-FDP and abundance data for HKK-FDP, however, enabled approximate comparisons of dispersal trait distributions that, though not completely analogous, may still be useful for exploration of dispersal limitations.

3.2.2 Projection

For this projection, we assumed that at an unspecified future date, the population of large trees (≥ 10 cm dbh) in the restoration plots will be comprised entirely of colonizing EGF trees and the offspring of plantation trees. We also assumed that the stand density of trees ≥ 10 cm dbh in the restored forest will be 437.5 trees ha^{-1}, equivalent to the stand density reported for HKK-FDP in a 1999 survey (Bunyavejchewin et al. 2004). This stand density is equivalent to 6.8% of the seedling density (6,837 seedlings ha^{-1}) on the restoration plots as measured by the seedling surveys (Sinhaseni 2008).

In the absence of long-term survival data for any of the seedlings, we assumed that rates of survival and growth are equivalent among species and that 6.8% is the percent probability that a recruited seedling will survive and mature to ≥ 10 cm dbh in the restored forest.

To estimate the number of trees from a given classification that will recruit and survive to attain sizes ≥ 10 cm dbh on a hectare of restored forest, we multiplied 0.068 by the number of recruited seedlings for each trait category (third column of Table 2.2) and then divided by 0.19 ha. We compared the projected abundance distributions of dispersal modes and seed sizes against that of trees ≥ 10 cm dbh in HKK-FDP. DS-EGF was not included in this comparison as species abundance data for DS-EGF were unavailable**.**

4. Results

4.1 Trait Categorization

The dispersal modes of nearly all tree species at all sites (forest restoration plots, DS-EGF, and HKK-FDP) were successfully assigned. Maxwell and Elliott (2001) list 340 tree and treelet species as growing in evergreen forest across the national park (250 trees, 90 treelets; Table 2.2). A 1999 survey of the CTFS plot recorded 240 tree species with dbh ≥ 10 cm at HKK-FDP, although species was not identified but rather listed as “unknown.” Using published fruit and seed descriptions, we assigned seed dispersal modes to all tree/treelet species in the restoration plots, DS-EGF, and to all but the unknown species in the HKK-FDP plot.

Of the animal-dispersed species, we categorized the seed size of 68.7% of EGF and 54.7% of HKK-FDP species, using available seed measurements, and an additional 28.1% of DS-EGF species and 40.4% of HKK-FDP species, using fruit size information, genus characteristics, and/or photographs. We could not determine the seed size categories of nine DS-EGF species (3.2%) and 11 HKK-FDP species (4.9%), assumed to be animal-dispersed based on their genera traits.

Sinhaseni (2008) identified 56 colonizing tree and treelet species (972 seedlings) in FORRU’s forest restoration plots, of which 38 (64.3%) were listed as characteristic EGF species (Maxwell and Elliott 2001, Sinhaseni 2008). Two additional colonizing species, not listed in Maxwell and Elliott, were assigned as EGF species, using information from Gardner et al. (2007) and FORRU (personal communication). Eighteen colonizing species (182 seedlings) had not previously been recorded as growing in EGF, at the time of the survey, but had been recorded as growing in other forest types within the national park (Maxwell and Elliott, 2001). In addition to the colonizing seedlings, the survey of the restored forest plots identified 508 seedlings of 17 plantation species. We were able to categorize the dispersal modes of all identified seedlings in the restored forest plots by using seed measurements, fruit measurements or generic traits.

4.2 Reference Forests

4.2.1 Dispersal traits across species

The percent frequency of dispersal traits among tree species was similar in both DS-EGF and HKK-FDP (Figures 2.1a and 2.1b). Most tree species in both reference forests were animal-dispersed (81.8% for DS-EGF and 74.6% for HKK-FDP). Although seed lengths of animal-dispersed species ranged from < 2 mm (e.g. *Ficus spp.*) to greater than 35 mm (e.g. *Mangifera spp.*), the frequency of seed sizes across animal-dispersed species was skewed towards S and VS seeds (with lengths ≤ 10 mm). Consequently, the majority of species in both references forests possessed either S or VS seeds (57.9% for DS-EGF and 55.9% for HKK-FDP; Table 2.2, Figure 2.1). The frequency of species with larger seeds declined with increasing seed size in both forests, such that VL-seeded species made up only 7.9% of animal-dispersed EGF species and 8.4% of animal-dispersed HKK species.

4.2.2 Dispersal traits across trees, irrespective of species

In HKK-FDP 79.7% of all trees (dbh ≥ 10 cm), irrespective of species, were animal-dispersed (Table 2.2, Figure 2.1c). This was similar to the percent frequency of dispersal modes across species. Tree abundances in HKK-FDP, however, were more evenly distributed across seed size categories than were species. M-seeded trees were the most abundant seed size category (36.0% of trees), despite making up just 19.0% of all tree species. The next most abundant seed size categories were S-seeded trees (32.9%), followed by L-seeded trees (24.1%), VS-seeded trees (3.3%), and VL-seeded trees (2.3%). VL-seeded species were generally rare (fewer trees per species, Table 2.2) compared to all size categories except the VS-seeded species. Although there were more than twice as many VS-species as VL-seeded species, on average VS-seeded species had fewer trees per species.

4.3 Colonizing Seedlings

4.2.3 Dispersal traits across species

In the restored forest plots, 75.0% of colonizing EGF species were animal-dispersed, a percentage roughly equal to the percentage of animal-dispersed tree species in the HKK-FDP, though slightly less than the percentage of animal-dispersed tree species in DS-EGF (Figure 2.1a). The S- and VS-seeded species comprised 73.3% of colonizing, animal-dispersed EGF species. This was > 15% larger than the percentage of animal-dispersed tree species that were S- and VS-seeded in either of the reference forests. VL- species, on the other hand, comprised a smaller percentage (3.3%) among colonizing EGF species than among trees species in either of the reference forests. Moreover, the percentage of VL-seeded colonizing EGF species belies the fact that the size category consisted of only one species, *Beilschmiedia assamica*, which was present as a single seedling.

4.2.4 Dispersal traits across seedlings, irrespective of species

Animal-dispersed seedlings were 84% of colonizing EGF seedlings, irrespective of species (Table 2.3, Figure 2.1c). Of the animal-dispersed seedlings, 96.4% were S- or VS-seeded. M- and L-seeded seedlings were nearly equal in number and together comprised 3.4% of seedlings. The single VL-seeded animal-dispersed seedling to colonize the restoration plots (*Beilschmiedia assamica*, discussed previously) comprised 0.2% of the animal-dispersed EGF colonizers.

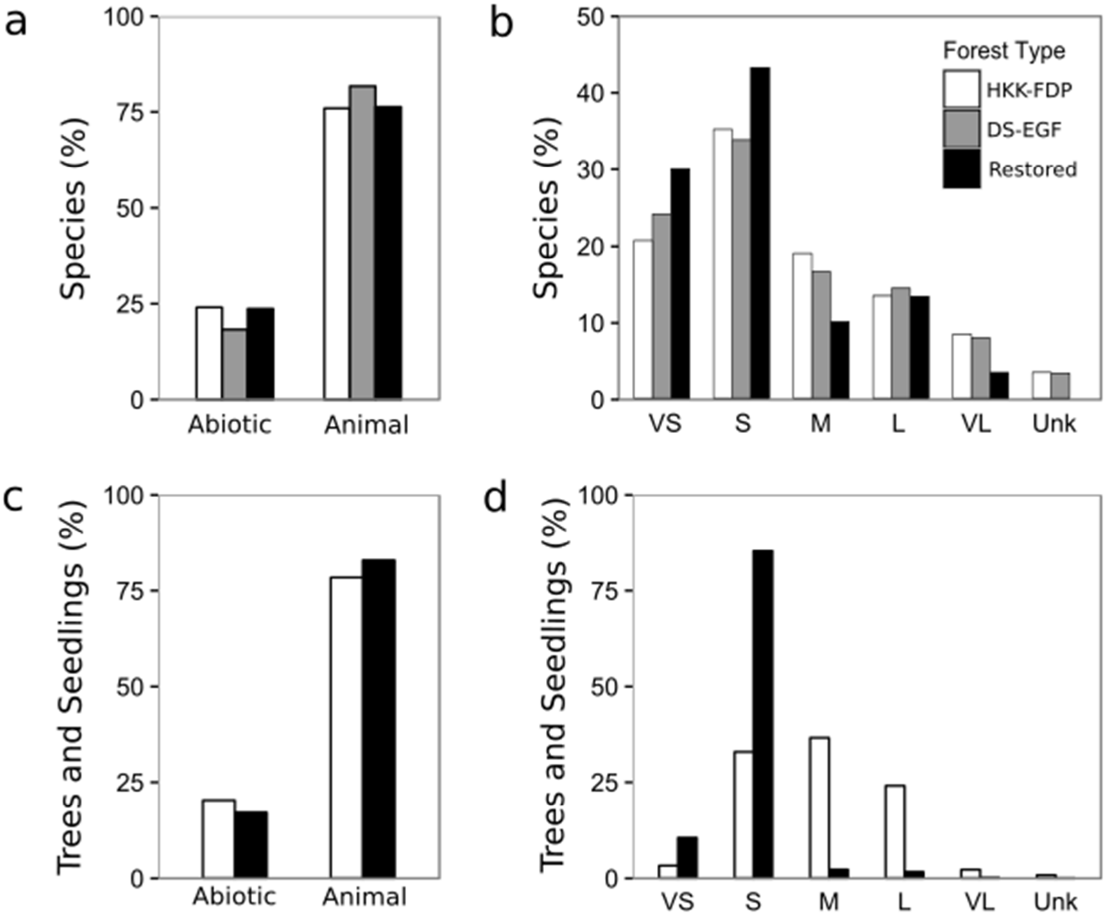
The distribution of dispersal traits across seedlings was heavily influenced by seedlings of *Litsea monopetala*, a S-seeded species that comprised nearly 60% (476) of all colonizing EGF seedlings (both abiotically-dispersed and animal-dispersed). *Litsea monopetala* seedlings were more than 14 times more numerous than the next most successful animal-dispersed species, *Litsea cubeba* (also S-seeded). However, even when we removed *L. monopetala* seedlings from the distribution, S- and VS-seeded seedlings still made up 87.9% of the animal-dispersed EGF colonizers (Table 2.2).

Table 2.2 The frequency of dispersal traits among tree and treelet species in intact evergreen forest in Doi Suthep National Park (DS-EGF) and Huai Kha Khaeng Wildlife Sanctuary 50-ha Forest Dynamics Plot (HKK-FDP). Also shown is the frequency of dispersal traits among trees (dbh ≥ 10 cm) in HKK-FDP and the mean number of trees per species with the standard deviation in parentheses

Dispersal Trait	DS-EGF species	HKK-FDP species	HKK-FDP trees	HKK-FDP trees/species
Abiotic	62	61	4,440	72.8 (182.9)
Animal	278	179	17,154	95.8 (291.7)
Very large	22	15	387	25.8 (41.1)
Large	40	24	4,135	172.3 (526.0)
Medium	46	34	6,275	184.6 (361.2)
Small	94	63	5,650	89.7 (242.4)
Very small	67	37	564	15.2 (27.1)
Unknown	9	6	143	23.8 (108.6)
Total	340	240	40	-

Table 2.3 The frequency of dispersal traits among tree and treelet species in intact evergreen forest in Doi Suthep National Park (DS-EGF) and among seedlings, irrespective of species, in 0.19 ha of EGF restoration plots in Doi Suthep National Park. Seedlings in the restoration plots are further subdivided into colonizing evergreen forest species (cEGF), colonizing species not previously recorded in evergreen forest (cNon-EGF) and species that were originally planted, to establish the restoration plots (Plantation).

	Number of species			Number of seedlings		
Dispersal Trait	cEGF	cNon-EGF	Plantation	cEGF	cNon-EGF	Plantation
Abiotic	10	6	3	129	25	121
Animal	30	12	14	675	157	374
Very large	1	0	3	1	0	80
Large	4	0	5	11	0	50
Medium	3	2	2	12	12	46
Small	13	4	4	582	77	198
Very small	9	6	0	69	68	0
Unknown	0	-	-	-	-	-
Total	40	18	17	804	182	495



Figure

Figure 2.1(a) Percent frequency distribution of seed dispersal modes among colonizing EGF tree species in restored forest plots, compared to that of trees recorded at HKK and DS-EGF. (b) Percent frequency of seed-sizes among animal-dispersed, colonizing, EGF tree species in restoration plots compared to the overall species distribution for animal-dispersed trees in HKK-FDP and DS-EGF. (c) Abundance distribution of seed dispersal modes for colonizing EGF tree and treelet seedlings (irrespective of species) on the restoration plots compared to trees ≥ 10 cm dbh in HKK-FDP. (d) Abundance distribution of seed-sizes among colonizing, animal-dispersed EGF seedlings on restoration plots compared to animal-dispersed trees ≥ 10 cm dbh in HKK-FDP. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 except for the category of species for which size is unknown. These are labeled as “Unk.”

4.3 Species evenness in restored forest

The abundance of colonizing EGF species on the restoration plots was highly uneven across species (Figure 2.2). As mentioned previously, seedlings from *L. monopetala* accounted for nearly 60% (476) of all colonizing seedlings. Seedlings belonging to the next ten highest colonizing species accounted for an additional 30% (238) of all seedlings. By contrast, half of all colonizing species were represented by three or fewer seedlings and comprised just 4.4% of all seedlings.

Both animal- and abiotically-dispersed species were present throughout the ranking distribution. The M-, L-, and VL- seeded, animal-dispersed species, however, were mostly confined to higher ranks (lower abundance) because they were generally represented by fewer seedlings.

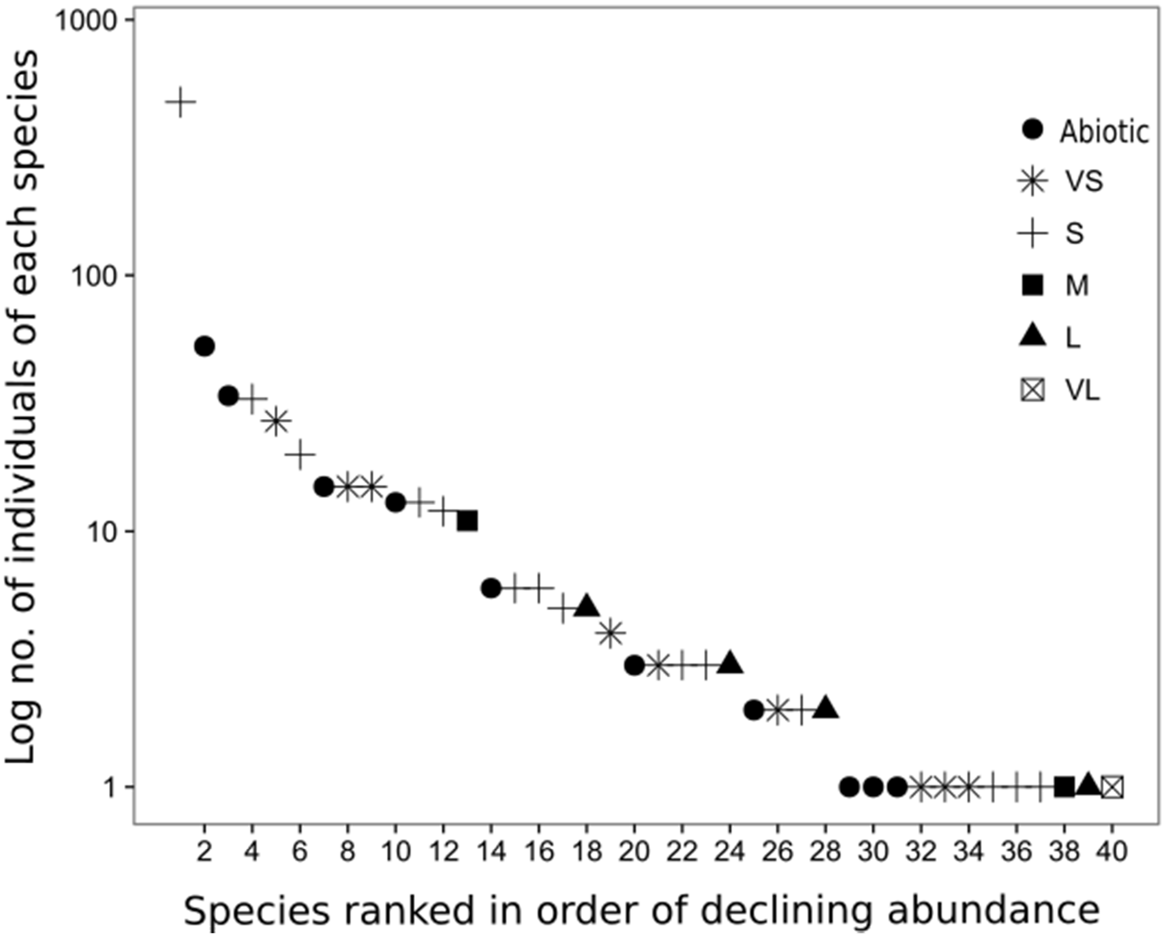


Figure 2.2 Rank abundance curve for colonizing seedlings of EGF tree and treelet species on 4- to 8-year old restoration plots. Abbreviations and measurement ranges for trait and size categories are given in Table 2.1.

4.4 Non-EGF species

In addition to colonizing EGF species, Sinhaseni et al.'s (2008) survey of the 4- and 8-year-old restoration plantations also identified 182 tree and treelet seedlings (on 0.19 ha) of belonging to 18 species that had not previously been recorded in DSNP-EGF (Maxwell and Elliott 2001). Similar to the colonizing EGF species, the majority of the colonizing non-EGF species (66.7%) and seedlings irrespective of species (86.2%) were animal-dispersed (Table 2.3).

In contrast to EGF colonists, however, animal-dispersed non-EGF colonists all had M or smaller seeds. This suggests that likely dispersal vectors for these species were small and medium-sized frugivorous birds.

4.5 Projection

We project that if the forest attains a stand density equal to that of HKK-FDP (437.5 trees $\geq$ 10 cm DBH ha^{-1}), the number of animal- and abiotically-dispersed trees per hectare of restored forest will be nearly identical to the number of animal- and abiotically-dispersed trees per hectare at present in the HKK-FDP (Figure 2.3a). However, the projected seed size composition among animal-dispersed trees in the restoration plots is predicted to become different from that at HKK-FDP (Figure 2.3b). Restoration plot trees with S seeds will outnumber all seed sizes combined (263 vs. 91 trees ha^{-1}). This contrasts with HKK-FDP where M-seeded trees edge out S-seeded trees (126 vs. 113 trees ha^{-1}) to be the largest animal-dispersed seed size category. Furthermore, the projection predicts fewer M- and L-seeded trees in the restored forest. The projected restored forest will have 84% fewer M-seeded trees and 75% fewer L-seeded trees than the HKK-FDP. Moreover, about 80% of the projected M and L seeded trees are predicted to belong to plantation rather than colonizing species. In the projected forest, VL-seeded trees will be considerably more numerous than at HKK-FDP (28 vs. 8 trees ha^{-1}); however, 98.8% of the VL-seeded trees will belong to one of three plantation species. Thus, it is predicted that there will be < 1 colonizing VL-seeded trees per ha of restored forest.

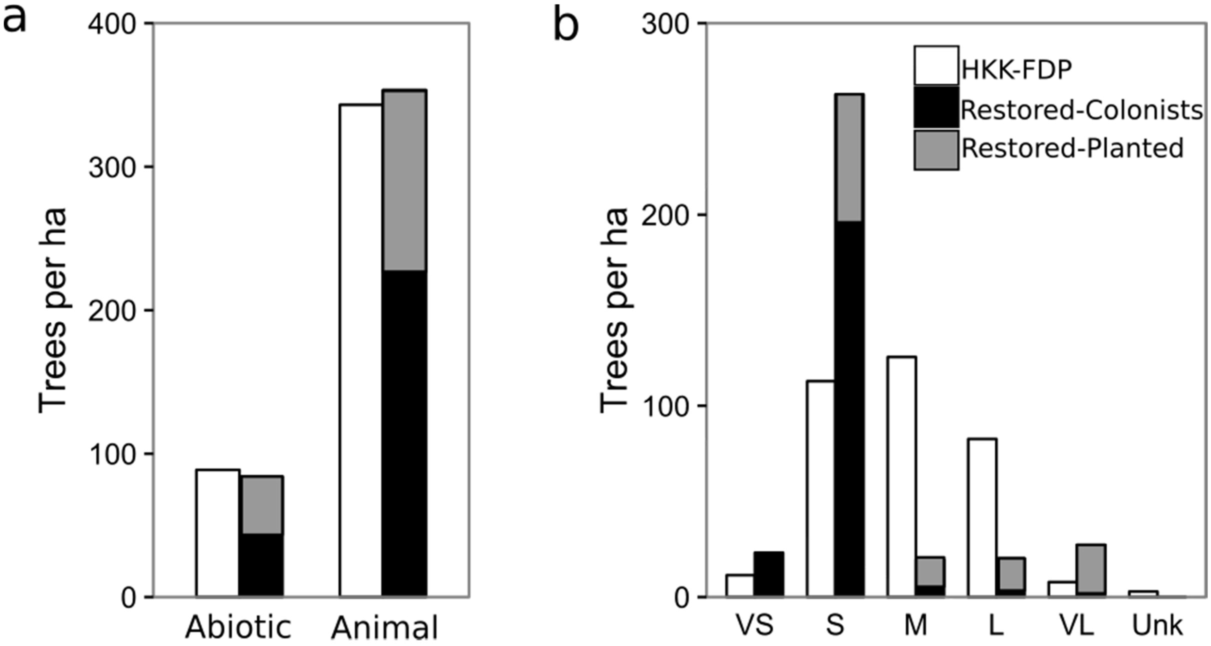


Figure 2.3 (a) The projected distribution (in trees ha^{-1}) of seed dispersal modes among EGF trees with dbh ≥ 10 cm on restoration plots compared to the actual distribution among trees with dbh ≥ 10 cm in HKK-FDP. (b) The projected distribution (in trees ha^{-1}) of seed sizes for animal-dispersed EGF tree and treelets with dbh ≥ 10 cm on restoration plots compared to the actual tree distribution of animal-dispersed trees with dbh ≥ 10 cm in HKK-FDP. The restoration plot distributions are subdivided by shade to indicate trees that colonized the forest (black) and the offspring of plantation trees (grey). All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 except the category of species for which size is unknown. These are labeled as "Unk."

5. Discussion

5.1 Reference Forests

As in most tropical forests in East Asia and throughout the world, the majority of tree species in intact evergreen forest in Doi Suthep National Park (DS-EGF) and Huai Kha Khaeng Wildlife Sanctuary 50-ha Forest Dynamics Plot's (HKK-FDP) are dispersed by frugivorous animals (Howe and Smallwood 1982, Corlett 1998b). Of these, more than half have S or VS seeds. The percentage of species declined with each successively larger seed-size category, such that VL-seeded species made up less than 8% of tree species in both forests. The skew towards smaller-seeds in the species distributions of both of these forests is similar to that reported for other tropical, subtropical and temperate forests (Herrera 1987, Corlett 1996, Peres and van

Roomalen 2002). The proportion of VL-seeded species, however, is less than that reported for similarly species-rich forests in the neo-tropics (15.9 – 19.6%) (Peres and van Roomalen 2002).

The abundance distribution of large trees in (dbh ≥ 10 cm) HKK-FDP suggests that although S- and VS- seeded categories are richest in species, distribution of trees across the seed sizes does not reflect the species richness of the category. For animal-dispersed trees, abundances are distributed more normally with M-seeded trees being more abundant than either S- or VS-seed trees.

5.2 Colonizing EGF Species

Most of the colonizing tree and treelet seedlings in the forest restoration plots belong to species that are reported to inhabit the reference ecosystem, DS-EGF (Maxwell and Elliott 2001). Altogether, these species comprise 68% of the colonizing species and 81% of the colonizing seedling population. However, we cannot be certain that dispersal from DS-EGF is responsible for recruitment of seedlings in the restoration plantations. Most of the colonizing species are generalists to some degree, inhabiting more than one forest type. Their recruitment may therefore be due to dispersal from non-EGF forest or forest patches rather than DS-EGF. There were, however, three animal-dispersed species among the colonizers that Maxwell and Elliott (2001) report as inhabiting DS-EGF exclusively and being “rare” in abundance These were *Ehretia acuminate, Michelia floribunda,* and *Aquilaria crassna*. Colonization by these species provides strong evidence of successful animal dispersal from intact EGF. This also suggests that the dispersal of other, more generalist species may have similarly occurred from intact EGF.

The percentage of colonizing, abiotically-dispersed EGF species and individual seedlings was similar to the percentage of abiotically-dispersed tree species in DS-EGF and tree species and trees in HKK-FDP. This suggests that abiotic dispersal neither favors nor limits recruitment in the forest restoration plots. The presence of abiotically-dispersed species throughout the rank-abundance curve, however, suggests that recruitment success for this dispersal mode varies by species. Although we did not subdivide abiotically-dispersed species by seed traits in this investigation, within this dispersal mode certain traits such as seed mass, area, and aerodynamics (for wind-dispersed seeds) may affect dispersal distances (Augspurger and Franson 1987, Greene and Quesada 2005). Future research should investigate whether and which abiotically-dispersed species are dispersal-limited in the forest restoration plantations in order to develop appropriate strategies for ensuring their presence in future restored forest.

Our results support the hypothesis that recruitment limitations in restored forests increase with increasing seed size. The majority of seedlings colonizing the restoration plots belonged to animal-dispersed species. This corresponds with the understory colonization by native species beneath restoration plantings and commercial tree plantations elsewhere in the tropics (Parrotta 1995, Reid et al. 2015). In our investigation, however, there were disparities in recruitment based on seed size with smaller-seeded seedlings overrepresented compared to larger-seeded species.

Furthermore, the absence or under-representation of large-seeded, colonizing seedlings in the restoration plots appears to be explained more by limited seed dispersal than by limited germination and/or early seedling establishment. Most forest restoration sites start with poor soil conditions due to histories of cultivation (Chazdon 2003). This severely limits the availability of suitable germination and recruitment microsites for naturally-recruited seeds (Doust et al. 2006). However, within about four years after tree planting, conditions on the forest floor beneath the developing forest canopy of the forest restoration plantations in this investigation had become sufficiently ameliorated to allow the offspring of large-seeded plantation species to establish. Moreover, in a separate direct-seeding experiment, we introduced previously absent L- and VL-seeded species (*Aglaia lawii, Baccaurea ramiflora, Calophyllum polyanthum, Horsfieldia amygdalina, Mangifera caloneura*) into the restoration plot understory and observed high germination rates (26.5% – 66.8%) for four out of five species as well as 2-year survival rates of 23.0% – 92.4% (Chapter 3, this dissertation). Cole et al. (2010) reported similar results for direct-seeded, large-seeded trees in young (3-year-old) native tree plantations in Costa Rica. Taken together, these provide evidence that restoration plantings rapidly ameliorate microsite conditions for large-seeded species recruitment. This suggests that recruitment of large-seeded species is more strongly limited by seed availability than microsite conditions.

The dispersal of many of the S- and VS-seeded species from DS-EGF is likely due to small- and medium-sized frugivorous birds. Bird surveys conducted in the 8-year-old restored forest plots during the same years as our seedling surveys recorded 17 frugivorous bird species {Wydhayagarn, 2009 #19}. The most common frugivorous birds were medium-sized and small passerines: bulbuls (Pycnonotidae) and white eyes (Zosteropidae) respectively. They are common throughout fragmented and degraded Southeast Asian forests and are important seed dispersal agents (Corlett 1998a). They are, however, unlikely to be responsible for dispersal of seeds larger than 15 mm (Corlett 1998b). Larger seeds may have been dispersed by some of DSNP's remaining medium-sized frugivorous mammals, such as Indian civets (*Viverra zibetha*), barking deer (*Muntiacus muntjak*), and hog badgers (*Arctonyx collaris*), all of which have been photo-trapped in the restoration plots. Civets, which are highly tolerant of degraded landscapes, commonly disperse seeds up to 20 mm in diameter (Corlett 2009). They and all other remaining mammalian frugivores within DSNP are in danger of extirpation from the study site by illegal hunting. The disappearance of these mammal species would further decrease the likelihood that large-seeded tree species will recolonize restoration plots.

To the best of our knowledge, no frugivorous animals currently recorded in DSNP can disperse VL seeds, yet one VL-seeded seedling belonging to a colonizing species was able to recruit into the forest. The presence of the seedling, identified as *Beilschmiedia assamica*, suggests one of two possibilities: Either remaining frugivores are occasionally able to disperse seeds larger than their gape or body size suggests or the seed arrived without the assistance of animal dispersal. Based on the location of the seedling, the latter explanation seems most likely. The plot on which *B. assamica* was found is at the base of a steep slope below a ridge that is home to an EGF/pine forest fragment (S. Elliott, personal communications). Although the trees in the fragment have never been surveyed, they may include a mature *B. assamica*. If so, the seed may have originated in the fragment and rolled downhill into the restoration plot. If this is the case, then we would not expect many other VL-seeded species to recruit into the restoration plots in the future.

5.3 Limitations

Our projection, as well as the species, seedling, and tree distribution comparisons, possessed a number of limitations. The first limitation was due to the initial seedling survey data. The surveys were conducted in forest restoration plantations within 2 km of one another all along the same watershed ridge. The close proximity of the survey sites limits its scope of inference; however, taken together with other recent studies of dispersal limitations in restored forests, this investigation adds to a growing body of evidence that natural recruitment of species in restored and secondary forests is filtered by dispersal traits, particularly for large-seeded, animal-dispersed species (Corlett 1991, Costa et al. 2012, Reid et al. 2015).

Furthermore, the survey data were acquired over a period of 18 months, a time frame that may have been insufficient to include periodic events that affect recruitment and early survival such as supra-annual seed production or intermittent weather variations (Gilbert et al. 2001, Wright et al. 2005, Engelbrecht et al. 2006). On the other hand, the survey included pre-existing seedlings, many of which can persist for years in the restored forest understory (Chapter 4, this dissertation). These seedlings, therefore, represented the accumulated recruitment over the four and eight years since forest establishment, potentially compensating for the survey's small time window.

The absence of seedling information from the reference forests limited this investigation to comparisons between seedlings in restored forest and adult trees in reference forests. The comparisons are not perfectly analogous because distribution of dispersal traits among colonizing seedlings may not persist as the forest matures. Moreover, the abundance of seedlings in the understory on a small time scale may be an inadequate predictor of future forest composition. Compared to the adult tree community, the seedling community of tropical forests may be less diverse than the adult tree community (Comita et al. 2007), possibly because seedling communities have not undergone ecological segregation by habitat (Baldeck et al. 2013). While recruitment of seedlings represents the first major bottleneck for the assembly of forest composition, Kanagaraj et al. (2011) found that the seedling community in a tropical forest was only weakly associated with habitat conditions. Habitat filtering, or the non-random survival of individuals as a result of habitat characteristics, increased as seedlings progressed into the next life stage (e.g. the seedling to sapling transition). This suggests that the trajectory of tree composition development may be substantially altered by the effects of conditions in restored forests on seedlings post-recruitment. Habitat filtering may alter the distribution of dispersal-traits in particular if some dispersal traits confer survival advantages, or are correlated with adaptations that do. For example, larger seed size is frequently associated with increased understory survival and growth (Foster 1986) and may be one of a suite of frequently co-occurring traits that facilitate regeneration in the resource-limited understory (Baraloto and Forget 2007). However, since almost nothing is known about long-term survival or maturation rates of seedlings recruited into restored forest, we were unable to predict the likelihood that seedlings of any dispersal type will transition to successive life stages. We were therefore compelled to project future forest composition based on the seedling community alone.

Shifts in dispersal patterns over time may alter both the composition of seedlings in the restoration plots and the trajectory of forest development. In secondary and restored tropical forest, the composition of seed rain and recruited seedlings is reported to increase in richness, diversity and evenness with time, particularly for animal-dispersed species (Oberhauser 1997, Aide et al. 2000, Reid et al. 2015). In our study sites as well, 8-year-old restoration plots recruited significantly more species and more animal-dispersed species than 4-year-old plots (Sinhaseni 2008). If animal-dispersed seedlings continue to increase over time as they have in other restored forests (Reid et al. 2015), our projection may overestimate the future density of abiotically-dispersed trees.

Over time, not only is dispersal likely to shift, but recruitment of offspring from species that were initially planted to establish the forest is likely to increase as well. Seedlings of plantation species were most abundant in the 8-year-old restored forest plots (Sinhaseni 2008), most likely because plantation trees in these plots had had more time to become reproductively mature. Even in these older plots, however, most plantation species were not yet reproductively mature and therefore had no offspring in the understory. Despite this, plantation seedlings already comprised a third of all the seedlings surveyed. As the restored forest ages, the offspring of plantation species may continue to increase, potentially altering the projected outcome of the distribution of dispersal traits.

Finally, our projection predicts only future densities of trees for each dispersal trait. Aside from providing the estimated proportion of plantation and colonizing trees for each dispersal trait category, the projection did not attempt to estimate species richness, diversity, or evenness of dispersal traits. It is clear though that there is wide variation within trait categories. For example, S-seeded seedlings were the most abundant seed size category in the DS-EGF understory. However, S-seeded species occurred throughout the rank abundance distribution for the initial seedling survey data. This suggests that not all S-seeded species are recruitment favored and that some small-seeded species may also be poorly represented in the future forest, even though their trait category is abundant.

5.4 Non-EGF Species

The majority of colonizing non-EGF seedlings in the restoration plots were M-, S- and VS-seeded animal-dispersed species. This suggests that likely dispersal vectors for these species were small and medium-sized frugivorous birds. It is reasonable to assume that abiotic dispersal and wide-ranging birds have made similar introductions of non-EGF species into the DS-EGF in the past. Although we do not know whether colonization by non-EGF species in the restored forest will impact the development of the forest composition, the absence of mature individuals in EGF suggests that non-EGF species are not well-adapted for the EGF environment. In this investigation we focused on colonizing EGF species because we assumed that as the restoration plots mature and the environment grows to more closely resemble DS-EGF, colonizing non-EGF species may be similarly excluded. However, it is also possible that conditions within the restoration plantations may be sufficiently different from those that prevailed at the time that the original DS-EGF established to allow colonizing non-EGF species to continue in the plantations. In this case the species composition of the future restored forest may never completely converge with that of the DS-EGF.

5.5 Research and Management Implications

The scarcity of animal-dispersed, L- and VL-seeded colonizers in the restoration plantations supports the hypothesis that these species are dispersal-limited in the absence of large frugivorous birds and mammals. Since large frugivorous seed dispersers are unlikely to return in the near future, restoration ecologists should consider additional measures to ensure the presence of large-seeded trees. Enrichment planting, the introduction of species to the forest without the removal of existing trees, may be used to further increase the diversity of larger-seeded species after the re-establishment of canopy cover has ameliorated microclimate conditions. Our research adds to the growing body of evidence that VL-seeded species are the most recruitment-limited of all animal-dispersed seeds. Based on this, we should consider prioritizing these species for enrichment planting. Additional research, however, is needed to determine which species would be best suited for planting and under what conditions planting is most likely to succeed.

The rarity of L- and VL-seeded species in the relatively young restoration plantations also raises the question about whether recruitment limitations will shift with time. Reid et al. (2015) found that limitations on animal seed dispersal decrease as forest restoration ages, though L-seeded species continue to be underrepresented in the seed rain. However, even if limitations on dispersal of L- and VL-seeded, animal-dispersed species decreases, late arriving species would arrive in older, more developed forest, which may further limit and delay their establishment and maturation (Finegan 1996, Chazdon 2008). Moreover, though density and richness of understory native tree seedlings has been shown to increase with restored forest age (for forests 10 – 55 years old), seedling establishment and growth is highest in the youngest forest, possibly due to higher light availability and fewer soil-borne pathogens in younger forests (Bertacchi et al. 2016). This suggests that enrichment planting in young restored forest may be the most effective means of offsetting the long-term effect of early dispersal limitations in forest restoration.

Practitioners should include L- and VL-seeded tree species among the species mix selected for planting. The total number of species that can be included in the mixture, however, is usually restricted by cost, logistics, and the availability of species suited to the harsh initial environment. Moreover, the large number of offspring of plantation species in this investigation highlights a subject that has yet to receive much research attention – the potential for offspring of actively planted species to influence the forest's long-term development trajectory. In the young restored forest under consideration here, the abundance of plantation seedlings suggests that at least some of the plantation species have a competitive advantage over colonizing species that are dispersal-limited. This advantage may become even more apparent as more plantation species become reproductively mature. Holl (2007) proposed that the composition of the planted overstory trees may decrease both the diversity and richness of the understory seedling community. Additional research to quantify the effect of overstory species composition in restoration settings may be useful for guiding selection of species for future restoration efforts.

The composition of the future mature forest is unlikely to perfectly reflect the present seedling composition. However, without additional information on the likelihood of seedling survival and maturation in restored forest conditions, more accurate projections of the forest composition trajectory are not possible. This investigation therefore emphasizes the need for research to quantify the likelihood that seedlings will transition to successive life stages. Such information will allow predictions of species outcomes, decades before restored forests mature (Howe and Miriti 2004) and make it possible for practitioners to create tools to guide effective restoration management decisions.

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Chapter 3 – Recruitment Microsite Limitations of Large-seeded Trees in Northern Thai Tropical Forest Restoration Plantations

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ABSTRACT

Restoration plantings of mixed native species can rapidly re-establish canopy cover on degraded, abandoned agricultural land; however, recruitment limitations may delay or prevent recolonization by large-seeded, animal-dispersed tree species. This affects composition, structure and function of the restored forest. The objective of this study was to evaluate the importance of seed availability and microsites on the recruitment (germination and early survival) of large-seeded tree species in 13-year-old seasonally dry tropical forest restoration plantations in northern Thailand. Our seed sowing experiment combined five large-seeded tree species with four microsite treatments in a split-plot design and measured germination and seedling survival and growth for two years. All five tree species were previously absent from the understories of the plantations. Four treatments simulated potential microsites that naturally-dispersed seeds may encounter. These were deposition on soil and on leaf litter, and burial beneath soil and beneath leaf litter. We recorded seedling height and stem diameter as measures of growth and light availability and dry season soil water as key components of understory environmental conditions. High overall germination (> 25% for four out of five species), high two-year survival of germinated seeds (59.7%), and the absence of statistically detectable effects of the microsite treatments on seed germination and seedling survival and growth suggest that basic microsite requirements for germination and early establishment of these species were met within 13 years of initiating tree planting and other restoration treatments. This supports the hypothesis that seedlings of large-seeded species are often absent from seasonally dry tropical forest restoration plantations due to inadequate seed availability, rather than inadequate microsite conditions. Direct seeding of large-seeded tree species, beneath the canopy of restoration plantations, may be an effective way to offset limited seed dispersal of these species into restoration sites. Broadcast sowing of large seeds is probably as effective as burying them, provided rainfall is sufficient.

1. Introduction

Seasonally dry tropical forests (SDTFs) are among Earth's most threatened tropical terrestrial ecosystems (Janzen 1988, Miles et al. 2006). Accounting for approximately 42% of all tropical forest area, SDTFs are distinct from aseasonal tropical forest because they grow where there is at least one prolonged season (≥ 4 months) of severe to absolute drought each year (Dirzo et al. 2011). Over the past century, large areas of SDTFs have been converted to agriculture and remaining forest has become fragmented or degraded (Murphy and Lugo 1986, Miles et al. 2006). This has resulted in widespread species extirpations and created potential extinction debts – pools of species that are likely to become extinct in the near future, if habitats are not regenerated or restored (Tilman et al. 1994). Today, however, millions of hectares of converted former forest lands have been abandoned, due to declining soil productivity (Murphy and Lugo 1986, ITTO 2002, Chazdon 2003). These lands represent an opportunity for tropical forest recovery and thus a possible safety net against the extinction of forest-dependent species that are threatened by habitat loss (Martínez-Garza and Howe 2003, Chazdon et al. 2009). Yet soil deterioration, harsh climatic conditions, competition with herbaceous weeds overstocking with livestock and the absence of tree seed sources (nearby remnant forest) present formidable barriers to natural forest succession on such sites (Parrotta et al. 1997, Chapman and Chapman 1999, Elliott et al. 2003). Under such circumstances, active intervention is required to catalyze succession and the development of ecosystems similar to natural forests within a reasonable time frame. Efforts to develop rapid, low-cost, low-tech restoration techniques are being independently undertaken in several tropical nations (Elliott et al. 2003, de Souza and Batista 2004, Lamb et al. 2005). One frequently employed strategy is to first protect and assist any naturally occurring regeneration and then complement it if necessary by planting indigenous tree species. The first major goal of forest restoration is canopy closure (usually within 3 – 4 years). This shades out herbaceous weeds, improves soil conditions, and ameliorates the microclimate. These changes then facilitate species recruitment through seedling establishment of unplanted (colonizing) species. Such recruitment depends entirely on natural seed-dispersal from nearby remnant forest into the restoration site to increase tree species diversity and re-assemble the floristic composition of the original forest ecosystem.

While recruitment of naturally-dispersed seedlings increases tree species richness and diversity in the understory of young, actively-restored forests (Sinhaseni 2008, Lamb 2011, Bertacchi et al. 2016), recolonization by some tree species is slow or does not happen at all, particularly for those with large, animal-dispersed seeds (Reid et al. 2015, Chapter 1 of this dissertation). Such trees are often long-lived, shade-tolerant, late-successional species that are able to regenerate in the forest understory (Leishman et al. 2000). Large-seeded trees tend to have higher wood density, larger size at maturity, and higher rates of CO_2 fixation than smaller-seeded species (Osuri and Sankaran 2016). Consequently, reduced recruitment of them may alter not only forest composition, but also forest structure and function. Moreover, the failure of large-seeded trees to regenerate may increase their risk of regional extirpation or even extinction (Brodie et al. 2009, Wotton and Kelly 2011, Caughlin et al. 2014).

Limited seed-dispersal is the likely cause of delayed recolonization of large-seeded trees in both actively-restored and naturally-regenerating tropical forest (Lamb 2011, Chazdon 2014, Reid et al. 2015). Although the majority of tropical tree species are dispersed by frugivorous birds and mammals (Howe and Smallwood 1982), larger seed sizes require larger seed-dispersing animals (with wider gapes). In general, however, there are fewer large frugivorous dispersers, so the larger the seed, the less likely it will be dispersed (Kitamura et al. 2002, Corlett 2017). Moreover, large frugivores are becoming increasingly rare. Hunting and habitat loss have extirpated many species of frugivores capable of dispersing the largest seeds (e.g. hornbills, elephants, wild cattle species, rhinos etc.) from vast stretches of their former ranges (Corlett 2007, Peres and Palacios 2007, Effiom et al. 2013). Even where they remain extant, such animals often cannot disperse seeds from forest into deforested sites due to distance, lack of forest connectivity and the barriers of agricultural land and infrastructure development (Cordeiro and Howe 2001).

Dispersal of seeds into deforested areas alone, however, does not guarantee recruitment. Establishment (i.e. germination and seedling survival) may also be limited by the availability of microsites with suitable abiotic conditions (Guariguata and Ostertag 2001). While these sites may be on a scale of no more than a few centimeters, they often determine germination and initial growth of individual plants (Harper 1977). In moist tropical forest where the primary limiting environmental factor for seedling survival is light availability, microsite research has usually focused on differences in understory light levels caused by canopy gaps (Augspurger 1984, Brown 1996, Schnitzer and Carson 2001). In SDTF, however, moisture may be as or more limiting than light, due to extended dry seasons (Vieira and Scariot 2006, Poorter and

Markesteijn 2008, Ferreira et al. 2015). In these forests, seedbed microsites may play a critical role in seedling establishment by preventing seed and seedling desiccation. The importance of seedbed microsites may be further amplified on restoration sites, as the conditions on such sites are usually poor (e.g. soil compaction, low levels of soil organic matter and low soil water retention) due to long-term, intensive, agricultural activity, such as repeated weeding and burning (Chazdon 2003).

The surface of a forest floor is highly heterogeneous, thus seeds that have naturally dispersed into restored SDTF may come to rest in a variety of microsites. For example, variable leaf litter distribution throughout the understory means that arriving seeds may be deposited on the surface of leaf litter or on bare forest soil. From there, seeds may work their way beneath litter, or seed-caching mammals may bury some seeds beneath soil. Each of these conditions poses both challenges and opportunities for seedling recruitment. Seeds deposited on bare soil may benefit from good seed-soil hydraulic conductivity and favorable aeration (Makana and Thomas 2005); however, seeds on bare soil as well as seeds on leaf litter may be at greater risk for desiccation. Furthermore, leaves may block the seedling radicles on the surface of litter, preventing them from reaching the mineral soil (Molofsky and Augspurger 1992). In contrast, seeds buried beneath soil or leaf litter may be shielded from desiccation, but forced to expend greater amounts of energy to grow above the substrate. This energy expenditure may reduce the robustness of seedlings that manage to emerge (Molofsky and Augspurger 1992, Peterson and Facelli 1992).

Large seed size itself may be an adaptation to challenging understory conditions. Large seeds typically have higher rates of germination and seedling survival than smaller seeds (Molofsky and Augspurger 1992, Dalling and Hubbell 2002). Larger seed energy stores may also enable seedling emergence from below litter or soil, hasten their growth above competing vegetation, and facilitate seedling persistence in deep shade (Leishman et al. 2000). Among tropical trees large seed size is also associated with desiccation sensitivity (Pritchard et al. 2004, Daws et al. 2006). Desiccation sensitivity may explain why some studies have found that seed burial increases germination and seedling survival of large-seeded tropical tree species in moisture-limited environments (Hardwick et al. 1997, Doust et al. 2006).

In many secondary forests, floristic composition often does not recover as rapidly as structural composition does (Aide et al. 2000, Chazdon 2003, Brearley et al. 2004, Chua et al.

2013). The composition of these forests may be distinct from primary forests for decades, following re-establishment of forest cover. This is in part due to slow recolonization of large-seeded tree species. In order to ensure the timely return of these species to restored tropical forests, we need to understand the role that seed and microsite limitations play in their recruitment and early development. To the best of our knowledge, however, explicit tests of seed and microsite limitations have not yet been conducted in restored tropical forest. In this study, we addressed this gap by conducting a seed sowing experiment, using five large-seeded tree species that have failed to naturally recolonize 13-year-old seasonal dry tropical forest restoration plantations in northern Thailand, despite being present in nearby forest. We sowed seeds using four different treatments to simulate microsite conditions that naturally-dispersed seeds might encounter in the forest understory. We then monitored seed germination, seedling survival, and seedling growth for two years. Furthermore, we explored the relationship of light availability and soil water content with seedling survival during the first dry season. Finally, we discuss the implications of the results of this investigation for future management of restored tropical forests.

2. Study Site

The field portion of this study was conducted on three 0.16 ha experimental forest restoration plantation plots located along or immediately below the ridge of a watershed (1,207 – 1,310 meters above mean sea level) in Doi Suthep-Pui National Park (DSNP), Northern Thailand. The site of the restoration pots was originally covered with seasonally dry evergreen forest (EGF). EGF is the most diverse of DSNP's six forest types. EGF supports over 250 tree species (~75% of which are evergreen) and contains the largest number of rare and endangered plant species restricted to a single DSNP forest type (Maxwell and Elliott 2001). However, EGF is also the park's most endangered forest type, since much of the DSNP's EGF has been cleared for cultivation. The site of the plots used in this investigation was also cleared for farming over two decades prior to restoration planting, but was later abandoned due to declining fertility. Following abandonment, the land became dominated by grasses and herbaceous weeds (Elliott et al. 2000).

The Forest Restoration Research Unit (FORRU) of Chiang Mai University established the restoration plantation plots in 1998 (13 years prior to initiation of our investigation) as experimental trial replicates to test and refine the Framework Species Method (FSM) for EGF restoration. The FSM seeks to accelerate the process of forest succession by using mixed plantings of 25–30 species of hardy, fast-growing, indigenous trees to create a canopy that shades out competing grasses and herbaceous weeds and moderates the understory climate for tree seedlings (Goosem and Tucker 1995, Elliott et al. 2003, Lamb et al. 2005). After canopy closure, the FSM relies on natural seed-dispersal from remnant trees and forest to increase tree species diversity within the plantings.

The restoration plantation plots used in our study were planted with the same mix of 29 tree species at a density of 3,125 ha^{-1} (averaging 1.8 m between trees). Canopy closure on the plots was complete within four years after planting (Anusarnsunthorn and Elliott 2004, FORRU 2005) and a dense, two-layered canopy had developed by the start of this study (Wydhayagarn et al. 2009). Each of the three plots was separated from its nearest neighboring replicate plot by at least 0.7 km. The land between the plots included older and younger restoration plantations, small secondary forest patches, and agricultural land. At the time of this investigation most of the slopes below the watershed ridge were still being cultivated to provide income and subsistence for the residents of Ban Mae Sa Mai (18º52´N, 98º51´E), a Hmong village community (population of about 1,700) within DSNP boundaries (Neef et al. 2004) and approximately 2 km south of the plots. The nearest extensive patch (> 100 ha) of intact, primary EGF was approximately 1 – 2 km east of the plots. Additional details regarding the planting, maintenance and monitoring of the plots can be found in Elliot et al. (2003).

We selected the 13-year-old plots because they were the oldest successfully-established restoration plantations in DSNP. Although FORRU began restoration planting trials a year earlier in 1997, survival of planted trees was mixed in that first year's plantings (Elliott, personal communication). The next year FORRU adjusted both the composition of planted species and the post-planting fertilization and weeding schedule. This increased seedling survival and within four years the plantings had achieved canopy closure (Anusarnsunthorn and Elliott 2004, FORRU 2005). Understory seedling communities developed soon after. Seedling surveys conducted across all three restoration plots 8-9 years after establishment identified 369 seedlings belonging to 30 colonizing EGF species within 942 m^2 of sampling subplots (Sinhaseni 2008). The presence of colonizing species indicated recruitment from seed dispersal into the plantations was occurring. Furthermore, most of the seedlings were animal-dispersed (82%). However, most of the animal-dispersed colonizers (93%) had smaller-sized seeds with seed lengths ≤ 1 cm (Chapter 2, this dissertation).

Average annual precipitation at the elevation of the plots is 2,095 mm (as recorded by the Kog-Ma Watershed Research Station, the weather station nearest to the plots) (Elliott et al. 2003),with virtually all rainfall occurring during the six-month wet season that extends from May through October. During the dry season (from November to April) precipitation averages less than 100 mm per month (Elliott 2003). The average annual volume of rainfall places the study site at the moist end of the precipitation spectrum for seasonally dry tropical forests as defined by several authors (Miles et al. 2006, Dirzo et al. 2011); however, this paper adopts the broader definition of SDTF used by Bunyavejchewin et al. (2011) which includes all forests that exhibit dynamics (e.g. flower, fruit, and leaf phenology as well as growth and mortality) synchronized with seasonal drought.

3. Methods

3.1 Species Selection

We selected five animal-dispersed, mature-forest tree species for this investigation: *Aglaia lawii, Baccaurea ramiflora, Calophyllum polyanthum, Horsfieldia amygdalina* and *Mangifera caloneura*. Adults of these species are present in intact, primary EGF in DSNP at low to moderate abundances (Maxwell and Elliott 2001), but colonizing juveniles of these species have never been identified in the understory of the restoration plots (Sinhaseni 2008).

Two of the five selected species, *A. lawii* and *H. amygdalina*, were among the species FORRU planted to establish the restoration plots in 1998. Both species, however, grew poorly under initial open field conditions and had only moderate or poor survival, so they were not recommended for future plantings (Elliott et al. 2003). Although it is possible that a few of the initially planted individuals persisted on the plots during the period of this investigation (2011 – 2013), as previously stated juveniles of these species were absent.

The selected species represent a range of seed sizes (Table 3.1). However, all five produce seeds with a mass > 0.4 g and a length > 1 cm. Thus, based on length, these species possess seeds that are within the top third of seed sizes for all tree species within intact EGF in DSNP (Chapter 2, this dissertation).

Table 3.1 Families and approximate sizes of seed length, width, and mass of planted species.

Species	Family	Length (mm)	Width (mm)	Mass (g)
A. lawii[1]	Meliaceae	21.5	13.3	1.89
B. ramiflora[2]	Phyllanthaceae	12.6	12.0	0.45
C. polyanthum[3]	Guttiferae	22.0	15.0	8.75
H. amygdalina[4]	Myristicaceae	33.4	18.3	4.92
M. caloneura[4]	Anacardiaceae	45.3	29.7	6.4

[1] (Saldanha and Nicholson 1976)' [2](Yu et al. 2008)' [3](Nair et al. 2005)' [4] (FORRU 2016)

We collected the seeds used in this investigation from adult trees within nearby remaining natural forest in DSNP. We collected seeds from 2 – 3 adult trees per species for *A. lawii*, *B. ramiflora*, and *H. amygdalina*. We were, however, only able to obtain seeds from one adult tree each for *M. caloneura* and *C. polyanthum* since individuals of these species appear to fruit irregularly in DSNP. We collected seeds from four of the five species in early June of 2011, one week prior to the initiation of the nursery germination trial. Fruiting of the fifth species, *H. amygdalina*, occurred earlier than the other species, and we acquired seeds of this species two weeks prior to the nursery trial. After collection we removed fruit flesh from the seeds and rinsed them gently with water. We then packed the seeds in moistened peat moss and stored them at approximately 10°C until planting.

3.2 Nursery Test of Seed Viability

On June 15, 2011, one week prior to the start of the field experiment (and within one week of seed collection), we initiated a germination test at FORRU's research nursery to determine the viability of the collected seeds. We sowed 100 *A. lawii, B. ramiflora, C. polyanthum,* and *M. caloneura* seeds and 75 *H. amygdalina* seeds in trays containing a mixture of 50% forest soil and 50% coconut coir. Seeds were housed beneath a plastic nursery roof and so received about 20% of full sunlight (Elliott et al. 2003). For 14 weeks we watered the trays daily and monitored the seeds for germination. We defined germination as emergence of the hypocotyl from the seeds.

3.3 Field Experiment Design

On June 22, 2011, approximately one month after the start of the wet season, we initiated the field portion of the seed sowing experiment. This experiment took the form of a split-plot design, in which we planted seeds of the five selected tree species in combination with four microsite treatments.

On each of the three forest restoration plots, we established two 5 m by 4 m subplots, at least 10 m from plot edges and at least 30 m from one another. To prevent seed predation by small mammals, we erected a 1.1 m tall chicken wire fence around the perimeter of each subplot. A 10 cm chicken wire skirt extended outwards from the base of the fence and we buried the skirt beneath a layer of soil and litter to prevent entry by burrowing rodents.

We further subdivided subplots into twenty 1 m by 1 m split-plots. We then randomly assigned split plots to one of the twenty combinations of species and microsite treatments. In each split-plot 25 seeds of a single species were planted in five rows of five, with each seed at least 15 cm from its nearest neighbor. We applied one of four microsite treatments to each split-plot by placing seeds (i) on top of the pre-existing leaf litter, (ii) on the mineral soil beneath pre-existing leaf litter, (iii) on mineral soil cleared of leaf litter, and (iv) 2-cm beneath mineral soil cleared of leaf litter (i.e. by burying seeds). The depth of pre-existing leaf litter on uncleared split-plots varied, but was generally 5 – 10 cm. For treatments requiring seeds be buried beneath leaf litter, we carefully lifted the litter by hand at each planting location, placed the seed on the soil, and replaced the leaf litter. We inserted 15-cm bamboo skewers into the substrate beside each seed in the investigation, to allow us to more easily relocate seeds for monitoring.

We monitored seed germination and seedling survival once a week for the first 10 weeks after planting, then once every three weeks through to week 16. As with the nursery experiment, we defined germination as the visible emergence of the hypocotyl from the seed or above the substrate. To maintain treatment integrity, at each monitoring event for the first 16 weeks we cleared leaf accumulation from split-plots assigned to the two microsite treatments requiring bare mineral soil, being careful not to disrupt seeds or developing seedlings on the split-plots. By week 16 most new germination had ceased; therefore subsequent monitoring events did not include microsite treatment maintenance. We conducted additional germination and survival monitoring 9, 20 and 26 months after planting.

3.4 Measuring Seedling Height and Diameter

To gauge seedling growth, we took stem height and diameter measurements for a subset of surviving seedlings nine and 20 months after seed sowing. Seedlings were selected for measurement nine months after seed sowing. When split-plots had more than eight surviving seedlings, we randomly selected eight seedlings for measurement. When there were eight or fewer seedlings in a split-plot, we measured all seedlings. We measured seedling stem diameter 2 cm above the soil and marked the stems with acrylic paint at the measurement location to ensure accurate re-measuring. We measured stem height from 2 cm above the soil to the tip of the apical bud. We tagged each measured seedling by encircling the base of the stem with a labeled, 1 cm wide aluminum cable tie. Eleven months after taking the initial measurements (20 months after seed sowing), we re-measured the height and diameter of the tagged seedlings.

3.5 Measuring Light Availability and Soil Moisture

In March 2012, we took hemispherical photographs of the forest canopy to estimate the proportion of sunlight available to the seedlings in each split-plot. We took photographs using a Nikon Coolpix 8700 digital camera, mounted on a self-leveling tripod and fitted with a FC-E9 fisheye converter lens. We took photographs at the center of each split-plot, at a height of approximately 40 cm. We used the HemiView Software package (Delta-T Devices, v 2.1) to analyze the photographs and estimate the Global Site Factor (GSF) for each split-plot. The GSF is the proportion of global solar radiation that is available under open sky, at a given location.

Also in March 2012, we estimated the average percent volumetric soil moisture content (θ_v) of each split-plot to a depth of 20 cm. Because March is the fifth month of the six-month dry season, soil moisture was at or near the annual low. We used a HydroSense Soil-Water Measurement System (CD620, CS620, Campbell Scientific, Inc.), fitted with two 20 cm soil moisture probes to conduct measurements. We took readings by inserting the probes vertically into the soil surface at three locations in each split-plot: the center and two opposing corners. The HydroSense system uses the soil dielectric permittivity between its two probes to estimate the average soil volumetric moisture content over the probe length. The system, however, is calibrated to provide θ_v estimates for agricultural rather than forest soils (Cambell Scientific 2010). To adjust estimates to accurately reflect soil moisture on the restoration plots, we used the method described in Cznarmoski et al. (2005) to create a calibration curve from intact soil columns taken from the restoration plots. We plotted the averaged readings from each split-plot along the calibration curve to estimate the average percent θ_v for each split-plot.

3.6 Data Analyses

We used three linear mixed models (LMMs) to test the effects of microsite treatment, species, and the interaction between microsite treatment and species on 1) seed germination, 2) survival of germinants, and 3) growth of seedlings

For LMM1, we defined germination as the proportion of planted seeds that had germinated at any time within the first four months of planting, when microsite treatments were still being maintained. For LMM2, we defined survival as the proportion of seedlings alive at the monitoring event at four months that were still alive at the monitoring event at 26 months. For LMM3, we defined growth as the height and diameter of seedlings 20 months after seed sowing.

At the monitoring events that occurred nine and 26 months after seed sowing we observed a small number of new *A. lawii* and *C. polyanthum* seedlings, but we excluded these from all LMM analyses because they had emerged after microsite treatments had ceased.

We excluded one species, *H. amygdalina*, from both LMM2 and LMM3 due to insufficient survival data. This species had low germination (approximately 5% of planted seeds germinated) and as a result, 20% of split-plots planted with *H. amygdalina* had no germinating seeds from which to obtain survival proportions or growth measurements. In addition, in LMM2 the number of surviving seedlings varied widely among the four included species. LMM2 therefore weighted each split-plot's survival proportions by the number of seedlings on the split-plot that were alive at the monitoring event conducted four months after seed sowing to compensate for bias from survival proportions derived from small numbers of seedlings.

To account for the nested structure of the experimental design, we included both plot and subplot as random effects in all LMMs. In addition, we logit transformed germination and survival proportions and log transformed height measurements to stabilize variance and normalize the data. For each model, we calculated the summary statistic R^2_{GLMM}, as described in Nakagawa and Schielzeth (2013), to quantify the amount of variance explained by the model, as well as to provide an absolute value describing the model's goodness-of-fit. We conducted all analyses in the R 3.0.2 software environment (R Development Core Team 2013).

4. Results

4.1 Nursery Germination

Nursery germination for all species except *H. amygdalina* was less than 50% of the mean germination observed in the field experiment (Table 3.2). Large numbers of seeds with fungal growth or rotting suggests that overwatering may have been the cause of low germination. Because germination in the field experiment indicated greater seed viability for these species than was demonstrated in the nursery, we could not use the results of the nursery trials to estimate the overall viability of the seed stock for these species. Furthermore, although more *H. amygdalina* seeds germinated in the nursery than in the field (Table 3.2), previous FORRU germination tests for this species reported germination rates of more than twice that of this investigation (FORRU 2016). This suggests that *H. amygdalina* seeds in our nursery trial may have also been affected by overwatering, albeit to a lesser extent than the other four species. Consequently, we were also unable to estimate *H. amygdalina* seed stock viability with confidence.

Table 3.2 Percent germination (Germ) for planted seeds (*n*) in nursery and field trials. The table also includes the results of FORRU nursery germination trials conducted between 1995 and 1997 (FORRU 2016).

	Nursery		Field		FORRU	
Species	*n*	Germ (%)	*n*	Germ (%)	*n*	Germ (%)
A. lawii	100	13.0	598	68.6	72	55.6
B. ramiflora	100	8.0	600	58.5	72	51.4
C. polyanthum	100	5.0	600	30.3	72	31.9
M. caloneura	100	13.0	600	26.5	72	70.8
H. amygdalina	75	28.0	599	5.3	72	94.4

4.2 Field Experiment

4.2.1 Seed Germination

In the field experiment, the mean germination percentage for all split-plots (n = 120) was 37.0% (sd = 27.4%). Mean germination percentages across split-plots by species (n = 24 for each species) ranged from a minimum of 5.4% (sd = 3.9%) for *H. amygdalina* to a maximum of 68.6% (sd = 27.2%) for *A. lawii* (Table 3.3 and Figure 3.1a).

Microsite treatments did not significantly affect overall germination ($F_{3,92} = 1.11$, p = 0.35), nor did the treatments affect species differently ($F_{12,92} = 1.31$, p = 0.23). Species germination rates (irrespective of treatments), however, were significantly different from one another ($F_{4,92} = 70.7$, $p < 0.0001$; Figure 3.1). The statistical model explained 70% of the variance in germination ($R^2_{GLMM} = 0.70$).

4.2.2 Germinant Survival

The mean percent 26-month survival of germinants across all split-plots (n = 120) was 58.5% (sd = 36.8%). Mean percent survival across split-plots by species (n = 24) ranged from a minimum of 23.0% (sd = 46.6%) for *M. caloneura* to a maximum of 92.4% (sd = 9.1%) for *A. lawii* (Table 3.3 and Figure 3.1b).

Microsite treatments did not significantly affect overall germinant survival ($F_{3,75} = 0.74$, p = 0.53), nor did treatments affect germinant survival differently by species ($F_{9,75} = 0.85$, p = 0.58). Germinant survival irrespective of treatment, however, was significantly different among species ($F_{3,75} = 15.97$, $p < 0.0001$; Figure 3.1). The statistical model explained 18% of the variance in survival ($R^2_{GLMM} = 0.18$).

Table 3.3 Mean percent germination of sown seeds across split-plots by species 4 months after sowing (*n* = 24 split-plots per species) and mean 26-month survival of germinants across split-plots by species. Standard deviations are in parentheses.

Species	Sown Seed Germination (%)	Germinant Survival (%)
A. lawii	66.8 (27.2)	92.4 (9.1)
B. ramiflora	58.7 (12.2)	34.8 (21.6)
C. polyanthum	27.8 (12.1)	83.8 (15.4)
M. caloneura	26.5 (13.5)	23.0 (21.3)
H. amygdalina	5.4 (3.9)	N/A*

* Mean germinant survival could not be calculated as five *H. amygdalina* split-plots had no germinants.

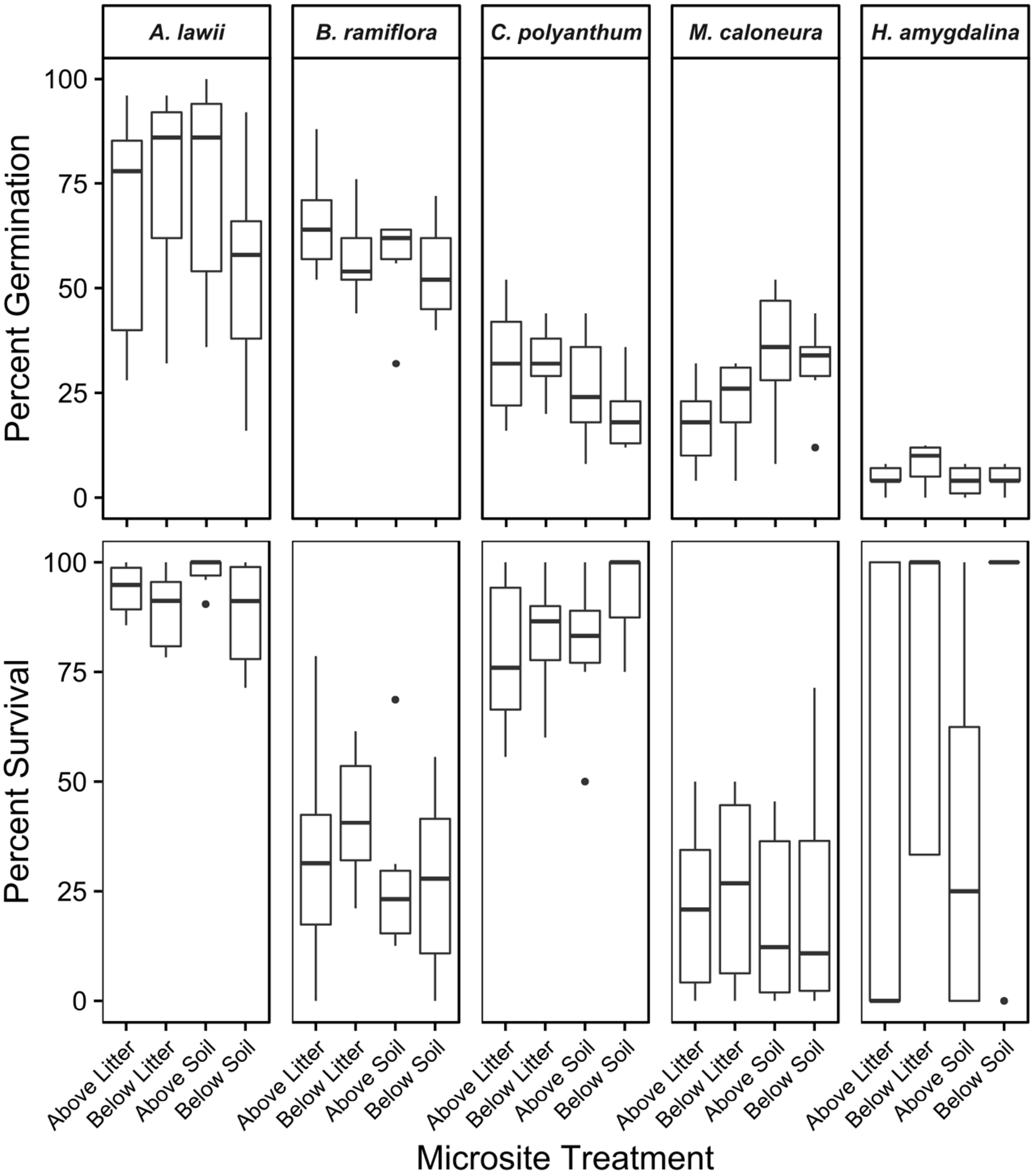

Figure 3.1 Box plots displaying (a) the percent germination of planted species by microsite treatment, 4 months after seed sowing and (b) the percent survival of germinants of planted species by microsite treatment, 26 months after seed sowing. Each box represents the interquartile range (IQR) of the data distribution. The horizontal line across the box represents the distribution median. Boxplot whiskers represent the most extreme data within 1.5 times of the IQR. Outliers outside of 1.5 times the IQR are represented by an individual dot. Note that the boxplots of *H. amygdalina* germinant survival were strongly skewed due to the small number of initial germinants (28).

4.2.3 Seedling Measurements

At 20-months after seed sowing the mean height across all seedlings ($n = 400$) was 17.2 cm (sd = 8.8) and the mean diameter was 3.1 mm (sd = 1.0). Mean height by species ranged from a minimum of 9.7 cm (sd = 2.5) for *B. ramiflora* to a maximum of 27.6 cm (sd = 8.7) for *C. polyanthum* (Table 3.4). Mean diameter by species ranged from a minimum of 1.6 mm (sd = 0.3) for *B. ramiflora* to a maximum of 3.0 mm (sd = 0.6) for *C. polyanthum.* Figure 3.2 provides a boxplot of height and diameter by species and microsite treatment.

Microsite treatments did not significantly affect overall seedling height ($F_{3,362} = 0.23$, $p = 0.88$), nor did the treatments affect the height of species differently ($F_{9,362} = 0.51$, $p = 0.87$). The height of seedlings by species irrespective of treatments, however, were significantly different from one another ($F_{3,362} = 81.39$, $p < 0.0001$). At 20 months, the mean height of the tallest species, *C. polyanthum,* was nearly three times that of *B. ramiflora*, the shortest species, and twice that of *A. lawii, M. caloneura,* and *H. amygdalina*, which all had similar heights (Figure 3.2, Table 3.4). The statistical model explained 97% of the variance in height measurements ($R^2_{GLMM} = 0.971$).

Microsite treatments had marginally significant effects on seedling diameter ($F_{3,362} = 2.22$, $p = 0.085$), though there was no evidence that the treatments affected the diameter of species differently ($F_{9,362} = 0.26$, $p = 0.98$). The diameter of seedlings by species irrespective of treatments were significantly different from one another ($F_{3,362} = 40.86$, $p < 0.0001$) (Figure 3.2). The mean diameters of the five species at 20 months were more evenly spread out than the mean heights; however, the species with largest mean diameter, *M. caloneura* was still more than twice as large as the species with the smallest mean diameter*, B. ramiflora* (Figure 3.2, Table 3.4). The statistical model explained 90% of the variance in diameter measurements ($R^2_{GLMM} = 0.902$).

Table 3.4 Mean seedling height and stem diameter 20 months after seed sowing by species. Standard deviations are in parentheses.

Species	*n*	Height (cm)	Diameter (mm)
A. lawii	143	14.0 (3.6)	2.1 (0.4)
B. ramiflora	75	9.7 (2.5)	1.6 (0.3)
C. polyanthum	117	27.6 (8.7)	3.0 (0.6)
M. caloneura	48	14.4 (2.9)	3.5 (0.5)
H. amygdalina	17	14.1 (3.4)	2.6 (0.6)

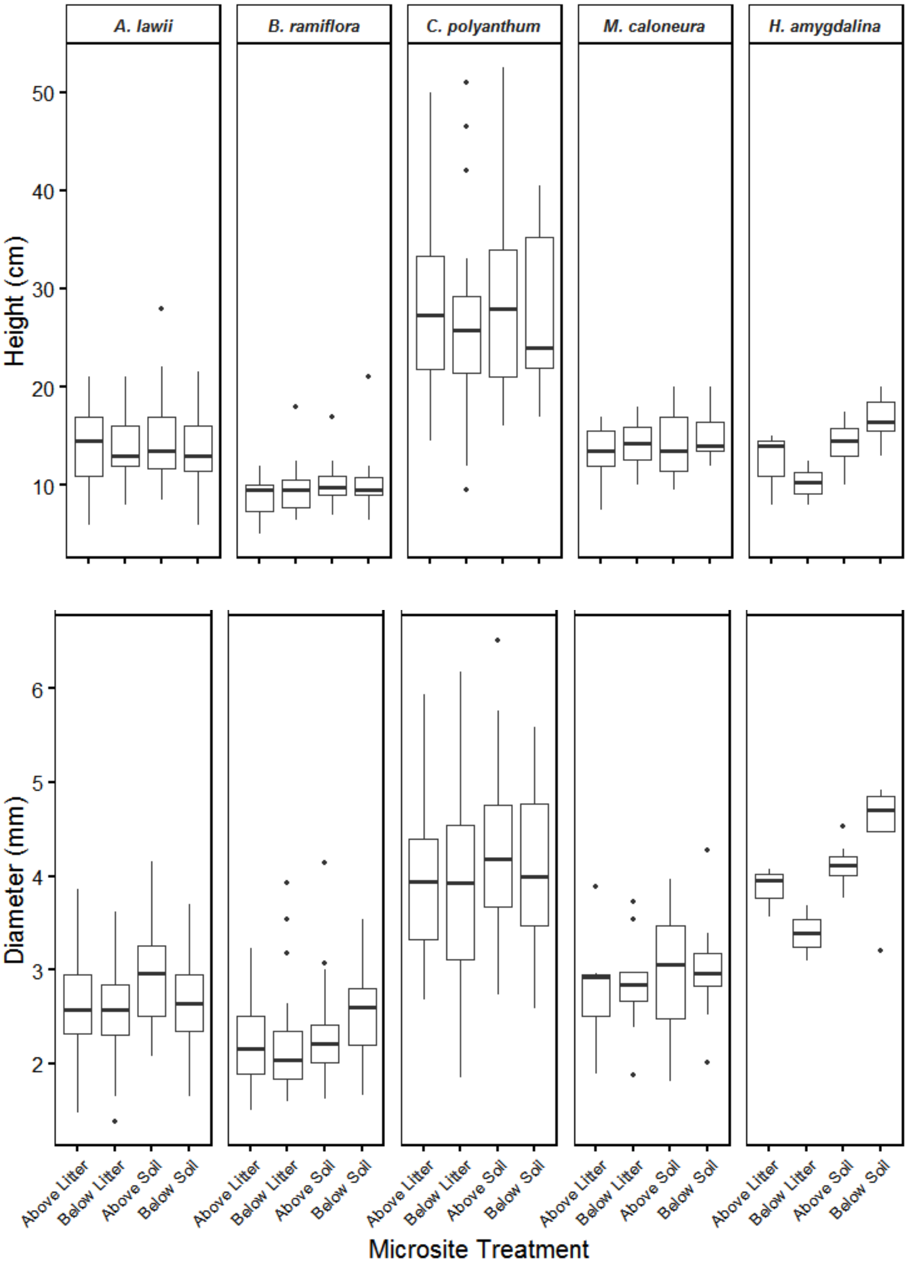

Figure 3.2 Box plots displaying (a) height (cm) of surviving seedlings of planted species by microsite treatment, 20 months after seed sowing and (b) the diameter (mm) of surviving seedlings of planted species by microsite treatment, 20 months after seed sowing. Each box represents the interquartile range (IQR) of the data distribution. The horizontal line across the box represents the distribution median. Boxplot whiskers represent the most extreme data within 1.5 times of the IQR. Outliers outside of 1.5 times the IQR are represented by an individual dot. Note that the boxplots of H. amygdalina measurements may have been skewed by the small number of seedlings (20) that germinated and were still alive at 20 months.

4.3 Patterns in Germination and Survival

Germination of all species peaked at or before the fourth month after planting (Figure 3.3). After the peak, two distinct patterns in seedling survival emerged. *B. ramiflora* and *M. caloneura* survival began to decline rapidly, with *B. ramiflora* survival beginning to decline slightly earlier than *M. caloneura*. Between the four- and nine-month monitoring, the number of surviving *B. ramiflora* seedlings declined by 33.7% and *M. caloneura* seedlings declined by 51.0%. This rate of decline continued through the end of the study. Between the nine- and 21-month monitoring *B. ramiflora* declined an additional 35.2% and *M. caloneura* declined an additional 44.4%. By contrast, survival of *A. lawii* and *C. polyanthum* seedlings remained high throughout the study, declining by just 2.2% and 9.3% respectively between the four- and nine-month monitoring events and an additional 4.6% and 5.2% respectively between the nine- and 21-month monitoring events. The survival of *H. amygdalina* seedlings differed from the other four species in that survival declined rapidly (28.6%) between the four- and nine-month monitoring but slowed between the nine- and 26-month monitoring (5% decline). There were, however, very few *H. amygdalina* seedlings (28 seedlings overall) and trends in this species' survival may have been obscured by the small sample size.

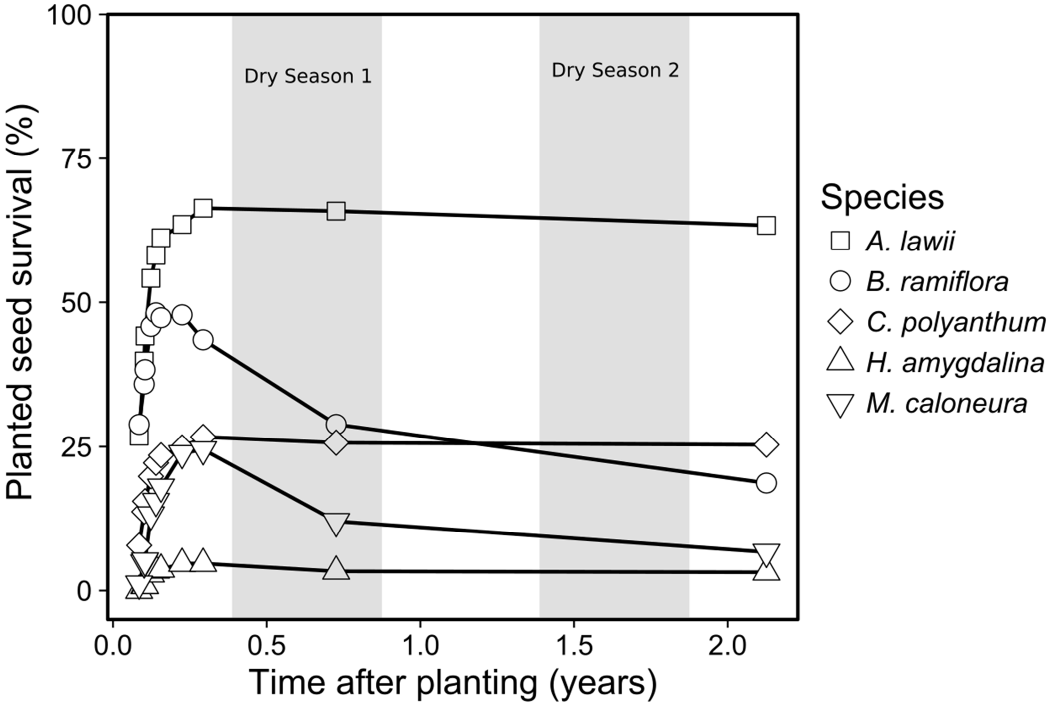

Figure 3.3 Percentage survival of sown seeds (i.e. the percentage of sown seeds that were present as seedlings) in the restored forest.

4.4 Light Availability and Soil Moisture

Dry season light availability estimates, across all split-plots (*n* = 120), ranged from 2.3 to 12.1% with a mean of 5.6% (sd = 1.9%). Dry season soil moisture (volumetric soil moisture content) ranged from 6.5 to 11.7%, across all split-plots (*n* = 120), with a mean of 9.1% (sd = 1.1). We were unable to determine whether there was any correlation between light availability, soil moisture, and seedling survival or growth due to insufficient variation in the estimates of light availability and soil moisture measurements.

5. Discussion

5.1 General Overview

Four of the five large-seeded tree species introduced as seeds into the restored forest had relatively high overall germination (> 25%) and 26-month germinant survival (59.7%), irrespective of microsite treatment. The absence of statistically detectable microsite treatment effects suggests that the basic microsite requirements for germination and early establishment of these species were generally met in the 13-year-old restored forest. Over the first 20 months of the investigation, surviving seedlings of all five species grew in both height and diameter, indicating that conditions were sufficient not only for persistence, but also seedling growth. Furthermore, initial microsite conditions were not correlated with seedling height and only marginally correlated with diameter at 20 months. Microsite treatment effects on seedling diameter appear to be due to slightly higher mean diameters of individuals initially buried beneath leaf litter and mineral soil compared to individuals initially sown on top of leaf litter and above bare mineral soil. The largest difference in mean diameters between treatments, however, was only 0.3 mm. The lack of effect on both post-germination seedling survival and growth suggests that the germination microsites of the type we investigated have little to no effect on the robustness of seedlings. Taken together, the results provide support for the hypothesis that seed availability more strongly limits the recolonization of these species in the restored forest than do understory microsite conditions. This further implies that the complete absence of these species from the understory prior to this investigation was primarily the result of severe to absolute seed limitation, and suggests that other, currently-absent, large-seeded tree species may be similarly limited.

The finding of significant seed limitation in the restored seasonal forest is consistent with the results of similar direct seeding studies of tropical rainforest trees (Makana and Thomas 2004, Svenning and Wright 2005, Vargas and Stevenson 2013) and contributes to the growing body of research that suggests that seed limitation is the norm not only for tropical trees, but also for plant species in general (Turnbull et al. 2000).

The germination and survival percentages in this investigation were comparable to those reported for large-seeded trees sown in similarly-aged, early successional seasonal and moist tropical forest (Bonilla-Moheno and Holl 2009, Cole et al. 2010). Additionally, measurements of understory light availability and dry season soil moisture content (both key limiting factors in tropical forests) were comparable to those in other primary and secondary seasonal forests (Fisher et al. 1991, Baker 1997, McLaren and McDonald 2003). Thus, after a little more than a decade, these understory conditions for seedling regeneration in this restored forest have become similar to naturally regenerating secondary forests. This investigation therefore adds to the growing body of evidence that restoration plantings rapidly ameliorate environmental barriers that once prevented natural forest regeneration (Cole et al. 2010, Bertacchi et al. 2016).

5.2 Seed Viability

Although seed viability may interact with seed availability to limit seedling establishment (Clark et al. 1999), we were unable to isolate viability as a factor in seedling recruitment this investigation due to overwatering of seeds in the nursery test. We were, however, able to make a few observations based on comparisons between field germination in this investigation and previous nursery germination tests that FORRU conducted as part of their effort to identify species suitable for restoration planting. Field germination rates for three of the five species, *A. lawii*, *B. ramiflora* and *C. polyanthum* (Table 3.2), were similar to or greater than those reported for previous FORRU germination tests (FORRU 2016). However, two species, *H. amygdalina* and *M. caloneura*, had considerably lower germination rates in the field experiment than in the FORRU germination tests. Comparatively poor germination for these two species may have been the result of extended seed storage and late seed harvesting, especially in the case of *H. amygdalina*. Future experiments should include additional tests of seed viability to determine the degree to which seed viability limits establishment in restored forest.

5.3 Microsite Effects

Neither placement of seeds on top of or below 5 – 10 cm of leaf litter affected seed germination and 26-month survival and growth of germinants. The absence of any leaf litter effect in this investigation contrasted with studies that have reported that, compared to placement on bare mineral soil, leaf litter inhibits both germination and survival of seedlings in the understory (Putz 1983, Vazquez-Yanes and Orozco-Segovia 1992, Dalling and Hubbell 2002). Species in these studies, however, were nearly all small-seeded pioneers. Studies that include late-successional species with seed sizes comparable to those in this investigation, on the other hand, have similarly found either small positive or no effect of litter on germination and seedling survival in forest understory (Molofsky and Augspurger 1992, Makana and Thomas 2005, Dupuy and Chazdon 2008). Furthermore, Makana and Thomas (2005) report that similar to the seedlings in our study, the presence or absence of litter has little effect on growth of large-seeded species in the understory. The results of this investigation therefore contribute to the growing body of research indicating that, while leaf litter may strongly influence the establishment of small-seeded species, it is neither an impediment nor a requirement for the establishment of large-seeded trees in the understory.

Although we found that burial of seeds in soil had no discernable effect on germination and survival, several studies have found that burial beneath soil strongly increases tropical tree recruitment, particularly for large-seeded species (Hardwick et al. 1997, Woods and Elliott 2004, Doust et al. 2006). These studies, however, have been conducted in abandoned agricultural fields, where climatic conditions are likely to be harsher. Under these conditions, burial may enhance recruitment by maintaining temperature and humidity at levels required for germination and preventing loss of recalcitrant seeds due to desiccation. In the restored forest, however, the canopy cover may be sufficient to maintain adequate temperature and humidity for germination without burial. Moreover, 2011, the year this investigation was initiated, was an exceptionally wet year throughout Thailand, with the annual rainfall reaching 24% above normal (Thai Meteorological Department 2012). It is therefore possible, given the high-year-to-year variability in levels and timing of precipitation, that seeds may be more sensitive to microsite environments in drier years. For example, in Panama survival of pioneer tree seedlings began to decrease after dry spells of only four days (Engelbrecht et al. 2006).

Increased recruitment of buried seeds may also be attributed to protection from seed predators (Cintra 1997, Brewer and Molly 2001). In this investigation, however, we attempted to limit the test to the effects of abiotic microsite factors alone on recruitment by erecting fences to exclude small mammalian seed predators. Although we did not take steps to prevent bird and insect seed predation, we also did not observe evidence of either form of predation. While it is not possible for us to quantify potential seed predation outside of fenced exclosures, the high density and species richness of naturally-recruited seedlings (1.1 seedlings m^{-1}, 58 species) observed during the understory seedling survey of the restored forest plots, suggests that recruitment limitation due to seed predation in the forest is low (Sinhaseni 2008).

5.4 Seasonal Microclimate Effects

Based on hemispherical photographs taken during the dry season, we estimated that the seedlings in this investigation received approximately 6% of full sun during the dry season. Although at present, we know very little about light conditions in intact EGF, dry season understory light in lower-elevation Thai mixed deciduous forest appears to be somewhat higher (approximately 10% of standard overcast sky distribution), possibly due to the higher proportion of deciduous trees in that forest type (Marod et al. 2004). Volumetric soil moisture during the height of the 2012 dry season was approximately 9%. This is intermediate between dry season θ_v reported for wetter (Meinzer et al. 1999) and drier SDTF (Baker et al. 2005).

Although we were able to characterize the light availability and volumetric soil moisture content of the research sites during the first dry season, we were unable to incorporate these measures into analyses of seedling survival and growth due to low variation in the environmental data. This was likely the result of the close proximity of split-plots within subplots. Seasonal changes in understory light availability, however, are characteristic of SDTF due to the prevalence of deciduous canopy trees in many of these forests (Murphy and Lugo 1986).

Several studies have suggested that, in seasonal forests, drought filters tree seedlings during the first dry season after germination (Lieberman and Li 1992, Gerhardt 1996, McLaren and McDonald 2003). In our investigation, three of the tested species (*B. ramiflora*, *M. caloneura*, and *H. amygdalina*) experienced substantial declines in survival (≥28.5%) over the course of the first dry season. *H. amygdalina* had very few seedlings due to low germination; therefore patterns in survival may be obscured by the small sample size. High mortality of *M. caloneura* during the first dry season, however, corresponds with Marod et al. (2002)'s investigation of seedling dynamics in a Thai mixed deciduous forest. In their study, all of the naturally-recruited first-year *M. caloneura* seedlings died as a consequence of dry-season drought. Survival of *B. ramiflora* seedlings contrasted with *M. caloneura* in that *B. ramiflora* seedling survival began to decline a month prior to the start of the first dry season (Figure 3.3). This suggests that factors in addition to drought may have contributed to reducing early survival of *B. ramiflora* seedlings. One potential factor may have been insect predation, which we frequently observed on young *B. ramiflora* leaves. After the first dry season, both *B. ramiflora* and *M. caloneura* survival continued to decline; however, there were too few monitoring events to determine whether the declines were continuous or corresponded with the second dry season. If the declines were continuous, this would suggest that other factors such as low light availability may be contributing to the filtering of seedlings from the understory. In contrast to *B. ramiflora* and *M. caloneura*, survival of the *A. lawii* and *C. polyanthum* remained very stable over the entire course of the investigation, declining by ≤ 14.4% between four- and 26-months after sowing (Figure 3.3). Low mortality over two dry seasons provides strong evidence of high drought tolerance for seedlings of these species and suggests that, while seasonal drought may filter some large-seeded tree species from the restored forest, drought tolerance may also be fairly common. Consequently, the impact of seasonal drought on seedling composition in the restored forest may be less important than the effects of factors such as seed availability for many species.

5.5 Effects of Seed Size on Early Establishment

Although we did not explicitly include seed size as a tested variable, the five species included in this investigation spanned a relatively wide range of seed sizes (Table 3.1) and there were significant differences in both seed germination and 26-month survival between species. We were therefore able to make some observations concerning the results based on the seed sizes of the five species.

Numerous studies have found strong positive correlations between larger seed size and increased rates of early establishment (see review in Leishman et al. 2000); however, the two smallest-seeded species in our study (*B. ramiflora* and *A. lawii*) had, by large margins, the highest germination rates. Furthermore, although survival of *B. ramiflora* later declined rapidly after germination, *A. lawii*, went on to have the highest overall survival in addition to the highest percent germination. This suggests that seed size alone does not predict establishment success, at least not in a year with high rainfall.

As was previously discussed, none of the tested species, including the two smallest-seeded species, were affected by the microsite treatments. Several studies have found that leaf litter affects recruitment of trees differently by seed size. Poor recruitment of species with smaller seeds in other studies has been attributed to light interception by leaf litter, and leaf litter acting as a barrier to both seedling radicles and seedling emergence above the litter (Molofsky and Augspurger 1992, Vazquez-Yanes and Orozco-Segovia 1992, Dalling and Hubbell 2002, Dupuy and Chazdon 2008). It should be noted, however, that the smallest seeds in this study were still two or more orders of magnitude larger than the seeds that were categorized as small in several of the previously cited investigations (e.g. 0.45 g in this investigation versus 0.0019 g in Molofsky and Augspurger (1992)). Thus even the smallest seeds in our investigation may meet the minimum size threshold required to overcome microsite obstacles to germination and establishment at rates similar to, or even greater than, other, larger-seeded species.

5.6 Implications for Tropical Forest Restoration

By demonstrating that seed availability more strongly limits colonization of young restored forest by large-seeded, late-successional trees than microsite conditions, this investigation underscores the critical importance of seed limitation in the restoration of the tree community. Given that sources of seed limitations (e.g. distant seed sources, low seed production, and poor animal-dispersal) are unlikely to decrease in the foreseeable future, active intervention will be required to ensure that large-seeded tree species are represented in the future forest. Enrichment planting, the interplanting of tree species into the existing forest, may augment forest species diversity by introducing absent species. Enrichment planting is most often carried out using nursery grown seedlings and saplings (Lamb et al. 2005); however, raising seedlings in a nursery is costly, labor intensive, and limits planting to just those species that are suitable for nursery propagation (Engel and Parrotta 2001, Zahawi and Holl 2009). Direct seeding (i.e. sowing seeds directly into restoration habitats), on the other hand, can be a far more efficient and cost-effective means of enrichment planting (Cole et al. 2010). Although we did not explicitly focus on testing the viability of direct seed enrichment planting, successful seedling establishment from introduced seeds in our investigation supports Cole et al.'s (2010) finding that direct-seed sowing is a viable means of introducing large-seeded, late-successional tree species into young restoration plantings. Furthermore, our results add to the growing body of research indicating large-seeded, late-successional trees are well-suited for direct-seeding under a range of early successional conditions (Hardwick et al. 1997, Camargo et al. 2002, Hooper et al. 2002, Bonilla-Moheno and Holl 2009) .

This investigation also has potential implications for the selection of direct seeding methods. Although some studies have reported increased recruitment following burial of large seeds (Hardwick et al. 1997, Doust et al. 2006), this study found that microsites did not significantly affect seed germination or survival and growth of seeds sown beneath the canopy of 13-year-old restored forest. This suggests that direct seeding by broadcast sowing of seeds onto the leaf litter may be just as effective as seed burial, while also being considerably easier and cheaper to implement. However, as previously discussed, there was unusually high precipitation in the first year of this investigation. In addition, our seeds were protected from some forms of seed predation by a fence. Consequently, additional research should first clarify the relationship between seedbed microsites and factors such as variable annual precipitation and seed predation prior to the use of broadcast sowing in large-scale enrichment planting,

Although the species tested in our investigation were all putatively shade-tolerant, mature-forest species, they manifested a wide range of germination, survival, and growth responses in the restored forest understory. These differences underscore the need for additional seed sowing experiments to test the suitability of desired species for direct seed enrichment planting. They also suggest the need for an objective means of comparing species suitability to facilitate species selection by forest managers. Tunjai and Elliott (2012) proposed one such method that scores species based on a combination of establishment (percent survival of seeds at one year after sowing) and height growth and then ranks those scores relative to other species. When we applied a version of this method to the results of our investigation, *C. polyanthum* and *A. lawii* were the highest ranked of the five tested species. This suggests that these two species are most suitable for direct seed enrichment planting *if* the primary objective of planting is maximizing seedling establishment and growth. Enrichment planting in the restoration setting, however, may have additional objectives such as increasing diversity and habitat value and conserving rare and endangered species. Future ranking methods should incorporate factors related to these objectives as well as efficient establishment and growth to ensure that the resulting rankings accurately represent the value of species towards meeting all enrichment planting goals.

Finally, final seedling heights in our investigation were similar to those reported by Cole et al. (2010) for two-year old, large-seeded, late successional tree seedlings sown into 8-10-year-old rainforest restoration plantings, but our results further indicate that most seedling height was attained within the first nine months after sowing. With the exception of *C. polyanthum*, growth of all seedlings slowed substantially between nine and 20 months after sowing, gaining only about 3 cm overall. Such slow growth may be characteristic of seedlings established by direct seeding in the understory of restoration plantings given the similarities in final seedling height between our investigation and Cole et al. (2010). This suggests that seedling establishment alone may be insufficient to ensure timely maturation of desirable large-seeded species in the restored forest. Research that pairs direct seeding with additional management interventions such as gap formation or seasonal watering may accelerate the rate of maturation. Moreover, similar treatments may also facilitate the recruitment and establishment of species that had relatively poor establishment in this investigation, thereby increasing their suitability for direct-seed enrichment planting.

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Chapter 4 – Seedling Dynamics in Seasonally Dry Tropical Forest Restoration Plantations and Their Response to Limiting Environmental Factors

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ABSTRACT

Seasonally dry tropical forest (SDTF) restoration plantings have catalyzed understory tree seedling recruitment, but little is known about post-recruitment seedlings dynamics (i.e. survival and growth) and their interaction with environmental filters. For two years we measured the survival and growth of naturally-recruited seedlings of thirteen tree species in 11 – 14 year old Thai SDTF restoration plantations. We also investigated the relationship between survival, growth, and microsite variations in understory light and dry season soil moisture. Sampled species included both new colonizers and the offspring of planted species. Among these were pioneer, intermediate and late-successional species. High two-year survival (≥ 69%) and continuous growth of intermediate and late-successional species indicate the understory environment is adequate for regeneration of these species. Three early successional species, however, had high mortality (≤ 50.5% survival) and may be less likely to successfully regenerate. Survival of intermediate and late successional planted species was comparable to that of intermediate successional colonizing species, suggesting many planted species may be able to regenerate in close proximity to parent trees. Although the range of light availability in understory microsites did not appear to limit survival, light availability strongly limited seedling growth. Neither survival nor growth appeared to be limited by dry season soil moisture. Neither of the two measured factors explained all growth; therefore additional factors (e.g. soil nutrients) should be investigated in future research. Results suggest management interventions to increase light and soil moisture are unnecessary to increase survival post-recruitment, but increasing light (e.g. thinning) may hasten maturity. Practitioners should focus on enrichment planting of dispersal-limited species to accelerate ecosystem reassembly. Enrichment planting in young restoration plantations may give seedlings a competitive advantage over the offspring of planted species, as well as enhance their access to light.

1. Introduction

Although seasonally dry tropical forest (SDTF) once comprised 42% of the world's tropical forest area, it is now the Earth's most threatened terrestrial tropical ecosystem (Janzen 1988, Miles et al. 2006). Regeneration of formerly forested lands may increase SDTF area and provide a safety net for endemic species threatened by habitat loss. However, barriers to regeneration may be particularly high in this forest type due to prolonged seasonal drought (≥ 6 months). Consequently, the development of strategies to accelerate tree recolonization and catalyze the regeneration cycle in former SDTF has become a research priority (Ray and Brown 1995, Vieira and Scariot 2006, Griscom and Ashton 2011, Lamb 2011).

In Northern Thailand, active forest restoration using mixed native species plantings has been shown to rapidly re-establish forest cover in former SDTF (Elliott et al. 2003). Planted trees generally established closed canopies within four years of planting. Soon after, seedling communities begin to develop in the understory. A survey conducted on ten-year-old restoration plantations found species-diverse tree seedling communities that included both new colonists and plantation species (Sinhaseni 2008, Lamb 2011). These seedlings spanned the spectrum of successional stages, from pioneers to late-successional species and included a number of different leaf and growth traits. Their recruitment is an encouraging indication that restoration plantations have catalyzed initial forest regeneration processes. Furthermore, the species composition of seedling communities suggests a development trajectory towards a forest that will be diverse in both species and functional traits.

Recruitment of a diverse seedling community, though necessary, is only the first step in the re-assembly of the tropical forest ecosystem. Seedlings experience high mortality compared to later life stages (Harper 1977). It is during the seedling stage that environmental filtering, the non-random survival of individuals as a result of environmental habitat characteristics, is strongest (Baldeck et al. 2013). Even when the environment does not impact seedling survival, it may still limit growth and maturation (Delissio et al. 2002, Montgomery and Chazdon 2002). Over time, filtering and repression of seedlings in the understory may be as consequential to the trajectory of forest development as initial seedling recruitment.

In tropical forest, understory light availability is widely presumed to be the key factor limiting seedling survival and growth. This is based largely on research from moist tropical forests where light availability has been shown to exert strong selection pressure on shadeintolerant species while also acting as the primary factor limiting growth of shade-tolerant seedlings on the forest floor (Whitmore 1996). Although shade-tolerant species may persist for years in the understory, many will not mature without increased light from canopy gaps (Denslow 1987). The role of light in the regeneration of SDTFs, however, is not as clear. In these forests light may be less limiting due to higher understory light levels resulting from lower, less complex canopies and higher proportions of deciduous trees (Murphy and Lugo 1986). Extended SDTF dry seasons may make drought rather than light the most important factor in seedling establishment and survival (Vieira and Scariot 2006, Poorter and Markesteijn 2008, Ferreira et al. 2015). In some cases, high levels of light may actually decrease survival of mature forest seedlings in SDTF by increasing water stress during the dry season (Lieberman and Li 1992, McLaren and McDonald 2003).

Given that the seedling dynamics and their interaction with key environmental factors may play a critical role in determining the trajectory of forest development, an understanding of these processes in restored forest plantations is necessary to evaluate the progress of ecosystem assembly and to determine whether additional intervention will be required to meet restoration objectives. In this observational study, we seek to address this need by 1) characterizing seedling survival and growth over two years in the understory of young Thai restoration plantation and 2) investigating the effect of microsite variations in understory light and dry season soil moisture on seedling dynamics in the developing SDTF. Because the monitored species spanned a range of functional groups and included species recruited from both inside and outside of the plantations, we also looked for patterns that might increase our understanding of regeneration strategies used by SDTF species. Finally, we discuss the potential management implications suggested by our results and observations.

2. Study Site

This study was conducted on ten experimental forest restoration plots, covering an area of approximately 1.6 ha, located along or immediately below the ridge of a watershed (1,207 – 1,310 m above mean sea level) in Doi Suthep-Pui National Park (DSNP), Northern Thailand. Average annual precipitation at this elevation is 2,095 mm (as recorded by the Kog-Ma Watershed Research Station, the weather station nearest to the forest restoration plots) (Elliott et al. 2003). Although this level of rainfall places the study site at the moist end of the precipitation spectrum for seasonally dry tropical forests (Dirzo et al. 2011), virtually all rainfall occurs during the six-month wet season that extends from May through October. Precipitation averages less than 100 mm per month during the dry season from November to April (Elliott 2003).

The study site was originally covered with tropical, seasonally dry, evergreen forest (EGF). Primary EGF represents the park's most species-rich forest type, providing habitat for approximately 250 documented tree species, two-thirds of which are evergreen (Maxwell and Elliott 2001). EGF is also the DSNP's most endangered forest type as much of it has been cleared for cultivation. The forest restoration plots under consideration had been cleared for farming for over two decades prior to plantation planting. The land was later abandoned due to declining fertility and became dominated by herbaceous weeds (Elliott et al. 2000).

At the time of this investigation, most of the slopes below the plots were still being cultivated to provide income and subsistence for the residents of Ban Mae Sa Mai, a Hmong village community (population of about 1,700) within park boundaries (Neef et al. 2004), approximately 2 km south of the experimental blocks (18º52´N, 98º51´E). The nearest extensive patch of intact, primary EGF is approximately 1 – 2 km east of the plots.

Chiang Mai University's Forest Restoration and Research Unit (FORRU) began establishing experimental forest restoration plots in 1997 to test and refine the Framework Species Method (FSM) for EGF restoration. Since then, FORRU has added new plots annually. The FSM uses mixed plantings of 25 – 30 species of hardy, fast-growing native trees to catalyze forest succession. Trees are planted at a density of approximately 3,125 trees ha^{-1} and canopy closure in the plantations is complete within four years of planting (Anusarnsunthorn and Elliott 2004, FORRU 2005). The canopy facilitates regeneration of tree seedlings in the understory by shading out herbaceous competitors and moderating the understory climate (Goosem and Tucker 1995, Elliott et al. 2003, Lamb et al. 2005). Following canopy closure, the FSM relies on natural seed dispersal from intact forest to continue the process of restoring the floristic composition.

We conducted our investigation on ten 0.16 ha forest restoration plots planted between 1997 and 2000. At the initiation of this investigation in 2011, the plots were between 11 and 14 years of age. They were chosen because they were the oldest and most developed forest restoration plots in DSNP. Seven of the ten plots were adjoining, forming a continuous stretch of forested land. The three remaining plots shared no borders, but were surrounded on at least three sides by other, younger, FSM plots or by regenerating secondary forest. At the start of this investigation, the plantations on the oldest of the ten plots had begun to develop a dense two-layered canopy (Wydhayagarn et al. 2009).

FORRU alters each year's species mixture in response to seedling availability and the results of previous field trials. There is, however, generally a high degree of species overlap in the planting mixtures. In the species mixtures used between 1997 and 2000, four species were included in all four years and 27 species overlapped at least two years. Additional details regarding the planting, maintenance, and monitoring of the plots can be found in Elliot et al. (2003).

3. Methods

3.1. Species Selection

For this investigation, we monitored naturally-recruited seedlings belonging to thirteen tree species. The selected species encompassed a range of putative successional types, growth habits, and leaf deciduousness (Table 4.1). Assignment of successional types was based on observations made by FORRU and descriptions of species habits in Maxwell and Elliott (2001) and Gardner et al. (2007). Our criteria for species selection also required that we be able to sample at least 100 seedlings for that species and the seedlings occur in at least three restoration plots. Nine of the species were also included in the planting mixtures used to establish the restoration plantations. We observed mature, seed-bearing individuals belonging to all but one of these nine species (*Cica*) on the restoration plantation plots, therefore we assumed that most, if not all of the seedlings belonging to plantation species are the offspring of planted individuals rather than the result of seed dispersal from outside of the plantations. Hereafter we refer to the offspring of the nine planted species as "plantation" seedlings and seedlings belonging to the remaining four unplanted species as "colonizing" seedlings, because they were dispersed into the plots from outside seed sources.

Table 4.1 The names and traits of the species used in this investigation.

Species	Abbrev.	Family	Recruitment	Seed Dispersal	Canopy Position	Leaf Type	Successional Type
Archidendron clypearia	*Arcl*	Leguminosae	Plantation	Wind	Sub-canopy	Evergreen	Intermediate
Artocarpus lakoocha	*Arla*	Moraceae	Colonizing	Animal	Canopy	Deciduous	Pioneer
Bauhinia variegata	*Bava*	Leguminosae	Plantation	Wind	Canopy	Deciduous	Pioneer
Castanopsis calathiformis	*Csca*	Fagaceae	Plantation	Animal	Canopy	Evergreen	Late
Cinnamomum caudatum	*Cica*	Lauraceae	Plantation*	Animal	Canopy	Evergreen	Late
Erythrina subumbran	*Ersu*	Leguminosae	Plantation	Wind	Canopy	Deciduous	Pioneer
Ficus hirta	*Fihi*	Moraceae	Colonizing	Animal	Sub-canopy	Evergreen	Intermediate
Heynea trijuga	*Hetr*	Meliaceae	Plantation	Animal	Sub-canopy	Evergreen	Intermediate
Litsea salicifolia	*Lisa*	Lauraceae	Plantation*	Animal	Canopy	Evergreen	Intermediate
Prunus cerasoides	*Prce*	Rosaceae	Plantation	Animal	Canopy	Deciduous	Pioneer
Rhus rhetsoides	*Rhrh*	Anacardiaceae	Plantation	Animal	Canopy	Evergreen	Pioneer
Schima wallichii	*Scwa*	Theaceae	Colonizing	Wind	Canopy	Semi-deciduous	Intermediate
Turpinia pomifera	*Tupo*	Staphyleaceae	Colonizing	Animal	Sub-canopy	Evergreen	Intermediate

*These species were included as part of the planting mixture for a single year; however, their seedlings were identified across plots of different ages. This indicates that seedlings on other plots have originated from planted trees in adjacent plots or from external seed sources.

3.2. Seedling Sampling

In January 2011, we tagged at least 100 seedlings of each species by encircling the stem of each seedling with a labeled aluminum wire tie. We also placed a flag bearing a duplicate tag in the soil beside each seedling to facilitate re-location and re-identification. We attempted to select seedlings such that conspecifics were spread out as widely as possible across multiple plots. At the minimum, however, each seedling was at least 1 m in distance from the nearest conspecific seedling.

In February 2011, we measured the diameter of each seedling at 2 cm above the soil and marked the location of measurement using white acrylic paint to facilitate accurate re-measurement at subsequent monitoring events. We also measured seedling height from 2 cm above the soil to the tip of the apical bud. In February 2012 and February 2013, we recorded seedling mortality, re-measured the diameter and height of surviving seedlings, and if needed, we re-applied white acrylic paint to the stems to mark the location of measurement.

3.3. Light Availability Estimates

We estimated the microsite light availability using hemispherical canopy photographs taken directly above each seedling in January and February 2011. We took the photographs during the dry season because the absence of rain and mist allowed us to take clear canopy photographs. Light estimates from these photographs are likely to be higher than the actual light received by seedlings throughout the course of a year because of seasonal changes in leaf cover due to the presence of deciduous species among the canopy trees. We attempted to take additional photographs during the 2011 rainy season to provide a more complete estimate of microsite light availability throughout the year, but were unable to use the photographs due to light diffusion caused by mist and droplets of water on the lens. Strong correlations between light estimates made from the dry season hemispherical photographs and seedling growth (discussed below), however, suggest that these estimates were sufficient to detect relationships between light and seedling dynamics in the understory.

We took photographs with a Nikon Coolpix 8700 digital camera mounted on a self-leveling tripod and fitted with a FC-E9 fisheye converter lens. Photographs were taken as close to the top of each seedling as possible, but at a minimum height of approximately 40cm above the ground. We used the HemiView Software package (Delta-T Devices, v 2.1) to analyze photographs and estimate the Global Site Factor (GSF) above each seedling. Prior to analysis we classified all photographs with a programming script. This script converted the photographs from RGB to CIE space and identified all blue and white hues as sky and all other hues as sky obstructions (i.e. canopy). Finally, it converted the photographs to binary black and white images where the sky was white and the canopy black. Classifying photographs in this manner allowed us to minimize operator bias and streamline the processing and analysis of photographs for 1,334 seedlings.

The GSF is an index of the proportion of global radiation reaching a location relative to that of a location with no sky obstructions, although in this investigation we converted GSF to a percentage for ease of interpretation. HemiView defines global radiation at any given time as the sum of diffuse and direct radiation that reaches a location after passing through openings in the canopy (Rich et al. 1999). Thus, GSF in this investigation is analogous to the percentage of full sun available at each seedling microsite. We should note that direct and diffuse light estimates used to determine GSF were based on interactions between the path of the sun and the canopy under clear conditions. Radiation estimates may be different from actual measurements since those depend on conditions at any given point in time. GSF should therefore be viewed as an estimate of potential long-term radiation at a given location.

3.4. Dry Season Soil Moisture

In March 2012, we measured microsite volumetric soil moisture content (θ_v) for each seedling to a depth of 20 cm. Since March is the fifth month of the six-month dry season, θ_v was assumed to be at or near the annual low. We used a HydroSense Soil-Water Measurement System (CD620, CS620, Campbell Scientific, Inc.), fitted with two 20-cm soil moisture probes to conduct measurements. We took two measurements for each seedling by inserting the probes vertically into the soil surface at two locations on opposite sides of the seedling. Both insertions were approximately 10 cm from the base of the stem to minimize damage to seedling roots. The HydroSense system uses the soil dielectric permittivity between its two probes to estimate the θ_v over the probe length. The system, however, is calibrated to provide θ_v estimates for agricultural rather than forest soils (Cambell Scientific 2010). To adjust estimates to accurately reflect soil moisture on the restoration plots, we used the method described in Czarnomoski et al. (2005) to create a calibration curve from intact soil columns taken from the restoration plots. We plotted the average of the two readings from each seedling along the calibration curve to determine the θ_v for the seedling.

3.5 Data Analysis

3.5.1 Linear mixed model overview

We used six linear mixed models (LMMs) to investigate the relationship between environmental variables (i.e. understory light availability and dry season soil moisture) and seedling survival and growth. All models included environmental variables as fixed effects and plot as a random effect to account for the influence of plot on seedling survival and growth. Models also included interactions between the environmental variable of interest and species. We calculated the summary statistic R^2_{GLMM} for each model as described in Nakagawa and Schielzeth (2013) to quantify the amount of variance explained by each model as well as to provide an absolute value describing the model's goodness-of-fit. We conducted all analyses in the R 3.0.2 software environment (R Development Core Team 2013).

Models of height growth included seedlings alive during the entire investigation period with height growth > 0.5 cm. Models of diameter growth included surviving seedlings with diameter growth > 0.5 mm. Models excluded seedlings with negative changes in height due to stem dieback and seedlings with changes in height < 0.5 cm or diameter growth < 0.5 mm as they may have been subject to measurement error. Height and diameter growth measurements were log transformed to stabilize variance. Models of height and diameter growth also included log-transformed initial seedling height and diameter measurements as fixed effects to account for differences in growth due to differences in initial seedling size.

We excluded one species, *Fihi*, from models investigating seedling survival. Nearly all *Fihi* seedlings survived to the end of the investigation. We therefore assumed that *Fihi* survival was unrelated to the measured ranges of light availability and soil moisture.

We also excluded four species from models investigating seedling growth. *Ersu* and *Prce* were excluded due to poor two-year survival. *Bava* had slightly better survival but was excluded due to large numbers of seedlings with stem dieback rather than growth. *Rhrh* also had large numbers of seedlings with stem dieback.

A few GSF estimates and θ_v measurements were not included in this investigation due to technical errors in photography and measurement or because seedlings could not be relocated at the time measurements were taken. Consequently, some seedlings had incomplete data sets. If, however, seedlings had sufficient data to conduct an analysis we included it in the LMM. For example, seedlings with survival data, but missing height measurements for one year, were excluded from LMMs testing the relationship between the environmental factors and growth, but included in LMMs testing the relationship between environmental factors and survival.

2.5.2 Light Availability LMMs

At the start of this investigation the canopy across all plots had been closed for several years and changes to canopy light penetration were likely to be slow. We therefore assumed that estimates of light availability taken during in 2011 were generalizable across both years of the investigation, at least in relative terms. We therefore modeled the relationships between light availability and seedling survival and light availability and seedling growth across both years of the investigation (2011 – 2013). The models included interactions between light availability and species to investigate potential species differences in response to light.

2.5.3 Dry Season Soil Moisture LMMs

In contrast to estimates of light availability, dry season soil moisture measurements vary strongly depending on recent weather and variable annual precipitation (Marod et al. 2002). Due resource constraints, however, we were only able to measure soil moisture levels during the 2011 dry season. We therefore modeled the relationship between dry season soil moisture and survival and dry season soil moisture and seedling growth for just the 2012 – 2013 year. The models included interactions between soil moisture and species to investigate potential species differences in response to soil moisture. Models with dry season soil moisture also included light availability to account for variability due to light. We did not, however, model interactions with light due to limited degrees of freedom. Prior to including the two environmental variables in the same model, we calculated their variance inflation factor to determine whether the degree of collinearity between them was within acceptable limits (VIF<3).

4. Results

4.1 Survival and Mortality

Of the 1,334 seedlings sampled in this investigation, 350 seedlings died (26.2%), with 206 dying during the first year and 145 dying during the second year. Overall, 984 (73.8%) survived the entire duration of the two-year investigation.

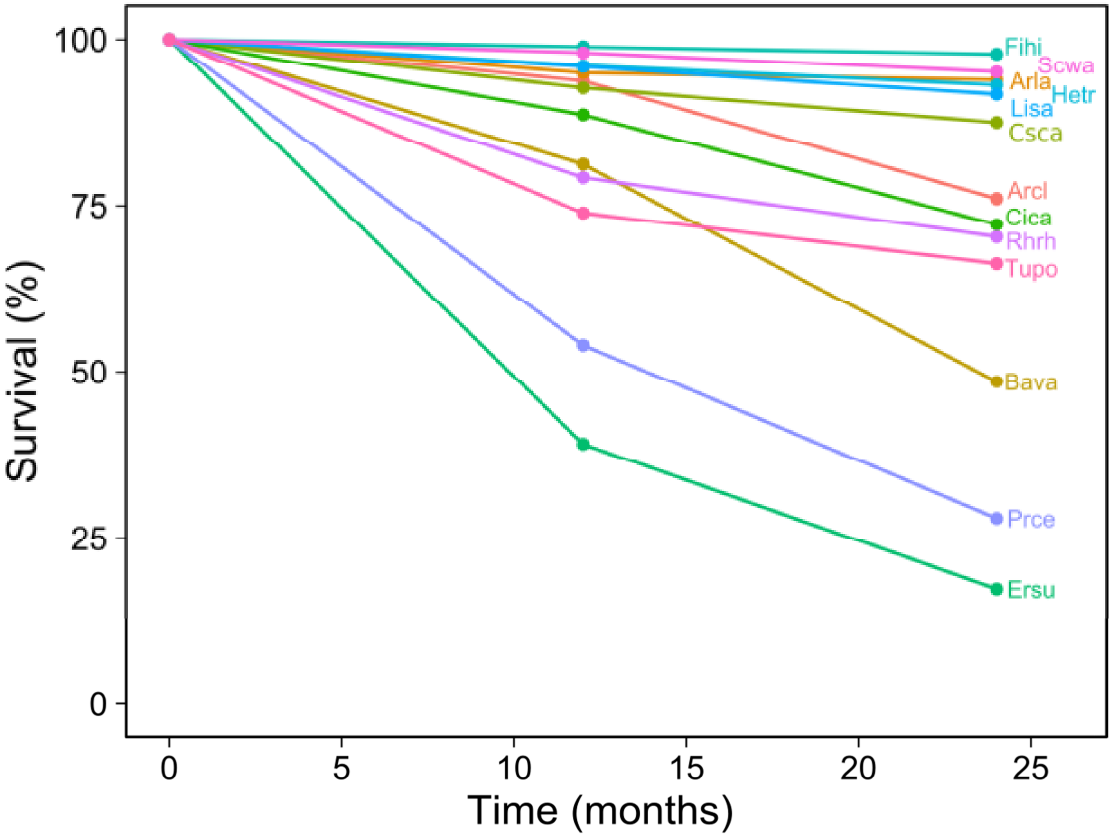

Figure 4.1 Percent survival of seedlings over two years. Species abbreviations are defined in Table 4.1.

Between the first and second year of the investigation, annual seedling mortality (irrespective of species) decreased by 2.6%. Changes in annual mortality, however, differed by species (Figure 4.1, Table 4.2). Annual mortality changed very little between the first and second year (< |4%|) for seven of the thirteen species. Of the six species with changes ≥ |4%|, three had increases in annual mortality (*Bava*, *Arcl*, and *Cica*) and three had decreases (*Tupo*, *Ersu*, and *Rhrh*).

Table 4.2 Seedling mortality by species. Species are listed in ascending order from lowest to highest mortality. Species abbreviations are defined in Table 4.1.

		Mortality (%)		
Species	Initial Sample (*n*)	Overall (2011 – 2013)	Year 1 (2011 – 2012)	Year 2 (2012 – 2013)
Fihi	102	2.0	1.0	1.0
Scwa	105	4.8	1.9	2.9
Arla	100	6.0	5.0	1.1
Hetr	105	6.7	3.8	3.0
Lisa	104	7.7	3.8	4.0
Csca	100	12.0	7.0	5.4
Arcl	101	22.8	5.9	17.9
Cica	102	26.5	10.8	17.6
Rhrh	105	28.6	20.0	10.7
Tupo	100	31.0	24.0	9.2
Bava	103	49.5	18.4	39.3
Prce	103	69.9	44.7	45.6
Ersu	104	73.1	53.8	41.7
Mean (SD)	102.6 (1.9)	26.2 (24.3)	15.4 (16.8)	15.3 (16.3)

4.2 Height and Diameter Growth

The mean and median height of all but two species, *Bava* and *Rhrh*, increased each year of the investigation (Figure 4.2). Heights of *Bava* and *Rhrh* decreased between Year 0 and Year 1 due to the large proportion of their seedlings that experienced dieback of leader stems during the first year. However, *Rhrh* growth between Year 1 and Year 2 exceeded the loss in height between Year 0 and Year 1 such that median *Rhrh* height increased slightly over the entire over the entire two-year investigation. *Bava* growth between Year 1 and Year 2, however, did not compensate for the loss in height due to dieback between Year 0 and Year 1, and median *Bava* height decreased over the entire two-year investigation. Finally, although mean diameters for all species increased between Year 0 and Year 2, five species: *Arla, Bava, Csca*, and *Scwa*, had either very small or no increases in median diameter in between Year 1 and Year 2.

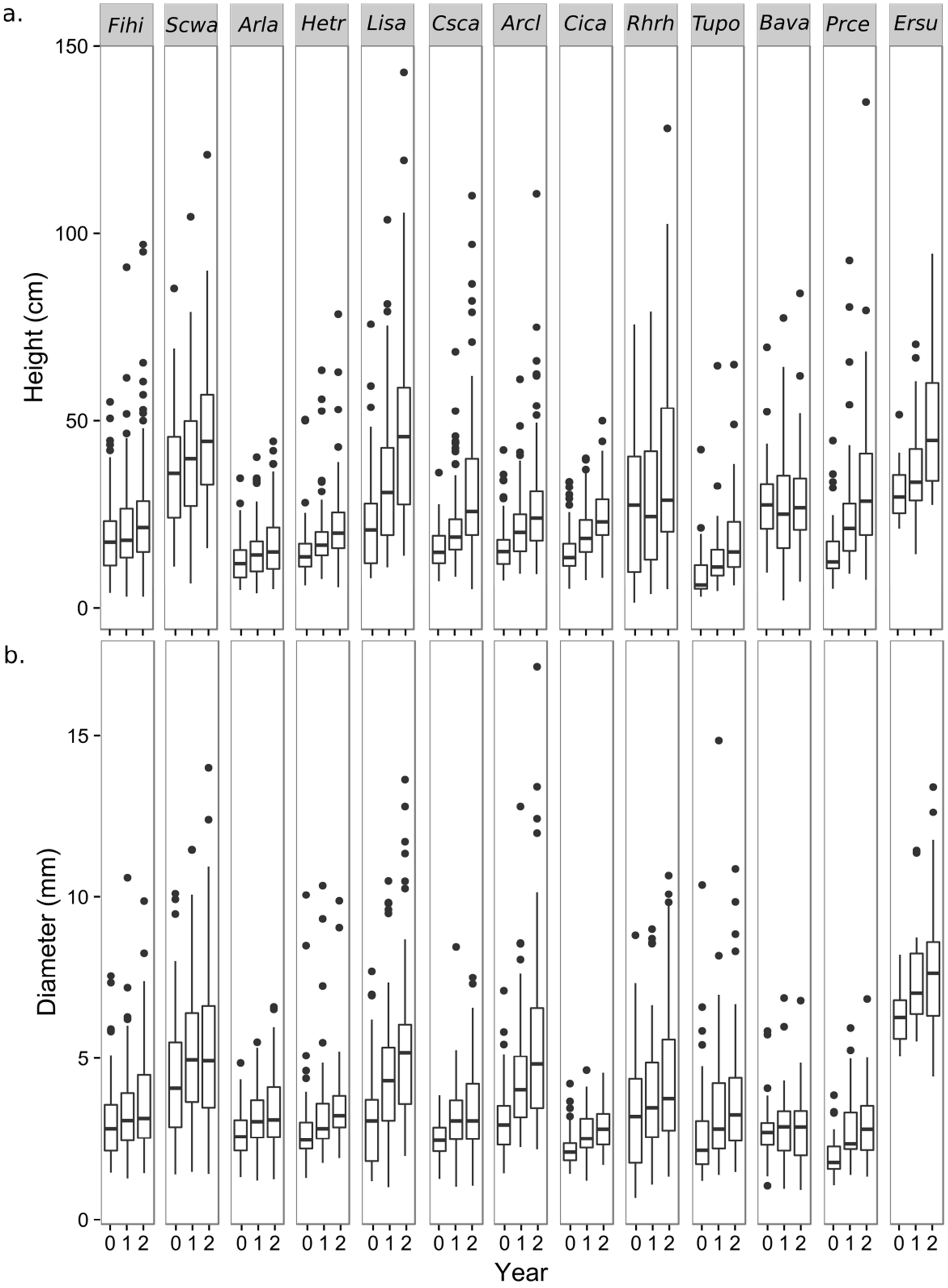

Figure 4.2 Box plots illustrating height (a) and diameter (b) measurements of seedlings by species at each of the measurement events held over course of the two-year investigation. Each box represents the interquartile range (IQR) of the data distribution. The horizontal line across the box represents the distribution median. Boxplot whiskers represent the most extreme data within 1.5 times of the IQR. Outliers outside of 1.5 times the IQR are represented by an individual dot. From left to right, species are arranged in order of highest to lowest percent overall survival. Species abbreviations are defined in Table 4.1.

4.3 Environmental Factors

Global site factor (GSF) estimates from hemispherical photographs taken directly above 1,239 seedlings ranged from 1.7% to 37.3%, with a mean of 11.0%, a median of 9.9%, and a standard deviation of 5.3%. GSF values below 20% comprise 93% of the estimates (Figure 4.3).

Values of dry season volumetric soil moisture content (θ_v) measured beside 1,221 seedlings ranged from 2.3% to 14.1%, with a mean of 9.5%, a median of 9.7%, and a standard deviation of 1.5%. Measurements of 6.1% to 12 % comprised 94% of all θ_v measurements (Figure 4.3).

The VIF value for GSF and θ_v was 1.02. A VIF below 3 indicates no collinearity between the variables (Zuur et al. 2007), therefore we incorporated GSF as a fixed effect in the analysis of height growth and θ_v.

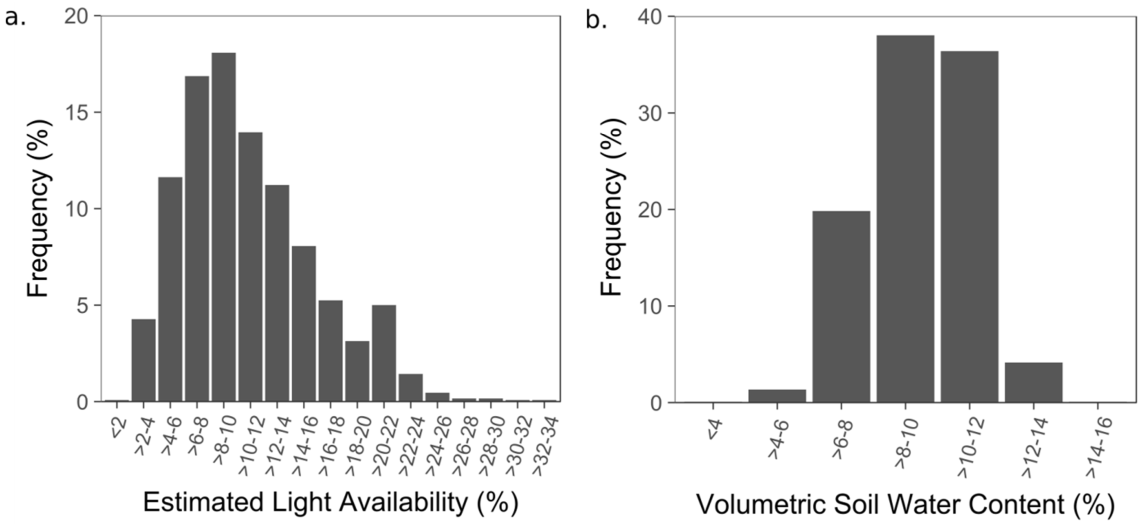

Figure 4.3 Percent frequency of (a) estimated percent light availability measurements (b) and dry season percent volumetric soil moisture content (θ_v).

4.4 Analyses

4.4.1 Environmental Factors vs. Survival

Neither GSF nor θ_v were significantly related to seedling survival in this investigation (Table 4.3).

Table 4.3 Results of linear mixed models (LMMs) of seedling survival and growth.

LMM	Time period	Response variable	Main explan. variable	No.of Species	Fixed effects	Statistic	*p*-value	R^2_{GLMM}
1	2011-2013	Survival	GSF	12	Species	$X^2_{11,1150} = 322.98$	<0.0001	0.388
					GSF	$X^2_{1,1150} = 0.30$	0.58	
					Species*GSF	$X^2_{11,1150} = 6.76$	0.82	
2	2012-2013	Survival	θ_v	12	Species	$X^2_{11,1105} = 330.85$	<0.0001	0.315
					GSF	$X^2_{11,1105} = 1.39$	0.24	
					θ_v	$X^2_{1,1105} = 0.52$	0.47	
					θ_v *Species	$X^2_{11,1105} = 15.96$	0.14	
3	2011-2013	Height Growth	GSF	9	Log Height in 2011	$F_{1,643} = 49.52$	<0.0001	0.387
					Species	$F_{8,643} = 7.63$	<0.0001	
					GSF	$F_{1,643} = 38.66$	<0.0001	
					Species*GSF	$F_{8,643} = 1.27$	0.2538	
4	2011-2013	Diameter Growth	GSF	9	Log Diameter in 2011	$F_{1,616} = 51.08$	<0.0001	0.264
					Species	$F_{8,616} = 3.58$	0.0004	
					GSF	$F_{1,616} = 26.90$	<0.0001	
					Species*GSF	$F_{8,616} = 1.14$	0.3356	
5	2012-2013	Height Growth	θ_v	9	Log Height in 2012	$F_{1,585} = 78.84$	<0.0001	0.386
					Species	$F_{8,585} = 15.35$	<0.0001	
					GSF	$F_{1,585} = 13.42$	0.0003	
					θ_v	$F_{1,585} = 2.80$	0.0948	
					θ_v *Species	$F_{8,585} = 0.59$	0.78	
6	2012-2013	Diameter Growth	θ_v	9	Log Diameter in 2012	$F_{1,433} = 29.42$	<0.0001	0.226
					Species	$F_{8,433} = 1.48$	0.1640	
					GSF	$F_{1,433} = 8.12$	0.0046	
					θ_v	$F_{1,433} = 0.12$	0.7336	
					θ_v *Species	$F_{8,433} = 1.28$	0.2535	

4.4.2 Understory Light Availability vs. Growth

There were strong and positive relationships between GSF and seedling height ($F_{1,643}$ = 38.66, $p < 0.0001$) and diameter growth ($F_{1,616}$ = 26.90, $p < 0.0001$) after accounting for the log of initial height and the log of initial diameter (Table 4.3).

Based on the results of the models comparing GSF and seedling growth, the median two-season height growth of seedlings is expected to increase by 3.43% for each 1% increase in GSF (95% CI [2.36%, 4.52%]; Table 4.4) and the median two-season diameter growth is expected to increase by 3.51% for each 1% increase in GSF (95% CI [2.18% 4.86%]). Although there was no statistically detectable interaction between species and GSF, predicted increases in median height growth by species in response to a 1% increase in GSF spanned a wide range (0.53% – 7.05%), as did predicted increases in median diameter growth (-0.03% – 6.47%). This suggests that there may be real species differences in growth responses to microsite variations in GSF. Furthermore, low R^2_{GLMM} values for the two models (R^2_{GLMM} = 0.39 for the model comparing GSF and height growth and R^2_{GLMM} = 0.26 for the model comparing light availability to diameter growth) suggest the models fail to explain a substantial proportion of variation in the growth response. Although some of this unexplained variability may be due to limitations GSF estimation, it also suggests that the models omit additional factors important to seedling growth.

4.4.3 Dry Season Soil Moisture vs. Growth

After accounting for the log of the initial height and GSF, θ_v was weakly negatively related to seedling height growth ($F_{1,585}$ = 2.80, p = 0.0948). However, there was no statistically detectable relationship between θ_v and diameter growth ($F_{1,433}$ = 0.12, p = 0.73) after accounting for the log of the initial diameter and GSF.

Table 4.4 Model predictions of percent change in median two-season height and diameter growth in response to each 1% increase in GSF by species. Species abbreviations are defined in Table 4.1.

Species	Δ Height growth (%)	df	95% CI		Δ Diameter growth (%)	df	95% CI	
			Lower	Upper			Lower	Upper
Arcl	7.05	643	3.18	11.06	2.49	616	-2.39	7.61
Arla	3.69	643	0.95	6.51	2.38	616	-1.07	5.96
Csca	4.63	643	1.77	7.56	4.88	616	0.02	9.97
Cica	2.52	643	-0.82	5.97	-0.30	616	-4.15	3.70
Fihi	6.18	643	2.50	9.98	2.29	616	-1.00	5.69
Hetr	3.12	643	0.46	5.84	5.62	616	2.13	9.23
Lisa	1.71	643	-1.11	4.62	3.32	616	-0.16	6.91
Scwa	2.32	643	-1.30	6.07	5.96	616	1.66	10.43
Tupo	0.53	643	-3.40	4.61	6.47	616	1.79	11.36
ALL	3.43	651	2.36	4.52	3.51	616	2.18	4.86

5. Discussion

5.1 Survival

Although nearly three quarters of the monitored tree seedlings survived through the end of the two-year investigation, there were significant survival differences among species. Ten of the thirteen sampled species demonstrated high long-term persistence (≥ 69% survival over two years). Of these, all but one is considered an intermediate or late successional forest species. By contrast, the three species with the lowest (≤ 50.5% survival over two years) were all pioneers. These results suggest that while understory conditions are sufficient for the recruitment and establishment of seedlings from intermediate and late stages of succession, they are insufficient for the long-term persistence of many early successional seedlings.

At present, little is known about long-term seedling survival in intact EGF, the forest originally present at the site of the restoration plots. However, even before taking into account significant survival differences between species, overall seedling survival in this investigation was substantially higher than seedling survival reported for other SDTF (Gerhardt 1996a, b, McLaren and McDonald 2003), including lower-elevation Thai evergreen forest (Marod et al. 2002). Since seedling mortality in SDTF is thought to be primarily the result of moisture stress during the dry season (Khurana and Singh 2001), differences in survival between the restored forest and other SDTF may be due to the relatively high levels of precipitation the restored forest receives during the wet season. This also suggests seedling dynamics in the restored forest may be more similar to humid tropical forest than drier SDTF. In fact, if we consider only intermediate and late successional seedlings, two-year survival exceeded 85%. This rate is comparable to multi-year survival rates reported for shade-tolerant seedlings and saplings in closed-canopy primary and secondary humid tropical forests (Welden et al. 1991, Montgomery and Chazdon 2002, O'Brien et al. 2013).

It is possible that similarities in seedling survival between the restoration plots and more humid tropical forests are artifacts of the exceptionally cool and moist weather the region experienced in 2011, the year we initiated the investigation (Thai Meteorological Department 2012). However, if that were the case, we might expect mortality to increase in the second year, since 2012 was both warmer and drier (Thai Meteorological Department 2013). Instead, overall annual seedling mortality decreased slightly and only three species experienced substantial increases in mortality between the first and second year. These species may have been more sensitive to water stress than the other ten, but there were no obvious similarities among them to indicate patterns in drought response. Overall, our results suggest that seedling survival was not substantially affected by anomalous weather in the first year, although a longer-term study may be useful for explicitly establishing the effects of year-to-year weather variability on seedling survival.

5.2 Growth

Although rates of growth varied by species, surviving seedlings of most species had two years of consecutive positive height and diameter growth in the understory. This suggests understory conditions were sufficient for the continuous growth of a range of naturally-establishing seedlings. Furthermore, we observed individual seedlings of six species grow to heights > 1 m, our cut-off height for differentiating seedlings from saplings. Most of these seedlings were of intermediate or late successional species, suggesting that conditions beneath the canopy of the forest restoration plantations are able to support not only establishment and persistence of intermediate to late successional species, but also the maturation of these species beyond the seedling stage.

Interestingly, even two of the high-mortality pioneer species, *Prce* and *Ersu*, had continuous positive growth among their surviving seedlings. Our results suggest that, although understory conditions in the restored forest plots are generally not conducive to the survival of seedlings of either species, some understory microsites may support both their survival and growth. We were unable to determine which factors limit their regeneration since neither light availability nor dry season soil moisture were correlated with their survival and there were too few survivors to determine the degree to which either of these factors limit growth. Furthermore, the length of this investigation was insufficient to determine whether high mortality rates would continue and eventually remove remaining survivors from the understory.

Two other sampled pioneer species, *Rhrh* and *Bava*, had high rates of stem dieback in the first year, resulting in decreases in their median height between the first and second monitoring event. While *Bava* also had high mortality, *Rhrh* had moderately high two-year survival (71%). *Rhrh*'s uneven growth, however, suggests that even apparently persistent pioneer species may be growth-limited in the understory.

5.3 Environmental Factors

5.3.1 Understory Light Availability

Based on hemispherical photographs taken during the dry season, we estimate that the seedlings in this investigation received a median of approximately 10% of full sun. Microsite variation, however, was relatively high and estimates ranged from as low as 1.7% to as high as 37.3%. Although at present we know little about light conditions in intact EGF, dry season understory light in lower-elevation Thai mixed deciduous forests appear to be similar to dry season light availability estimates in our investigation (Marod et al. 2004). Seasonal changes in understory light availability are characteristic of SDTF due to the prevalence of deciduous canopy trees in many of these forests (Murphy and Lugo 1986). In the Thai mixed deciduous forest, light intensity estimated from hemispherical photos taken during the wet season was 80% lower in the understory and 20% lower beneath a large canopy gap than estimates from the photographs taken during the dry season (Marod et al. 2004). Seasonal changes on the forest restoration plots are likely to be smaller than those observed in the mixed deciduous forest because, while deciduous trees comprise nearly three-quarters of Thai mixed deciduous forest tree species (Maxwell and Elliott 2001), they made up less than a third of the species planted to establish the plots (FORRU, personal communication). Our own efforts to obtain wet season hemispherical photographs for comparison of seasonal light availability on the restoration plots were stymied by mist and rainfall in 2011. Consequently our estimates of light availability were limited to photographs taken during the dry season, when canopy openness was highest. Although this very likely led to overestimation of annual light availability, the strength of the relationship between these estimates and seedling height and diameter growth (discussed below) indicate the estimates were adequate for gauging relative levels of microsite light availability to seedlings.

5.3.2 Dry Season Soil Moisture

During the 2012 dry season the median θ_v for the initial 20 cm of soil was approximately 10%. This is intermediate between dry season θ_v reported for wetter (Meinzer et al. 1999) and drier SDTF (Baker et al. 2005). Compared to estimates of light availability, the range of measured θ_v values was narrow, with almost all θ_v measurements between 6.1% and 12%. Soil moisture declines rapidly during the dry season, especially within the first 20 cm (Becker et al. 1988, Wright 1991) and the small range in θ_v in this investigation suggests that, at least by the end of the dry season, soil moisture on the restored forest plots has become largely homogenous at the shallow rooting depth.

5.3.3 Survival and Growth vs. Light Availability

Although understory light availability is widely considered the primary factor limiting both seedling survival and growth in tropical forests, we were unable to detect a relationship between microsite variations in understory light availability (GSF) and seedling survival in this investigation. Relatively high light in the restored forest understory may have obscured relationships between light and survival of seedlings belonging to intermediate and late successional species, since even the low end of light estimates in the restored forest plots was higher than the levels required for the long-term persistence of shade-tolerant seedlings in rainforest understory (Clark et al. 1993, Chazdon et al. 1996). By contrast, the high end of the light range may have been either too low for pioneer species to persist or occur too infrequently for us to detect relationships with pioneer species survival.

In contrast to seedling survival, there were strong positive relationships between microsite variations in light availability and seedling height and diameter growth among persistent seedlings. For these seedlings, 1% increases in GSF were predicted to increase median two-year seedling growth by 3.4% median diameter growth by 3.5%. This corresponds with previous investigations that have found that growth and carbon gain of tropical plants is highly responsive to microsite variations in light availability in the closed canopy understory (Oberbauer et al. 1993, Chazdon et al. 1996). In tropical rainforests, the responsiveness of individuals and species to light variations in closed canopy microsites may determine their long-term persistence and therefore the likelihood that they will mature (Montgomery and Chazdon 2002). In the restored forest, sensitive growth responses to light likely serve a similar purpose, although higher understory light may allow some species to mature beyond the seedling stage even in the absence of canopy gaps.

Understory light availability explains less than half of the variance in the growth data. Although this may be in part due to previously discussed limitations in light estimations, high unexplained variance also suggests that influential factors were omitted from the investigation. Soil nutrients may represent one category of these key factors. Recently, Holste et al. (2011) reported that the growth effects of many soil nutrients on seedlings growing in the understory of wet tropical forest are similar to that of understory irradiance, suggesting that soil nutrients play an equally important role in seedling growth, even in the shade. Previously researchers have assumed that slow-growing seedlings in the shade are not limited by soil nutrients for months or possibly even years (Kitajima 1996). Our investigation, however, indicates that intermediate and shade-tolerant seedlings are able to persist for years in the restored forest understory. Thus they are likely at some point to have exhausted their seed nutrient reserves and become dependent on soil nutrients. Mean light estimates of 10% in the forest restoration plantations are high compared to the light range reported for closed canopy wet and rainforest (0.3 – 6.5% full sun) (Montgomery and Chazdon 2002). High light in the forest restoration plantations may stimulate seedling growth and accelerate the rate of soil nutrient dependency.

5.3.4 Survival and Growth vs. Volumetric Soil Moisture

Several studies have found that water stress due to seasonal drought acts as the primary filter for seedling survival in SDTF (Lieberman and Li 1992, Gerhardt 1996a, McLaren and McDonald 2003). Our investigation, however, was unable to detect a relationship between the dry season volumetric soil moisture (θ_v) between 0 and 20 cm in depth and seedling survival in the second year of the investigation. Relationships between seedling growth and dry season soil moisture were also weak to undetectable.

Our results contrast with research demonstrating positive relationships between soil moisture and increased seedling growth during the dry season (Bunker and Carson 2005, Paine et al. 2009); however, these investigations included experimentally irrigated seedlings.

Low variance in natural levels of microsite θ_v in this investigation may have obscured the relationship between soil moisture and seedling growth and survival. Seedlings of many SDTF species have been shown to have deep, extensive root systems that allow them access to moisture in deeper soil (Engelbrecht and Kursar 2003, Markesteijn and Poorter 2009). Consequently the seedlings monitored in our investigation may be unaffected by low θ_v at the rooting depth from which we sampled.

The seedling selection itself may also have been biased in favor of drought-tolerant species and individuals. For a species to be included in the investigation, we required a minimum of 100 seedlings spread out across multiple restoration plots. High seedling survival in this investigation suggests that many of the sampled plants, which were categorized as seedlings by size rather than age, may have been the result of seedling accrual over multiple years. They may therefore represent a pre-filtered population of seedlings that had already passed through one or more dry seasons. Finally, while growth of SDTF and other tropical forest seedlings has been shown to decrease dramatically in response to seasonal decreases in soil moisture and rise again in response to seasonal rains (Gerhardt 1993, Comita and Engelbrecht 2009, Chaturvedi et al. 2013), one-time soil moisture readings and annual rather than seasonal measurements of seedling growth may have been too coarse a temporal scale to detect the effect of dry season soil moisture on growth. Despite the limitations in our analyses, high two-year survival among most seedlings and the insensitivity of both seedling survival and growth to dry season soil moisture provides strong evidence that the dry season is not a bottleneck for the sampled species.

5.3.5 Plantation vs. Colonizing Seedling Recruitment

We initially intended to focus this investigation on the regeneration of tree species that were dispersed into the restoration plots from outside (colonizing seedlings) and exclude the offspring of planted species (plantation seedlings). We discovered, however, that although restoration plots have a large number of colonizing species (Sinhaseni 2008), most of these species are rare. Only a handful of colonizing species met the criteria of having at least 100 seedlings spread out across at least three restoration plots. Plantation seedlings, on the other hand, were far more common – presumably due to the presence of seed trees on the plots. We therefore decided to incorporate both plantation and colonizing species into this investigation in order to compare their regeneration dynamics and their potential impact on the trajectory of forest development.

The majority of sampled species, both plantation and colonizing species, had high two-year survival (≥ 69%), and most of the survivors grew in both height and diameter. The demonstrated ability of these seedlings to persist and grow in the restored forest provides strong evidence that restoration efforts have succeeded in creating understory conditions favorable to the natural regeneration of a wide range of species. The observed rarity of colonizers compared to plantation seedlings suggests that colonizers are recruitment-limited. This limitation is likely due in large part to poor seed availability or dispersal, since experimental seed introductions into the restored forest understory resulted in high rates of seedling establishment for several previously-absent species (Chapter 3, this dissertation).

We observed that one plantation species, *Csca*, a fagaceous late-successional species, had formed dense monospecific seedling stands in the areas immediately surrounding parent trees. This species produced large crops of large acorns (with length ≥ 20 mm) both years of the investigation. Annual seed production coupled with the high survival and consistent growth of *Csca* seedlings measured in this investigation suggests that monospecific stands are the result of multiple years of seedling accrual. *Csca* and other persistent species may pursue a regeneration strategy of “seedling banking,” in which understory accumulations of repressed or slowly growing seedlings persist for years or even decades until high light from canopy gaps release them to mature (Clark and Clark 1992). This regeneration strategy may give persistent seedlings a large competitive advantage since they are able to more quickly capitalize on transient increases in understory light than seedlings that must start from seed.

Seedling banks have been observed in both tropical and temperate forests (Clark and Clark 1992, Catovsky and Bazzaz 2002, Delissio et al. 2002) and most rainforest canopy gaps are filled by advanced regeneration from seedling banks rather than recently recruited seedlings (Lomascolo and Aide 2001). While this strategy may foster continuous tree cover on the restored forest plots, dense banks of plantation seedlings may also inhibit the recruitment and maturation of colonizing tree species. Dispersal limitations place colonizing species at an initial disadvantage early in forest development, and although dispersal limitations may decrease over time as the forest matures (Reid et al. 2015), late-arriving species may encounter less favorable understory conditions than earlier recruits due to darker conditions from a more developed canopy (Bertacchi, 2016) and competition from pre-existing banks of plantation seedlings. This may be similar to naturally-regenerating secondary forests where early-colonizing tree species inhibit rather than facilitate the growth of late-arriving species by limiting their access to key resources, particularly sunlight (Wunderle Jr. 1997). Some researchers have predicted that in these instances, recruitment and maturation of late-arriving species may be delayed until initial colonizers senesce and create canopy gaps that permit late-arriving species in the seedling bank to mature (Finegan 1996, Chazdon 2008). Thus, though we may expect seed dispersal from outside the plantation to increase with time (Reid et al. 2015), the impact of early recruitment of plantation species may remain evident in the forest composition for years or even decades to come.

6. Management Implications

The results of this investigation contribute to the growing body of research indicating that restoration using mixed native species plantations creates conditions conducive to the regeneration of mature-forest tree species (Keenan et al. 1997, Parrotta and Knowles 2001, Lamb et al. 2005). High survival of intermediate and late-successional tree seedlings suggests that additional management interventions to increase light availability and soil moisture may be unnecessary to promote seedling survival after recruitment; however, the strong positive relationship between seedling growth and light availability suggests that management to increase understory light (e.g. thinning) may hasten seedling maturity. Light availability and soil moisture, however, did not explain all the variance in seedling growth. Additional factors, such as soil nutrients, may also strongly influence seedling growth and should be investigated in future research.

Since a wide range of seedlings persist and grow without assistance, managers may be best served by re-directing limited resources towards accelerating the re-assembly of a species-diverse seedling community. This may involve strategies for enrichment planting to increase the understory diversity of mature-forest seedlings. The performance of intermediate and late-successional tree species in this investigation suggests that restoration plantation understories are suitable for the enrichment planting of similar species. Enrichment planting, or the active planting of seeds or seedlings of desired species in the forest understory, may be particularly important for facilitating the recruitment of highly dispersal-limited species (e.g. species with large, animal-dispersed seeds) that are unlikely to recolonize on their own (Lamb 2011).

Observations made during this investigation also suggest that the most effective time to conduct enrichment efforts maybe while the forest is still young. The less developed canopy of younger forest may allow higher light levels which enable seedlings to mature more rapidly. Bertacchi et al. (2016), for example, attributed higher survival of enrichment planted seedlings in younger Brazilian restoration plantations to greater light availability in these forests compared to older plantations. Enrichment planting before many of the plantation trees reach reproductive maturity may also give enrichment planted seedlings a developmental head start and potentially offset the numerical advantage of plantation species.

Finally, managers should also consider excluding from the initial planting mix species with seedlings that may inhibit regeneration of colonizing species. This may include species that regularly produce large numbers of large seeds and have highly shade-tolerant seedlings, such as *Csca*. Thorough investigation of regeneration characteristics of potential plantation species prior to selection may prevent this occurrence given that, otherwise, the regeneration characteristics of plantation species will not be evident for some time after planting.

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Chapter 5 – Dissertation Summary and Conclusion

Hathai A. Sangsupan

1. Dissertation Summary

Restoration practitioners require an understanding of how ecological filters may affect community assemblage in tropical forest restoration in order to develop strategies that avoid or minimize the development of alternative pathways of succession. This dissertation addressed this need by investigating potential ecological filters to seedling regeneration in young Thai seasonally dry evergreen forest (SDTF) restoration plantations. Here we provide a brief summary and synthesis of the results of these investigations, as well as a discussion of the management implications of our research and some suggestions for future research directions.

In Chapter 2 we investigated whether recruitment of colonizing tree species in the restoration plantation plots can be attributed to dispersal mode (i.e. abiotic or animal dispersal) or seed size. We compared the distribution of these traits among colonizing seedlings in the understory of 4- to 8-year-old restoration plantation plots to the distribution of the same traits among trees in two intact reference forests. Furthermore, we investigated the potential impact of early seedling composition on future stand composition by using the distribution of dispersal traits among seedlings in the restored forest to project the future distribution of dispersal traits among large trees ($\geq$ 10 cm dbh). We found that the distribution of dispersal modes and seed sizes among colonizing seedlings in the restoration plantation was similar to the distribution among trees in an intact reference forest. There were, however, far fewer large-seeded species among the animal-dispersed colonizers than might be expected from the proportion of large-seeded trees in the reference forest. This supported the hypothesis that seed size limits dispersal and recruitment of large-seeded species in tropical forest restoration. Based on the distribution of dispersal traits of all seedlings (both colonizing and planted species), we projected that the mature restored forest will have about the same proportion of animal-dispersed trees as an intact reference forest; however, most of those trees will have small or very small seeds (< 10 mm length). We project that there will be 80% fewer medium- and large-seeded trees (15-25 mm length) in the mature restored forest than in the intact reference forest. Furthermore, nearly all very-large-seeded trees (> 25 mm length) will be the offspring of plantation species, while very-large-seeded colonizers will be extremely rare (< 1 tree ha^{-1}).

In addition to being dispersal-limited in the restoration plantations, establishment (i.e. germination and seedling survival) of larger-seeded, animal-dispersed species may also be limited by the availability of microsites with suitable abiotic conditions (Guariguata and

Ostertag 2001). In Chapter 3 we described the results of an experiment that explicitly tested seed and microsite limitations for large-seeded tree species that have failed to naturally recolonize young restoration plantation, despite being present in nearby forest. This study found that germination and establishment of five large-seeded tree species was not limited by seedbed microsite conditions in the restoration plantation understory. Moreover, although there were significant differences between species, relatively high overall germination (> 25%) and two-year survival of seedlings from germinated seeds (59.7%) suggested basic microsite requirements for germination and early establishment of large-seeded species were generally met in the 13-year old restoration plots. This supported the hypothesis that seedlings of large-seeded species are absent due to inadequate seed availability, rather than inadequate microsite conditions. The length of this study, however, was insufficient to determine whether seedlings would mature beyond the seedling stage. Continued mortality of two species over the two-year investigation suggests that they may not be able to successfully transition to the sapling stage. Mortality for these species was particularly high during the first dry season following germination, which suggests that their young seedlings may be susceptible to dry season drought stress.

Chapter 4 continued exploring seedling dynamics in the understory of restoration plantations by measuring the survival and growth of seedlings belonging to 13 naturally-recruited tree species in 11 – 14 year-old restoration plantation and investigating the relationship between seedling dynamics and microsite variations in understory light and dry season soil moisture. We found that once recruited, seedlings of intermediate and late successional tree species have high two-year survival and slow but continuous growth in the plantation understory. By contrast, several, though not all, pioneer species had low survival and/or poor growth. This suggests that the understory environment is adequate for intermediate and late successional species regeneration, but may act as a filter for most pioneers. Although neither light availability nor dry season soil moisture were significantly related to seedling survival, microsite light availability was strongly related to understory seedling growth. Still, neither of the two measured factors explained all growth. This suggests that additional factors, such as microsite variations in soil nutrients, may also be influential.

2. Implications for Tropical Forest Restoration

Our investigations indicate that the understory environment of young Thai SDTF restoration plantations was generally adequate not only for the recruitment of intermediate and late-successional tree species, but also for their two-year persistence and growth. This contributes to the growing body of research indicating that restoration using mixed native species plantations can create conditions conducive to the regeneration of mature-forest seedlings (Keenan et al. 1997, Parrotta and Knowles 2001, Lamb et al. 2005). The investigation in Chapter 2, however, found that the distribution of early colonizers was skewed towards smaller-seeded species which have larger numbers of potential animal dispersers. By contrast, larger-seeded colonizers were underrepresented in the plantation understory, despite being able to recruit and establish when introduced as seeds. This suggests seed dispersal limitations filtered species that were able to reach the plantations. If dispersal limitations continue, they may alter the trajectory of forest development, creating forests that are floristically and structurally different from intact forests.

Causes of seed limitation (e.g. distant seed sources, low seed production, and poor animal-dispersal) are unlikely to decrease in the foreseeable future. Active intervention may therefore be required to ensure that large-seeded tree species are represented in restored forests. Enrichment planting, the interplanting of tree species into the existing forest, may augment forest species diversity by introducing absent species. Although enrichment planting is most often carried out using nursery grown seedlings and saplings (Lamb et al. 2005), successful seedling establishment from introduced seeds in our investigation supports Cole et al.'s (2010) finding that direct-seeding is a viable means of introducing large-seeded, late-successional tree species into young restoration plantation. Direct seeding may also be a far more efficient and cost-effective means of enrichment planting (Cole et al. 2010). The results of our investigation in Chapter 3 also add to the growing body of research indicating large-seeded, late-successional trees are well-suited for direct-seeding under a range of early successional conditions (Hardwick et al. 1997, Camargo et al. 2002, Hooper et al. 2002, Bonilla-Moheno and Holl 2009). Although the species tested in Chapter 3 were all putatively shade-tolerant, mature-forest species, they manifested a wide range of germination, survival, and growth responses in the understory. These differences underscore the need for additional seed sowing experiments to determine which desired species are suitable for direct seed enrichment planting and which species may require different approaches for successful re-introduction.

Observations made in Chapters 3 and 4 also suggest that the most effective time to conduct enrichment efforts may be while the forest restoration plantations are still young. The less developed canopy of younger forest may provide higher understory light levels thereby enabling seedlings to mature more rapidly. Bertacchi et al. (2016), for example, attributed higher survival of enrichment planted seedlings in younger Brazilian restoration plantations to greater light availability in these forests compared to older plantations. Moreover, we observed that the seedlings of tree species that were planted to establish the plantations appear to have a numerical advantage over colonizing species due to the presence of seed sources in the restored forest. Enrichment planting of either seeds or seedlings before plantation species have reached reproductive maturity may give enrichment-planted species a developmental head start that offsets the numerical advantage of plantation species

The results and observations described in Chapter 4 suggest that managers should also consider excluding species from the initial planting mix species with regeneration characteristics that may later inhibit regeneration of colonizing species. This may include species that regularly produce substantial crops of large seeds and have highly shade-tolerant seedlings. *Castanopsis calathiformis* (*Csca*), for example, has formed dense monospecific stands of *Csca* seedling in the areas surrounding parent trees in the restoration plantation plots. These stands are likely the result of multiple years of seedling accrual since *Csca* produces heavy annual crops of large acorns and its seedlings have high survival and consistent growth in the understory. This strategy of seedling banking may give *Csca* a strong competitive advantage over dispersal-limited colonizing species since dense *Csca* stands can monopolize resources and more quickly capitalize on transient increases in understory light (e.g. from canopy gaps) than species that must start from seed.

Finally, high understory survival of seedlings belonging to mature-forest species in Chapters 3 and 4 suggests that additional management interventions to increase light availability and soil moisture may be unnecessary to promote the seedling survival after recruitment. The strong positive relationship between seedling growth and light availability in Chapter 4, however, suggests that management to increase understory light (e.g. thinning) may hasten seedling development. This may be important to ensure desirable species are able to move into canopy positions within a reasonable time frame.

3. Future Research Directions

The composition of the future mature forest is unlikely to perfectly reflect the present seedling composition as described in Chapter 2. Although our investigation of seedling dynamics in Chapter 4 found that many species had high seedling persistence, to develop more accurate projections of forest development trajectories, more long-term study is needed to quantify the likelihood that these seedlings will transition to successive life stages. Such information will allow us to predict species outcomes, decades before restored forests mature (Howe and Miriti 2004), and to generate tools to guide effective restoration management decisions. Annual variations in precipitation may also be important to seedling establishment, persistence, and growth, but the effects of these variations could not be determined in our two-year investigations. Longer-term studies may also clarify the role variable precipitation plays in seedling regeneration on the restoration plantations.

The large number seedlings of plantation species recruiting into restoration plantation plots (described in Chapters 2 and 4) highlight a subject that has yet to receive much research attention – the potential for the offspring of plantation species to influence the forest's long-term development trajectory. The high two-year survival rate of several intermediate and late successional plantation species (Chapter 4) suggests that these species are also able to persist for long periods in the restored forest understory. Their abundance suggests that at least some plantation species have a numerical competitive advantage over colonizing species that are dispersal-limited. This advantage may become even more apparent as more plantation trees become reproductively mature. Holl (2007) proposed that the composition of the planted overstory trees may decrease both the diversity and richness of the understory seedling community. To develop strategies that minimize or prevent this, practitioners need additional research to quantify the effect of plantation species regeneration on forest development.

The investigations of seedling recruitment and dynamics in this dissertation (Chapters 3 and 4) focused on the role of abiotic factors in limiting seedling regeneration; however, biotic factors such as seed and seedling predation are also hypothesized to act as key ecological filters in other tropical forests (Janzen 1970). Future research should investigate the degree to which these factors influence early tree regeneration in the restoration plantations.

Unexplained variance in growth in Chapter 4 may be due to additional factors such as microsite variations in soil nutrients. Recently, Holste et al. (2011) reported that soil nutrients were as or more strongly correlated with seedling growth as irradiance among seedlings in the understory of wet tropical forests. This suggests that soil nutrients play a key role in seedling growth, even in the shade, and hints at the potential for practitioners to augment soil nutrient levels to increase seedling growth. We conducted a small exploratory investigation of the relationship between seedling growth and soil nutrients levels (Appendix B). This investigation found some suggestive evidence that microsite variations in N, K, Ca, Mg, and Fe may be related to seedling growth; however, the study was limited by both sample size and time. Additional research is needed to clarify the relationships between seedling growth and soil nutrients and to determine whether nutrient addition might be an effective means of increasing the growth of desirable seedlings.

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APPENDICES

Appendix A – Supplemental material associated with Chapter 2

Table A.1 Seedling survey results on 4- and 8-year-old (yo) tropical forest restoration plots. Habitat is subdivided into EGF and non-EGF species. Numeric citations for sources of dispersal mode and seed size information for non-EGF species are included beside corresponding species names. All dispersal mode and seed size citations for EGF species are in Table A.2. Seed sizes are for animal-dispersed species. Columns headed “Planted in” indicate species that were originally part of the initial planting mix used to establish the plots. The number of seedlings in restoration plantations per plot age is per 942.5 m^{2}. Habitat is subdivided into EGF and non-EGF species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation).

Species	Habitat	Dispersal mode	Seed sizes	Planted in 4 yo plots	Planted in 8 yo plots	No. of seedlings 4 yo plots	No. of seedlings 8 yo plots
Albizia chinensis (Osb.) Merr.	EGF	Abiotic	–			0	1
Albizia garrettii Niels. [1]	non-EGF	Abiotic	–			1	5
Alseodaphine andersonii (King ex Hk. f.) Kosterm.	EGF	Animal	VL		Yes	0	1
Antidesma acidum Retz.	EGF	Animal	VS			14	13
Antidesma bunius (L.) Spreng.	EGF	Animal	S			1	0
Antidesma ghaesembilla Gaertn. [1, 2]	non-EGF	Animal	VS			44	4
Aporosa octandra (B.-H. ex D. Don) Vick. var. octandr*a [2]*	non-EGF	Animal	S			5	44
Aporosa villosa (Lindl.) Baill.[1]	non-EGF	Animal	S			1	24
Aquilaria crassna Pierre ex Lec.	EGF	Animal	S			0	3
Archidendron clypearia	EGF	Animal	M		Yes	0	2
Areca laosensis Becc. Arenga caudata (lour.) H.E. Moore	EGF	Animal	L			0	1
Artocarpus lakoocha Roxb. [3]	non-EGF	Animal	M			5	6
Bauhinia variegata L.	EGF	Abiotic	–			1	0
Beilschmiedia assamica	EGF	Animal	VL			1	0
Bombax anceps Pierre var. anceps [2]	non-EGF	Abiotic	–			1	4

Table A.1 (Continued) Seedling survey results on 4- and 8-year-old (yo) tropical forest restoration plots. Habitat is subdivided into EGF and non-EGF species. Numeric citations for sources of dispersal mode and seed size information for non-EGF species are included beside corresponding species names. All dispersal mode and seed size citations for EGF species are in Table A.2. Seed sizes are for animal-dispersed species. Columns headed "Planted in" indicate species that were originally part of the initial planting mix used to establish the plots. The number of seedlings in restoration plantations per plot age is per 942.5 m^2. Habitat is subdivided into EGF and non-EGF species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation).

Species	Habitat	Dispersal Mode	Seed Size	Planted in 4 yo plots	Planted in 8 yo plots	No. of Seedlings 4 yo plots	No. of Seedlings 8 yo plots
Bridelia glauca Bl. var. glauca	EGF	Animal	S			1	5
Broussonetia papyrifera (L.) Vent. [1, 3]	non-EGF	Animal	S			1	0
Canthium parvifolium Roxb.	EGF	Animal	L			0	3
Castanopsis acuminatissima (Bl.) A. DC.	EGF	Animal	S	Yes		2	0
Castanopsis calathiformis (Skan) Rehd. & Wils.	EGF	Animal	VL		Yes	0	76
Castanopsis diversifolia (Kurz) King ex Hk. f.	EGF	Animal	VL	Yes		3	0
Castanopsis tribuloides	EGF	Animal	S	Yes		5	5
Cinnamomum caudatum Nees [2, 4]	EGF	Animal	L			0	5
Chionanthus ramiflorus Roxb.	non-EGF	Animal	M			0	1
Clausena excavata Burm. f. var. excavate	EGF	Animal	S			0	1
Cratoxylum formosum (Jack) Dyer ssp. pruniflorum (Kurz) Gog. [1]	non-EGF	Abiotic	–			0	2
Dalbergia cultrata Grah. ex Bth.	EGF	Abiotic	–			1	1
Dalbergia oliveri	EGF	Abiotic	–			1	0

Table A.1 (Continued) Seedling survey results on 4- and 8-year-old (yo) tropical forest restoration plots. Habitat is subdivided into EGF and non-EGF species. Numeric citations for sources of dispersal mode and seed size information for non-EGF species are included beside corresponding species names. All dispersal mode and seed size citations for EGF species are in Table A.2. Seed sizes are for animal-dispersed species. Columns headed “Planted in” indicate species that were originally part of the initial planting mix used to establish the plots. The number of seedlings in restoration plantations per plot age is per 942.5 m^2. Habitat is subdivided into EGF and non-EGF species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation).

Species	Habitat	Dispersal Mode	Seed Size	Planted in 4 yo plots	Planted in 8 yo plots	No. of Seedlings 4 yo plots	No. of Seedlings 8 yo plots
Debregeasia longifolia (Burm. f.) Wedd. [1, 2]	non-EGF	Animal	VS			1	0
Diospyros glandulosa Lace	EGF	Animal	L		Yes	0	4
Ehretia acuminata R. Br. var. acuminate	EGF	Animal	VS			0	1
Engelhardia spicata Lechen. ex Bl. var. spicata	EGF	Abiotic	–			0	3
Erythrina stricta Roxb.	EGF	Abiotic	–	Yes		2	15
Erythrina subumbrans (Hassk.) Merr.	EGF	Abiotic	–	Yes	Yes	1	107
Eugenia albiflora Duth. ex Kurz	EGF	Animal	L	Yes	Yes	6	33
Eugenia fruticosa (DC.) Roxb. [2]	non-EGF	Animal	S		Yes	2	8
Ficus hirta Vahl var. hirta	EGF	Animal	VS			8	7
Ficus hispida L. f. var. hispida [3]	non-EGF	Animal	VS			1	2
Ficus subulata Bl. Var subulata	EGF	Animal	VS			3	1
Ficus tinctoria	EGF	Animal	VS			0	2
Glochidion kerrii Craib	EGF	Animal	VS			0	1

Table A.1 (Continued) Seedling survey results on 4- and 8-year-old (yo) tropical forest restoration plots. Habitat is subdivided into EGF and non-EGF species. Numeric citations for sources of dispersal mode and seed size information for non-EGF species are included beside corresponding species names. All dispersal mode and seed size citations for EGF species are in Table A.2. Seed sizes are for animal-dispersed species. Columns headed "Planted in" indicate species that were originally part of the initial planting mix used to establish the plots. The number of seedlings in restoration plantations per plot age is per 942.5 m^2. Habitat is subdivided into EGF and non-EGF species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation).

Species	Habitat	Dispersal Mode	Seed Size	Planted in 4 yo plots	Planted in 8 yo plots	No. of Seedlings 4 yo plots	No. of Seedlings 8 yo plots
Glochidion acuminatum M.-A. var. siamense A.S. [5]	non-EGF	Animal	VS			0	6
Heynea trijuga Roxb. ex Sims	EGF	Animal	M	Yes	Yes	0	44
Ixora cibdela Craib	EGF	Animal	S			1	1
Litsea cubeba (lour.) Pers. var. cubeba	EGF	Animal	S			29	4
Litsea monopetala (Roxb.) Pers.	EGF	Animal	S			265	211
Litsea salicifolia (Roxb. ex Nees) Hk.f.	EGF	Animal	M			0	1
Machilus bombycina King ex Hk. f.	EGF	Animal	VS			0	3
Maesa ramentacea (Roxb.) A.DC.	EGF	Animal	VS			1	0
Mallotus philippensis (Lmk.) M.-A.	EGF	Animal	VS			13	2
Markhamia stipulata (Wall.) Seem ex K. sch. Var. kerrii Sprague	EGF	Abiotic	–		Yes	13	11
Michelia baillonii Pierre	EGF	Animal	S			0	3

Table A.1 (Continued) Seedling survey results on 4- and 8-year-old (yo) tropical forest restoration plots. Habitat is subdivided into EGF and non-EGF species. Numeric citations for sources of dispersal mode and seed size information for non-EGF species are included beside corresponding species names. All dispersal mode and seed size citations for EGF species are in Table A.2. Seed sizes are for animal-dispersed species. Columns headed "Planted in" indicate species that were originally part of the initial planting mix used to establish the plots. The number of seedlings in restoration plantations per plot age is per 942.5 m^2. Habitat is subdivided into EGF and non-EGF species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation).

Species	Habitat	Dispersal Mode	Seed Size	Planted in 4 yo plots	Planted in 8 yo plots	No. of Seedlings 4 yo plots	No. of Seedlings 8 yo plots
Michelia floribunda Fin. & Gagnep.	EGF	Animal	S			0	6
Micromelum hirsutum Oliv.	EGF	Animal	S			12	0
Micromelum minutum (Forst. f.) Wight & Arn.	EGF	Animal	S			0	13
Millettia macrostachya Coll. & Hemsl. var. macrostachya [1]	non-EGF	Abiotic	–			0	1
Morinda tomentosa Hey. ex Roth [2]	non-EGF	Animal	S			1	0
Oroxylum indicum (L.) Kurz [1]	non-EGF	Abiotic	–			4	0
Phoebe lanceolata (Wall. ex Nees) Nees	EGF	Animal	S		Yes	20	124
Prunus cerasoides Ham. ex D. Don	EGF	Animal	S	Yes	Yes	3	64
Pterocarpus macrocarpus Kurz	EGF	Abiotic	–			6	0
Rhus chinensis Mill. [1, 2]	non-EGF	Animal	VS			0	9
Sapindus rarak DC.	EGF	Animal	L	Yes	Yes	0	2
Sarcosperma arboreum Bth.	EGF	Animal	L	Yes	Yes	1	0

Table A.1 (Continued) Seedling survey results on 4- and 8-year-old (yo) tropical forest restoration plots. Habitat is subdivided into EGF and non-EGF species. Numeric citations for sources of dispersal mode and seed size information for non-EGF species are included beside corresponding species names. All dispersal mode and seed size citations for EGF species are in Table A.2. Seed sizes are for animal-dispersed species. Columns headed "Planted in" indicate species that were originally part of the initial planting mix used to establish the plots. The number of seedlings in restoration plantations per plot age is per 942.5 m^2. Habitat is subdivided into EGF and non-EGF species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation).

Species	Habitat	Dispersal Mode	Seed Size	Planted in 4 yo plots	Planted in 8 yo plots	No. of Seedlings 4 yo plots	No. of Seedlings 8 yo plots
Schima wallichii (DC.) Korth.	EGF	Abiotic	–			7	46
Spondias axillaris Roxb.	EGF	Animal	L	Yes	Yes	3	1
Sterculia villosa Roxb.	EGF	Animal	M			3	8
Turpinia pomifera (Roxb.) Wall. ex DC.	EGF	Animal	S			0	1
Wendlandia scabra Kurz var. scabra	EGF	Abiotic	–			34	0
Wendlandia tinctoria (Roxb.) DC. ssp. floribunda (Craib) Cowan [1]	non-EGF	Abiotic	–			0	7
Xantolis burmanica (Coll. & Hemsl.) P. Royen	EGF	Animal	L			0	2

Table A.2 Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Acer laurinum Hassk.	Abiotic	—	[1]
Acrocarpus fraxinofolius	Abiotic	—	[2]
Acronychia pedunculata (L.) Miq	Animal	S	[2]
Actinodaphne henryi Gamb.	Animal	S	[2]
Adinandra integerrima T. And. Ex Miq	Animal	S	[2]
Aglaia lawii	Animal	L	[2, 4]
Aidia yunnanensis (Hutch) yaha.	Animal	VS	[2]
Alangium barbatum (R.Br.) Baill. Var barbatum	Animal	S	[1]
Alangium chinense (Lour) Harms	Animal	S	[4]
Alangium kurzii Craib	Animal	M	[2]
Albizia chinensis	Abiotic	—	[1]
Alchornea tiliifolia	Animal	S	[1]
Aleurites moluccana (L.) Willd	Animal	L	[2]
Allophylus cobbe	Animal	VS	[4]
Alseodaphne andersonii	Animal	L	[1]
Alstonia rostrata Fischer	Abiotic	—	[1]
Alstonia scholaris	Abiotic	—	[1]
Anacolosa ilicoides Mast.	Animal	L	[2]
Anneslea fragrans Wall.	Animal	S	[1]
Antidesma acidum Retz.	Animal	VS	[1]
Antidesma bunius	Animal	S	[1]
Antidesma montanum	Animal	VS	[2]
Antidesma sootepense Craib	Animal	VS	[2]
Aphanamixis polystachya (Wall.) R. Parker	Animal	M	[2]
Apodytes dimidiata E. Mey. Ex Arn.	Animal	S	[2]
Aquilaria crassna	Animal	S	[2]
Aralia montana Bl.	Animal	VS	[3]
Archidendron clypearia	Abiotic	—	[2]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Archidendron glomeriflorum	Abiotic	—	[3]
Ardisia attenuata Wall. Ex A. DC.	Animal	S	[1]
Ardisia corymbifera	Animal	S	[1]
Ardisia crenata Sims var. crenata	Animal	S	[4]
Ardisia maculosa Mez	Animal	S	[1]
Ardisia villosa Roxb.	Animal	S	[1]
Aridisa virens Kurz	Animal	S	[1]
Artocarpus gomezianus Wall. Ex Trec.	Animal	M	[2, 4]
Artocarpus lanceolata Trec.	Animal	S	[2]
Baccaurea ramiflora Lour	Animal	M	[2, 4]
Balakata baccata (Rosb.) Ess.	Animal	S	[2, 4]
Bauhinia variegata	Abiotic	—	[1]
Beilschmiedia percoriacea Allen var. ciliata H. W. Li	Animal	L	[1]
Beilschmiedia intermedia Allen	Animal	L	[1]
Betula alnoides Ham. Ex D. Don	Abiotic	—	[1]
Boehmeria chiangmaiensis Yaha	Animal	Unk	—
Boehmeria zollinggeriana Wedd.	Animal	Unk	—
Bischofia javanica	Animal	S	[2]
Brassiopsis glomerulata (Bl.) Regel	Animal	S	[2]
Breynia fruticose (L.) Hk. F.	Animal	VS	[1]
Bridelia glauca	Animal	VS	[1]
Brucea mollis Wall ex Kurz	Animal	S	[1]
Buddleja asiatica Lour	Abiotic	—	[1]
Callerya atropurpurea (Wall.) Schot	Animal	L	[3]
Calophyllum polyanthum	Animal	L	[2]
Camellia oleifera Abel var. confusa (Craib) Sealy	Animal	L	[1]
Camellia sinensis (L) O.K. var. assamica (Mast.) Kita	Animal	M	[1]
Canarium subulatum Guill.	Animal	L	[1, 2]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Canthium glabrum Bl.	Animal	M	[2]
Canthium parvifolium Roxb.	Animal	S	[2]
Canthium umbellatum Wight	Animal	S	[3]
Capparis kerrii Craib	Animal	S	[2]
Capparis pyrifolia Lmk.	Animal	S	[2]
Carallia brachiata (Lour.) Merr.	Animal	M	[2]
Casearia grewiifolia Vent. Var. gelionoides (Bl.) Sleum	Animal	VS	[2, 4]
Cassia bakeriana Craib	Abiotic	—	[2, 3]
Castanopsis acuminatissima (Bl.) A. DC.	Animal	M	[2]
Castanopsis armata (Roxb.) Spach	Animal	L	[2, 3]
Castanopsis diversifolia (Kurz) King ex Hk. F.	Animal	L	[2, 3]
Castanopsis rockii A. Camus	Animal	M	[1]
Castanopsis tribuloides (Sm.) A. DC.	Animal	L	[2]
Celtis tetrandra Roxb.	Animal	S	[1]
Celtis timorensis Span.	Animal	S	[1]
Cephalotaxus griffithii Hk. F.	Animal	L	[1]
Chionanthus sutepensis (Kerr) P.S. green	Animal	L	[2, 3]
Cinchona pubescens Vahl	Abiotic	—	[1]
Cinnamomum camphora	Animal	S	[1]
Cinnamomum caudatum	Animal	L	[1, 2]
Cinnamomum iners	Animal	S	[4]
Cinnamomum longipetiolatum	Animal	M	[1]
Cipadessa baccifera (Roth) Miq.	Animal	VS	[2]
Clausena excavata Brum. F. var. excavata	Animal	S	[4]
Clausena lenis Drake	Animal	S	[1]
Cleidion spiciflorum	Animal	M	[6]
Clerodendrum disparifolium B.	Animal	S	[7]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Clerodendrum infortunatum L.	Animal	S	[4]
Clerodendrum paniculatum L.	Animal	S	[4]
Clerodendrum serratum (L.) Moon var allichii Cl.	Animal	S	[8]
Crotalaria assamica Bth.	Abiotic	—	[9]
Croton lachnocarpus	Animal	S	[10]
Croton robustus	Animal	S	[10]
Cryptocarya amygdalina Nees	Animal	L	[1]
Cyathea chinensis Copel.	Abiotic	—	[11]
Dalbergia cultrata Grah. Ex Bth.	Abiotic	—	[2, 3]
Dalbergia oliveri	Abiotic	—	[2, 3]
Dalbergia ovata	Abiotic	—	[2, 3]
Daphniphyllum laurinum	Animal	M	[2]
Debregeasia longifolia (Burm f.) Wedd.	Animal	VS	[1]
Decaspermum parviflorum (Lmk.) A.J. Scott ssp. Parviflorum	Animal	VS	[2, 4]
Desmos sootepense (Craib) Maxw.	Animal	M	[4]
Dichroa febrifuga	Animal	VS	[1]
Dillenia aurea Sm. Var. aurea	Animal	S	[12]
Dimocarpus longan Lour. Ssp. Longan var. longan	Animal	M	[4]
Diospyros glandulosa Lace	Animal	M	[4]
Diospyros martabanica Cl.	Animal	S	[3]
Dipterocarpus costatus	Abiotic	—	[2]
Dracaena angustifolia Roxb.	Animal	S	[1]
Duabanga grandiflora (Roxb ex DC.) Walp.	Abiotic	—	[1, 3]
Duperrea pavettifolia (Kurz) Pit.	Animal	S	[1]
Dysoxylum aff. Hamiltonii Hiern	Animal	M	[13]
Ehretia acuminata R. Br. Var. acuminata	Animal	VS	[1]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Elaeocarpus floribundus Bl.	Animal	L	[14]
Elaeocarpus lanceifolius Rxob.	Animal	L	[1]
Elaeocarpus petiolatus (Jack) Wall. Ex Kurz	Animal	M	[1]
Elaeocarpus prunifolius Wall. Ex C. Muell.	Animal	M	[2]
Elaeocarpus sphaericus (Gaertn.) K. Sch	Animal	M	[3]
Elaeocarpus stipularis Bl.	Animal	M	[2, 3]
Engelhardia spicata Lechen ex. Bl var. spicata	Abiotic	—	[7]
Engelhardtia serrata Bl. Var. serrata	Abiotic	—	[7]
Engelhardtia spicata Lechen. Ex Bl. Var. integra (Kurz) Mann.	Abiotic	—	[2]
Eriobotrya bengalensis (Roxb.) Hk. F. forma bengalensis	Animal	L	[1, 2]
Erythrina stricta Roxb.	Abiotic	—	[1, 2]
Erythrina subumbrans	Abiotic	—	[1, 2]
Eugenia aff. Globiflora Craib	Animal	M	[1]
Eugenia albiflora Duth. Ex Kurz	Animal	L	[2]
Eugenia cinerea Kurz	Animal	S	[1, 2]
Eugenia claviflora Roxb.	Animal	M	[1, 2]
Eugenia megacarpa Craib	Animal	L	[1]
Eugenia tetragona Wight	Animal	S	[1, 2]
Euodia meliifolia (Hance) Bth	Animal	VS	[1]
Euodia triphylla DC.	Animal	VS	[1, 4]
Euodia viticina Wall. Ex Kurz	Animal	S	[1]
Euonymus similis Craib	Animal	S	[2]
Eurya acuminata DC. Var. wallichiana Dyer	Animal	VS	[1, 2]
Eurya nitida Korth. Var. siamensis	Animal	VS	[1]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Fagraea ceilanica Thunb.	Animal	VS	[1]
Ficus auriculata Lour	Animal	VS	[2]
Ficus benjamina L. var benjamina	Animal	VS	[2]
Ficus callosa Willd.	Animal	VS	[3]
Ficus capillipes Gagnep.	Animal	VS	[2]
Ficus cyrtophylla Wall. Ex Mi	Animal	VS	[3]
Ficus hirta Vahl var. hirta	Animal	VS	[3]
Ficus hirta Vahl var. roxburghii	Animal	VS	[3]
Ficus microcarpa L. f. var. microcarpa forma microcarpa	Animal	VS	[2]
Ficus piscocarpa Bl.	Animal	VS	[3]
Ficus semicordata B.-H. exJ.E. Sm. Var senucirdata	Animal	VS	[2]
Ficus subulata Bl. Var subulata	Animal	VS	[3]
Ficus superba (Miq) Miq. Var superba	Animal	VS	[2]
Ficus variegata Bl. Var. variegata	Animal	VS	[3]
Fraxinus floribunda Wall.	Abiotic	—	[1, 2]
Garcinia cowa Roxb	Animal	L	[2]
Garcinia mckeaniana Craib	Animal	L	[2]
Garcinia merguensis Wight	Animal	M	[2, 4]
Garcinia thorelii Pierre	Animal	Unk	—
Garcinia xanthochymus Hk. F. ex T. And	Animal	L	[2]
Glochidion kerii Craib	Animal	VS	[2]
Glochidion sphaerogynum	Animal	VS	[2]
Gluta obovata	Unknown	Unk	[2]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Glycosmis puberula Lindl. Ex Oliv. Var. craibii (Tana.) stone	Animal	S	[2]
Gmelina arborea Roxb.	Animal	M	[2, 4]
Goniothalamus griffithii Hk. F.& Thoms	Animal	M	[2]
Gordonia dalglieshiana Craib	Abiotic	—	[1, 2]
Harpullia cupanioides Roxb.	Animal	L	[1, 2]
Helicia formosana	Animal	L	[4]
Helicia nilagirica Bedd.	Animal	L	[2]
Heliciopsis terminalis	Animal	L	[2]
Heynea trijuga Roxb. Ex Sims	Animal	M	[2]
Hibiscus mutabilis L. l	Animal	s	[1]
Hopea odorata Roxb. Var. odorata	Abiotic	—	[1, 3]
Horsfieldia thorelii Lec.	Animal	L	[2]
Horsfielida amydalina (Wall.) Warm. Var. amydalina	Animal	L	[2]
Hovenia dulcis Thunb.	Animal	S	[2]
Ilex englishii Lace	Animal	VS	[2, 3]
Ilex umbellulata (Wall.) Loesn.	Animal	VS	[2, 3]
Indigofera dosua	Abiotic	—	[1]
Indigofera laxiflora Craib	Abiotic	—	[15]
Itea puberula Craib	Animal	S	[1]
Ixora cibdela var. puberula Craib	Animal	S	[16]
Ixora kerrii Craib	Animal	S	[3]
Knema conferta (King) Warb.)	Animal	L	[7]
Knema laurina (Bl.) Warb	Animal	L	[7]
Lasianthus kurzii Hk. F.	Animal	VS	[13]
Lasianthus lucidus Bl.	Animal	VS	[1]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Leea herbacea Ham. Ex Cl.	Animal	VS	[1]
Lepionurus sylvestris Bl.	Animal	S	[1]
Lepisanthes tetraphylla (Vahl) Radlk.	Animal	M	[4]
Lespedeza parviflora Kurz	Animal	VS	[1]
Lespedeza pinetorum Kurz	Abiotic	—	[1]
Lindera caudata	Animal	S	[1]
Lithocarpus garrettianus (Craib) A. Camus	Animal	M	[1, 2]
Lithocarpus spicatus (Sm.) Rehd. & Wils. Var brevipetiolatus (A.DC.) Rehd& Wils	Animal	L	[7]
Lithocarpus truncatus (King) Rehd &Wils.	Animal	L	[1]
Litsea albicans Kurz	Animal	Unk	—
Litsea cubeba	Animal	VS	[2]
Litsea firma	Animal	S	[7]
Litsea monopetala	Animal	S	[1]
Litsea salacifolia	Animal	M	[2]
Litsea semecarpifolia Wll. Ex Nees	Animal	L	[2]
Litsea zeylanica	Animal	VS	[1]
Livistona speciosa Kurz	Animal	L	[1]
Macaranga kurzii	Animal	S	[2]
Machilus bombycina King ex. Hk.f.	Animal	S	[1]
Maclura fruticosa (Roxb.) Corn.	Animal	VS	[1]
Macropanax dispermus (Bl.) O.K.	Animal	VS	[1]
Maesa permollis Kuirz	Animal	VS	[1]
Maesa ramentacea (Roxb.) A. DC.	Animal	VS	[1]
Magnolia liliifera(L.) Baill. Var. obovata (Korth) Gov.	Animal	S	[2]
Mallotus khasianus	Animal	M	[2, 17]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Mallotus oblongifolius	Animal	VS	[17]
Mallotus paniculatus	Animal	VS	[2]
Mallotus philippensis	Animal	VS	[17]
Mangifera caloneura	Animal	L	[2]
Manglietta garrettii Craib	Animal	M	[1, 2]
Markhamia stipulata (Wall.) Seem ex K. sch. Var. kerrii Sprague	Abiotic	—	[1, 2]
Mastixia euonymoides Prain	Animal	L	[2, 3]
Melastoma malabathricum L. ssp. Normale (D. Don) K. Meyer	Animal	VS	[18]
Melia toosendan Sieb. & Zucc.	Animal	M	[2]
Meliosma pinnata	Animal	VS	[2]
Meliosma simplicifolia	Animal	VS	[2]
Mesua ferrea L	Animal	L	[2]
Metadina trichotoma (Zoll. & Mor.) Bakh. F.	Animal	VS	[1]
Michelia baillonii Pierre	Animal	S	[4]
Michelia champaca L. var. champaca	Animal	S	[4]
Michelia floribunda Fin. & Gagnep.	Animal	S	[1]
Micromelum falcatum (Lour.) Tana	Animal	S	[1]
Micromelum hirsutum Oliv.	Animal	S	[2]
Micromelum minutum (Forst.f.) Wight & Arn.	Animal	S	[4]
Miliusa cuneata Craib	Animal	S	[1]
Miliusa thorellii Fin. & Gagnep.	Animal	M	[3]
Miliusa velutina (Dun.) Hk. F. & Thoms	Animal	M	[2, 4]
Millettia xylocarpa Miq.	Abiotic	—	[3]
Mischocarpus pentapetalus (Roxb.) Radlk.	Animal	S	[4]
Mitragyna hirsuta Hav.	Animal	VS	[1, 4]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Mitrephora vandaeflora Kurz	Animal	M	[1, 3]
Morinda angustifolia Roxb. Bvar scabridula Craib	Animal	S	[1]
Morus macroura Miq.	Animal	VS	[1, 4]
Mycetia glandulosa Criab	Animal	VS	[1, 3]
Mycetia rivicola Craib	Animal	VS	[1, 3]
Nyssa javanica (Bl.) Wang	Animal	M	[1, 2]
Olea dioica Roxb	Animal	S	[19]
Olea rosea Craib	Animal	M	[1]
Olea salicifolia Wall. Ex G. Don	Animal	M	[1]
Ormosia sumatrana (Miq.) Prain	Abiotic	—	[1]
Ostodes paniculata Bl.	Animal	M	[2]
Palaquium garrettii Flet.	Animal	M	[4]
Pavetta indica L.	Animal	VS	[2]
Persea chartacea	Animal	S	[3]
Phlogacanthus curviflorus (Wall.) Nees var. curviflorus	Animal	S	[1]
Phoebe cathia	Animal	M	[2]
Phoebe lanceolata (Wall. Ex Nees)	Animal	L	[2]
Phoebe neuranthoides	Animal	S	[1]
Phoebe pallida	Animal	S	[1, 3]
Phyllanthus roseus	Animal	S	[4, 20]
Picrasma javanica Bl.	Animal	S	[2, 4]
Pittosporopsis kerrii Craib	Animal	L	[21]
Pittosporum napaulense (Dc.) Rehd. & Wils.	Animal	VS	[1, 2]
Platea latifolia Bl.	Animal	L	[4]
Podocarpus neriifolius D. Don	Animal	M	[1]
Polyalthia simiarum (Ham. Ex Hk. F. & Th.)	Animal	L	[22]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Polyosma elongata Gedd	Animal	Unk	—
Potameia siamensis Kosterm	Animal	L	[2]
Pouteria grandifolia (Wall.) Baeh	Animal	L	[1]
Premna pyramidata Wall. Ex Schauer	Animal	VS	[1]
Premna villosa Cl. (accepted: Premna coriacea)	Animal	VS	[3, 23]
Prismatomeris tetrandra (Roxb) K. Sch ssp. Tetrandra	Animal	S	[1, 4]
Protium serratum (Wall. Ex Colebr.) Engl.	Animal	S	[2]
Prunus arborea (Bl.) Kalk. Var. montana (Hk.f.) Kalk	Animal	S	[4]
Prunus cerasoides D. Don	Animal	M	[2]
Prunus javanica	Animal	S	[2]
Prunus wallichii Steud.	Animal	S	[2]
Pseuderanthemum latifolium (Vahl) B. Han	Animal	VS	[1]
Psychotria monticola Kurz. Var. monticola	Animal	S	[1]
Psychotria ophioxyloides Wall	Animal	VS	[4]
Psychotria siamica (Craib) Hutch	Animal	VS	[2]
Pterocarpus macrocarpus Kurz	Abiotic	—	[2]
Pterospermum acerifolium Willd.	Abiotic	—	[1, 2]
Pterospermum grandiflorum	Abiotic	—	[2]
Pyrenaria garrettiana Craib	Animal	L	[1]
Quercus glabricupula Barn	Animal	M	[1]
Quercus incana Roxb.	Animal	L	[1]
Quercus lineata Bl. Var hildebrandii	Animal	L	[1]
Quercus semiserrata Roxb.	Animal	L	[2]
Quercus vestita Rehd. & Wils.	Animal	L	[3]
Radermachera glandulosa (Bl.) Miq.	Abiotic	—	[1, 2]
Rapanea yunnanensis Mez	Animal	VS	[1]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Rauvolfia verticillata (Lour.) Baill.	Animal	S	[1]
Rhododendron moulmainense Hk.	Animal	VS	[1]
Rhus rhetsoides	Animal	S	[4]
Rothmannia sootepensis (Craib) Brem	Animal	L	[2]
Salix tetrasperma Roxb.	Abiotic	—	[3]
Sapindus rarak DC.	Animal	L	[2, 4]
Sarcosperma arboreum Bth.	Animal	L	[2]
Saurauia napaulensis DC	Animal	VS	[1]
Saurauia roxburghii Wall.	Animal	VS	[1, 3]
Schima wallichii (DC.) Korth.	Abiotic	—	[1, 2]
Schefflera pueckleri (C.Koch) Frod	Animal	S	[3]
Schoepfia fragrans Wall.	Animal	S	[4]
Scleropyrum wallichianum	Animal	L	[2]
Semecarpus cochinchinensis	Animal	L	[2]
Sloanea tomentosa (Bth.) Rehd. & Wils.	Animal	M	[2]
Solanum macrodon Wall. Ex Nees	Animal	VS	[1]
Sorbus verrucosa (Decne.)Rehd. Var verrucosa	Animal	S	[1]
Spondias axillaris	Animal	M	[2]
Sterculia balanghas L.	Animal	L	[2]
Sterculia lanceolata Cav. Var. lanceolata	Animal	M	[1]
Sterculia principis Ganep.	Animal	M	[1]
Sterculia villosa Roxb	Animal	M	[2]
Stereospermum colais	Abiotic	—	[1]
Stereospermum neuranthum	Abiotic	—	[1]
Styrax benzoides Craib	Animal	S	[2]

Table A.2 (Continued) Doi Suthep EGF species, dispersal modes, and seed sizes (for animal-dispersed species). All abbreviations and measurement ranges for dispersal mode and seed size categories are given in Table 2.1 (Chapter 2, this dissertation) with the exception of species for which size is unknown (Unk).

Species	Dispersal Mode	Seed Size	Ref. no
Symplocos cochinchinensis (Lour.) S. Moore ssp. Laurina (Retz.) Noot.	Animal	S	[4]
Symplocos hookeri Cl.	Animal	M	[1]
Symplocos macrophylla Wall. Ex DC. Ssp. Sulcata (Kurz.) Noot. Var. sulcata	Animal	S	[2, 3]
Symplocos sumuntia B.-H. ex D. Don	Animal	S	[1]
Tarennoidea wallichii (Hk. F.) Tirv. & Sastre	Animal	S	[2]
Tephrosia kerrii Drum. & Craib	Abiotic	—	[1]
Terminalia mucronata Craib&Hurxh	Abiotic	—	[2]
Ternstroemia gymnanthera	Animal	S	[1]
Tetrameles nudiflora R. Br. Ex Benn.	Abiotic	—	[1]
Toona ciliate M. Roem	Abiotic	—	[1]
Trevesia palmata (DC) Vis.	Animal	M	[3]
Turpinia nepalensis (Roxb) Wall. Ex Wight	Animal	VS	[2, 4]
Turpinia pomifera (Roxb.) Wall. Ex DC.	Animal	S	[2, 4]
Viburnum cylindricum Ham. Ex D. Don	Animal	VS	[1]
Viburnum inopinatum Craib	Animal	VS	[1]
Vitex quinata (Lour.) Will.	Animal	S	[2]
Wendlandia scabra Kurz var. scabra	Abiotic	—	[1]
Xanthophyllum flavescens Roxb.	Animal	M	[1, 2]
Xantolis burmanica (Coll.& Hemsl.) P. Royen	Animal	L	[2, 3]
Xylosma brachystachys Craib	Animal	VS	[1]

Table A.3 Species information for large trees (dbh > 10 cm) in the Huai Kha Kaeng 50-ha Forest Dynamics Plot (HKK-FDP) [24]. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Acer oblongum	Abiotic	—	226	[1]
Acronychia pedunculata (L.) Miq	Animal	S	10	[2]
Adenanthera microsperma (syn = *Adenanthera pavonina*)	Animal	S	25	[2]
Afzelia xylocarpa	Animal	VL	29	[3]
Aglaia lawii	Animal	L	14	[2, 4]
Aglaia odorata	Animal	S	148	[1]
Aglaia spectabilis	Animal	VL	124	[4]
Ailanthus triphysa	Abiotic	—	12	[1]
Alangium chinense (Lour) Harms	Animal	S	15	[4]
Alangium kurzii Craib	Animal	M	5	[2]
Albizia chinensis	Abiotic	—	1	[1]
Albizia lucidior	Abiotic	—	7	[1]
Albizia odoratissima	Abiotic	—	7	[1]
Alchornea rugosa	Animal	S	39	[25]
Alphonsea ventricosa	Animal	S	679	[19]
Alstonia rostrata Fischer	Abiotic	—	2	[1]
Alstonia scholaris	Abiotic	—	16	[1]
Anacolosa ilicoides Mast.	Animal	L	2	[2]
Anisoptera costata	Abiotic	—	74	[26]
Anogeissus acuminata (Roxb. ex DC.) Guill.	Abiotic	—	4	[2]
Anthocephalus chinensis	Animal	VS	3	[2]
Antidesma bunius	Animal	S	8	[1]
Antidesma montanum	Animal	S	10	[2]
Aphanamixis polystachya (Wall.) R. Parker	Animal	L	87	[2]
Aphananthe aspera	Animal	S	2	[1]
Apodytes dimidiata E. Mey. Ex Arn.	Animal	S	1	[1, 2]
Aporosa octandra (B.-H. ex D. Don) Vick. var. octandra (syn may be: A. wallichii Hk. F.	Animal	S	4	[2]

Table A.3 (Continued) Species information for large trees (dbh > 10 cm) in the HKK-FDP. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Aporosa willichii	Animal	S	1	[2]
Ardisia polycephala	Animal	VS	21	[3]
Artocarpus chaplasha	Animal	S	7	[1]
Artocarpus gomezianus Wall. Ex Trec.	Animal	M	30	[2, 4]
Artocarpus lakoocha	Animal	M	3	[3]
Arytera littoralis	Animal	S	1,160	[24]
Baccaurea ramiflora Lour	Animal	M	1,117	[2, 4]
Balakata baccata (Rosb.) Ess.	Animal	S	7	[2, 4]
Beilschmiedia assamica	Animal	VL	1	[2]
Beilschmiedia gammieana	Animal	M	47	[24]
Beilschmiedia roxburghinana	Animal	VL	5	[1]
Beilschmiedia velutinosa (B. velutina)	Animal	VL	3	[2, 27]
Bischofia javanica	Animal	S	6	[2]
Callicarpa arborea	Animal	VS	14	[3]
Cananga latifolia	Animal	M	7	[3]
Canarium euphyllum	Animal	VL	2	[2]
Canarium subulatum Guill.	Animal	L	3	[2]
Canthium glabrum Bl.	Animal	M	3	[2]
Carallia brachiata (Lour.) Merr.	Animal	M	32	[1, 2]
Casearia grewiifolia Vent. Var. gelionoides (Bl.) Sleum	Animal	S	6	[2, 4]
Cassia fistula	Animal	M	35	[1]
Castanopsis tribuloides (Sm.) A. DC.	Animal	S	7	[1, 2]
Celtis tetrandra Roxb.	Animal	S	7	[1]
Celtis timorensis Span.	Animal	S	2	[1]
Champereia manillana	Unknown	Unk	96	—
Chionanthus callophyllus	Animal	M	28	[2, 3]
Chionanthus ramiflorus	Animal	M	9	[2]

Table A.3 (Continued) Species information for large trees (dbh > 10 cm) in the HKK-FDP. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Chukrasia tabularis	Abiotic	—	126	[2, 3]
Cinnamomum porrectum	Animal	S	9	[2, 3]
Cinnamomum tavoyanum	Animal	S	1	[2]
Citrus macroptera	Animal	M	3	[1]
Clausena excavata Brum. F. var. excavata	Animal	S	1	[4]
Cleidion spiciflorum	Abiotic	—	57	[2, 6]
Cleistocalyx nervosum (syn:*Syzygium nervosum)*	Animal	S	21	[1-3]
Colona floribunda	Abiotic	—	3	[2, 3]
Colona javanica	Abiotic	—	5	[3]
Colona winitii	Abiotic	—	0	[3]
Cordia clarkei	Unk	Unk	5	—
Cordia dichotoma	Animal	M	6	[28]
Crateva magna	Animal	S	10	[1, 3]
Cratoxylum cochinchinensis	Abiotic	—	1	[1]
Croton hutchinsonianus	Abiotic	—	2	[29]
Croton roxburghii	Abiotic	—	1,120	[3, 29]
*Cyathocalyx martabanicus*_var.harmandii	Animal	L	585	[30]
Dalbergia assamica	Abiotic	—	3	[1, 29]
Dalbergia cana	Abiotic	—	63	[1, 29]
Dalbergia cochinchinensis	Abiotic	—	33	[29]
Dalbergia oliveri	Abiotic	—	62	[2, 3, 29]
Derris dalbergioides	Abiotic	—	19	[3]
Dillenia indica	Animal	S	3	[19]
Dillenia obovata (syn with *D. aurea*)	Animal	S	1	[29, 31]
Dimocarpus longan Lour. Ssp. Longan var. longan	Animal	M	1,029	[1, 4]
Diospyros	Unknown	Unk	0	—

Table A.3 (Continued) Species information for large trees (dbh > 10 cm) in the HKK-FDP. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Diospyros coaetanea	Animal	M	4	[32]
Diospyros dasyphylla	Animal	M	19	[1, 3]
Diospyros ferrea	Animal	S	209	[1]
Diospyros montana	Animal	M	8	[3]
Diospyros variegata	Animal	M	399	[33]
Diospyros winitii	Animal	M	999	[24]
Diplospora singularis	Animal	S	13	[1, 34]
Dipterocarpus alatus	Abiotic	—	211	[1]
Dipterocarpus obtusifolius	Abiotic	—	14	[1, 2]
Drypetes hoaensis	Unknown	Unk	33	—
Drypetes roxburghii (syn: *Putranjiva roxburghii*)	Animal	S	13	[19]
Duabanga grandiflora (Roxb ex DC.) Walp.	Abiotic	—	32	[1, 3]
Dysoxylum cyrtobotryum	Animal	L	21	[4]
Dysoxylum grande	Animal	L	110	[1, 29]
Ehretia laevis	Animal	VS	9	[1]
Elaeocarpus lanceifolius Roxb.	Animal	VL	4	[1, 2]
Elaeocarpus robustus	Animal	L	16	[4]
Ellipanthus tomentosus	Animal	L	1	[7]
Engelhardtia spicata Lechen. Ex Bl. Var. integra (Kurz) Mann.	Abiotic	—	5	[2, 29]
Eriobotrya bengalensis (Roxb.) Hk. F. forma bengalensis	Animal	VL	7	[2]
Erythrina stricta Roxb.	Abiotic	—	10	[1, 2]
Fernandoa adenophylla	Abiotic	—	87	[2]
Ficus albipila	Animal	VS	2	[3]
Ficus altissima	Animal	VS	10	[3]
Ficus annulata	Animal	VS	11	[3]
Ficus calciola	Animal	VS	4	[3]
Ficus callosa Willd.	Animal	VS	3	[3]

Table A.3 (Continued) Species information for large trees (dbh > 10 cm) in the HKK-FDP. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Ficus capillipes Gagnep.	Animal	VS	1	[2]
Ficus curtipes	Animal	VS	7	[3]
Ficus drupaceae	Animal	VS	5	[3]
Ficus geniculata	Animal	VS	12	[3]
Ficus hederacea	Animal	VS	4	[3]
Ficus racemosa	Animal	VS	4	[3]
Ficus retusa	Animal	VS	14	[3]
Ficus sp.1	Animal	VS	1	[3]
Ficus sp.2	Animal	VS	4	[3]
Ficus stricta	Animal	VS	14	[3]
Ficus variegata Bl. Var. variegata	Animal	VS	6	[3]
Ficus vasculosa	Animal	VS	1	[3]
Firmiana pallens	Animal	M	2	[35]
Flacourtia jangomas	Animal	S	2	[3, 36]
Fraxinus floribunda Wall.	Abiotic	—	1	[1, 2]
Garcinia merguensis Wight	Animal	M	1	[2, 4]
Garcinia speciosa	Animal	M	466	[24]
Garuga pinnata	Animal	S	60	[2]
Garuga sp.1 (Must be *G. floribunda)*	Animal	S	1	[3]
Gluta obovata	Animal	L	193	[2, 24]
Glyptopetalum sclerocarpum	Animal	M	3	[1]
Gmelina arborea Roxb.	Animal	L	8	[2, 4]
Harpullia arborea	Animal	L	229	[4]
Harpullia cupanioides	Animal	L	89	[1, 2]
Heliciopsis terminalis	Animal	VL	2	[2]
Heynea trijuga Roxb. Ex Sims	Animal	M	9	[2]
Holoptelea integrifolia	Abiotic	—	2	[2]
Homalium ceylanicum	Abiotic	—	9	[37]
Hopea odorata Roxb. Var. odorata	Abiotic	—	274	[3]
Horsfieldia glabra	Animal	L	3	[4]

Table A.3 (Continued) Species information for large trees (dbh > 10 cm) in the HKK-FDP. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Ilex umbellulata (Wall.) Loesn.	Animal	VS	11	[1-3]
Irvingia malayana	Animal	VL	123	[1, 2]
Ixora finlaysoniana	Animal	S	2	[1]
Knema globularia	Animal	M	12	[3, 29]
Lagerstroemia balansae	Abiotic	—	34	[29]
Lagerstroemia calyculata	Abiotic	—	22	[29]
Lagerstroemia macrocarpa	Abiotic	—	6	[29]
Lagerstroemia tomentosa	Abiotic	—	206	[2]
Lagerstroemia venusta	Abiotic	—	2	[29]
Lagerstroemia villosa	Abiotic	—	18	[29]
Lepisanthes rubiginosa	Animal	M	74	[1, 3]
Lithocarpus grandifolius (syn: *L.elegans*)	Animal	M	1	[2, 3]
Lithocarpus thomsonii	Animal	L	26	[2, 3]
Macaranga siamensis	Animal	VS	112	[24, 29]
Mallotus philippensis	Animal	VS	130	[1, 19]
Mangifera caloneura	Animal	VL	4	[2]
*Mangifera quadrifida*_var.longipetiolata	Animal	VL	35	[7]
Margaritaria indica	Animal	VS	7	[1]
Markhamia stipulata (Wall.) Seem ex K. sch. Var. kerrii Sprague	Abiotic	—	99	[1, 2]
Melia azedarach (syn: *M. toosendan*)	Animal	S	52	[1, 2]
Meliosma simplicifolia	Animal	VS	6	[1, 2]
Memecylon ovatum	Animal	VS	38	[4]
Memecylon plebejum var.ellipsoideum	Animal	S	18	[3]
Michelia baillonii Pierre	Animal	S	12	[2, 4]
Microcos paniculata	Animal	S	44	[3]

Table A.3 (Continued) Species information for large trees (dbh > 10 cm) in the HKK-FDP. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Micromelum minutum (Forst.f.) Wight & Arn.	Animal	S	1	[3, 4]
Millettia erythrocalyx	Abiotic	—	3	[1]
Mischocarpus pentapetalus (Roxb.) Radlk.	Animal	S	106	[2, 4]
Mitrephora thorelii (syn:*M. thorelii and M. vandaeflora*)	Animal	M	697	[1, 3]
Morus macroura Miq.	Animal	VS	5	[4, 29]
Murraya paniculata	Animal	S	462	[2]
Neocinnamomum caudatum Nees	Animal	L	1	[1, 2]
Neolitsea obtusifolia	Animal	S	654	[1, 2]
Nephelium hypoleucum (syn: *Dimocarpus longan*)	Animal	VL	18	[1, 2]
Nothapodytes foetida (syn: *N. nimmoniana*)	Animal	M	7	[1]
Orophea polycarpa	Animal	S	18	[19]
Oroxylum indicum (L.) Kurz	Abiotic	—	10	[1]
Parkia leiophylla	Abiotic	—	1	[1]
Phoebe paniculata	Animal	S	1,251	[3]
Phyllanthus collinsiae	Unknown	Unk	8	—
Phyllanthus emblica	Animal	S	1	[2]
Picrasma javanica Bl.	Animal	S	22	[2, 4]
Polyalthia cerasoides	Animal	VS	23	[3]
Polyalthia suberosa	Animal	S	3	[3, 19]
Polyalthia viridis	Animal	L	2,570	[24]
Premna pyramidata Wall. Ex Schauer	Animal	VS	2	[1]
Premna villosa Cl. (accepted: *Premna coriacea*)	Animal	VS	2	[3, 23]
Protium serratum (Wall. Ex Colebr.) Engl.	Animal	S	29	[2]

Table A.3 (Continued) Species information for large trees (dbh > 10 cm) in the HKK-FDP. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Prunus arborea (Bl.) Kalk. Var. montana (Hk.f.) Kalk	Animal	S	68	[4]
Pterocarpus macrocarpus Kurz	Abiotic	—	10	[2]
Pterocymbium tinctorium	Abiotic	—	14	[19]
Pterospermum cinnamomeum	Abiotic	—	1	[29]
Pterospermum grandiflorum	Abiotic	—	138	[2]
Pterospermum semisagittatum	Abiotic	—	2	[29]
Radermachera ignea	Abiotic	—	149	[1]
Rapanea yunnanensis Mez	Animal	VS	14	[1]
Saccopetalum lineatum (syn: *Miliusa horsfieldii* and *M. lineata*)	Animal	M	1,132	[1]
Sapindus rarak DC.	Animal	L	8	[2, 4]
Sapium insigne (syn: *Falconeria insignis*)	Animal	VS	26	[38]
Schefflera elliptica	Animal	VS	5	[1]
Schima wallichii (DC.) Korth.	Abiotic	—	1	[1, 2]
Scleropyrum pentandrum (syn: *S. wallichianum*)	Animal	M	37	[1, 2]
Semecarpus albescens	Animal	L	41	[2, 24]
Senna timoriensis	Abiotic	—	12	[3]
Shorea roxburghii	Abiotic	—	2	[1]
Shorea siamensis	Abiotic	—	1	[1]
Siphonodon celastrineus	Animal	M	16	[2, 24]
Spondias pinnata	Animal	VL	25	[2, 3]
Sterculia balanghas	Animal	VL	5	[2]
Sterculia hypochroa	Animal	M	29	[2, 3, 29]
Stereospermum colais	Abiotic	—	39	[1, 2, 39]
Stereospermum cylindricum	Abiotic	—	1	[39]
Styrax benzoides Craib	Animal	S	2	[2]
Suregada multiflora	Animal	S	10	[2]

Table A.3 (Continued) Species information for large trees (dbh > 10 cm) in the HKK-FDP. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Syzygium claviflorum (syn: *Eugenia claviflora*)	Animal	M	6	[1, 2]
Syzygium cumini (syn: *Eugenia cumini*)	Animal	S	22	[2]
Syzygium helferi	Unknown	Unk	1	—
Syzygium megacarpum (syn: *Eugenia megacarpa*)	Animal	L	28	[1, 39]
Syzygium syzygioides	Animal	S	90	[3, 40]
*Syzygium tetragonum*_cf. (syn: *Eugenia tetragona*)	Animal	S	13	[1, 2]
Tarennoidea wallichii (Hk. F.) Tirv. & Sastre	Animal	S	14	[1, 2]
Terminalia bellirica	Animal	L	11	[2]
Terminalia mucronata Craib&Hurxh	Abiotic	—	1	[2, 3]
Terminalia triptera (syn. *T. nigrovenulosa*)	Abiotic	—	12	[1]
Tetradium glabrifolium	Animal	VS	1	[1]
Tetrameles nudiflora R. Br. Ex Benn.	Abiotic	—	326	[1, 3]
Toona ciliata M. Roem	Abiotic	—	15	[1, 29]
Trema orientalis (L.) Bl.	Animal	VS	2	[1]
Trewia nudiflora	Animal	S	171	[2]
Turpinia pomifera (Roxb.) Wall. Ex DC.	Animal	S	10	[2, 4]
Ulmus lancaefolia	Abiotic	—	11	[3]
Unidentified	Unk	Unk	280	—
Vatica odorata	Abiotic	—	811	[7]
Vitex canescens	Animal	S	2	[2, 29]
Vitex glabrata	Animal	S	18	[29, 41]
Vitex limonifolia	Animal	S	1	[1]
Vitex peduncularis	Animal	S	60	[2]
Vitex quinata (Lour.) Will.	Animal	S	3	[2]

Table A.3 (Continued) Species information for large trees (dbh > 10 cm) in the HKK-FDP. Seed sizes are given for animal-dispersed species. All abbreviations and measurement ranges for trait and size categories are given in Table 2.1 (Chapter 2, this dissertation) except for those species for which size is unknown (Unk). The last column provides references for sources of dispersal mode and seed size information.

Species list	Dispersal Mode	Seed Size	No. of trees with dbh >10 cm	Ref. no
Walsura villosa (syn: *W. trichostemon*)	Animal	L	1	[2]
Wrightia viridiflora	Abiotic	—	1	[1, 29]
Xanthophyllum virens	Animal	L	82	[3, 42]
Xantolis burmanica (Coll.& Hemsl.) P. Royen	Animal	L	6	[2, 3, 39]
Xylosma longifolia	Animal	VS	30	[1]
Zanthoxylum limonella	Animal	S	3	[3]
Zollingeria dongnaiensis	Abiotic	—	4	[2]

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Appendix B – Supplemental material associated with Chapter 4

Exploring the relationship between seedling growth and soil nutrients in Thai tropical forest restoration plantations

1. Introduction

In the seedling dynamics investigation reported in Chapter 4 of this dissertation, understory light availability explained less than half of the variance in the growth data. Although this may be due in part to previously discussed limitations in light estimations, high unexplained variance also suggested that influential factors were omitted from the investigation. Soil nutrients may represent one category of these key factors. Recently, Holste et al. (2011) reported that soil nutrients were as or more strongly correlated with seedling growth as irradiance among seedlings in the understory of wet tropical forests. This suggests that soil nutrients play a key role in seedling growth, even in the shade and hints at the potential for practitioners to augment soil nutrient levels to increase seedling growth. Furthermore, Salinas-Peba et al. (2013) reported that adding nutrients to understory seasonally dry tropical forest seedlings increased both seedling survival and growth, though the magnitude of the effects differed by site and species. Prior to these studies, researchers assumed that slow-growing seedlings in the shade are not limited by soil nutrients for months or possibly even years (Kitajima 1996). Our seedling dynamics investigation, however, indicated that intermediate and shade-tolerant seedlings are able to persist for years in the restored forest understory. Thus they are likely at some point to have exhausted their seed nutrient reserves and become dependent on soil nutrients. Moreover, relatively high light conditions in the young restoration plantations may stimulate growth and accelerate the rate of soil nutrient dependency.

This investigation seeks to explore the relationship between microsite levels of soil nutrients and seedling growth for a subset of nine intermediate and late successional species sampled in Chapter 4. We also discuss future research directions and forest management implications suggested by the results.

2. Study Site

This study was conducted on ten experimental forest restoration plots, covering an area of approximately 1.6 ha, located along or immediately below the ridge of a watershed (1,207 – 1,310 m. above sea level) in Doi Suthep-Pui National Park (DSNP), Northern Thailand. Average annual precipitation at this elevation is 2,095 mm (as recorded by the Kog-Ma

Watershed Research Station, the weather station nearest to the forest restoration plots). Although this level of rainfall places the study site at the moist end of the precipitation spectrum for seasonally dry tropical forests (Dirzo et al. 2011), virtually all rainfall occurs during the six-month wet season that extends from May through October. Precipitation averages less than 100 mm per month during the dry season from November to April (Elliott 2003).

The study site was originally covered with tropical, seasonally dry, evergreen forest (EGF). Primary EGF represents the park's most species-rich forest type, providing habitat for approximately 250 documented tree species, two-thirds of which are evergreen (Maxwell and Elliott 2001). EGF is also DSNP's most endangered forest type as much of it has been cleared for cultivation. The forest restoration plots under consideration had been cleared for farming for over two decades prior to plantation planting. The land was later abandoned due to declining fertility and became dominated by herbaceous weeds (Elliott et al. 2000).

At the time of this investigation, most of the slopes below the plots were still being cultivated to provide income and subsistence for the residents of Ban Mae Sa Mai, a Hmong village community (population of about 1,700) within park boundaries (Neef et al. 2004), approximately 2 km south of the experimental blocks (18º52´N, 98º51´E). The nearest extensive patch of intact, primary EGF is approximately 1-2 km east of the plots.

Chiang Mai University's Forest Restoration and Research Unit (FORRU) began establishing experimental forest restoration plots in 1997 to test and refine the Framework Species Method (FSM) for EGF restoration. Since then, FORRU has added new plots annually. The FSM uses mixed plantings of 25-30 species of hardy, fast-growing native trees to catalyze forest succession. Trees are planted at a density of approximately 3,125 trees ha^{-1} and canopy closure in the plantations is complete within four years of planting (Anusarnsunthorn and Elliott 2004, FORRU 2005). The canopy facilitates regeneration of tree seedlings in the understory by shading out herbaceous competitors and moderating the understory climate (Goosem and Tucker 1995, Elliott et al. 2003, Lamb et al. 2005). Following canopy closure, the FSM relies on natural seed dispersal from intact forest to re-establish the floristic composition of the original forest. At the start of this investigation, the oldest experimental restoration plots had begun to develop a dense two-layered canopy (Wydhayagarn et al. 2009).

We conducted this investigation on ten 0.16 ha plantation plots established between 1997 and 2000. At the initiation of this investigation in 2011, the plots were between 11 and 14 years of age. Six of the ten plots were adjoining, forming a continuous stretch of forested land. The four remaining plots shared no borders, but were surrounded on at least three sides by other FSM plots or by regenerating secondary forest. For the purpose of this investigation, three of the isolated plots are referred to by their year of establishment followed by their replicate number (1998-2, 1998-3, and 1999-3). The fourth plot is referred to as Plot 1997 as it is the only replicate of that year incorporated into this investigation. Due to the difficulty in determining the plots on which seedlings were located when at the border of immediately adjacent plots, we grouped some plots together. Plot 1998-1 refers to both the first replicate of three plots planted in 1998 as well as the adjacent 1999-1 and 1999-2 plots. Finally, Plot 2000 refers to the entire stretch of three contiguous plots planted in 2000.

Prior to plantation establishment, the soil on the sites displayed evidence of degradation. Compared with soil in the corresponding intact EGF, the soil on the restoration plantation plots prior to planting was significantly more acidic (mean pH=5.44, s.d. = 0.423), and had less organic matter and nitrogen (mean N = 0.26%, s.d. = 0.045). Mean K was 274.84 ppm (s.d. 137.64) The soil composition also had significantly more sand and less silt and clay, (Elliott et al. 2000). At the time of plot establishment, planted seedlings were fertilized with 100g of 15-15-15 NPK fertilizer at planting. At 4-6 week intervals, they were fertilized with an additional 100g of the same fertilizer three times more during the first rainy season (Elliott et al. 2003). Fertilizer application ceased at the end of the first rainy season. Additional details regarding the planting, maintenance, and monitoring of the plots can be found in Elliot et al. (2003).

3. Methods

3.1 Species Selection

From the species sampled by the investigation in Chapter 4, we selected the nine intermediate and late successional species with the highest overall two-year seedling survival: *Archidendron clypearia (Arcl), Artocarpus lakoocha (Arla), Castanopsis calathiformis (Caca), Cinnamomum caudatum (Cica), Ficus hirta (Fihi), Heynea trijuga (Hetr), Litsea salicifolia (Lisa)*, *Schima wallichii (Scwa)*, and *Turpinia pomifera (Tupo)*. *Rhus rhetsoides (Rhrh)*, a pioneer tree was also initially included for soil nutrient sampling due to its high survival. This species had been excluded from Chapter 4 statistical analyses because of its tendency to die back and because the range of light availability (GSF) for its seedlings was restricted to the low end of the range for seedlings overall. Since the subset sampled in this study also had a lower light range, we also excluded it from the analyses in this investigation, though we include soil nutrient rates in our results summarizing nutrients by species and across and within plots.

3.2 Growth Measurements

This investigation used the two-year (2011-2013) height and diameter growth measurements described in Chapter 4 of this dissertation.

3.3 Seedling Selection

We initially selected a subset of 21 surviving seedlings belonging to each of the nine species. All seedlings demonstrating net positive height and diameter growth and light availability measurements represented the range of light availability for their species. A few initially selected seedlings were later excluded from the analyses because they could not be relocated following initial probe placement or because either height or diameter growth was later deemed insufficient for inclusion (see Chapter 4 Methods, this dissertation).

3.4 Soil Nutrient Measurements

In August 2013, we measured the availability of soil nutrients for selected seedlings. We determined soil nutrient availability to seedlings using Plant Root Simulator (PRS) probes (Western Ag Innovations, Inc.). The probes are ion exchange resin membranes in plastic frames that can be inserted into the soil with minimal disturbance. Ion adsorption on the resin membrane provides a measure of ion flux over time across a constant surface. Probes are either positively charged to adsorb soil anions or negatively charged to adsorb soil cations. PRS probes provide soil nutrient measurements as a nutrient supply rate (μg nutrient/10 cm^2 ion-exchange membrane/2 weeks burial).

In August 2013, we inserted two anion and two cation probes into the soil in an approximately 10 cm by 10 cm square surrounding each seedling, with probes of the same type inserted into opposite corners of the square. We chose to deploy the probes during the wet season because both growth and soil nutrient cycling increases with soil moisture availability in SDTFs (Singh et al. 1989, Jaramillo et al. 2011). After two weeks, we removed the probes from the soil, rinsed off loose soil particles from the probe surfaces with deionized water, and returned them to Western Ag Innovations for laboratory analyses. Nutrient measurements reported for each seedling represent the combined nutrient sorption of two probes (either anion or cation, depending on the nutrient), with the exception of N, which was determined by combining the nitrogen supply rates of both NH_4^+ and NO_3^- supply rates from both cation and anion probes.

3.5 Analysis

We used linear mixed models (LMMs) to model the relationship between two-year seedling growth and each soil nutrient (N, K, S, Ca, Mg, Fe, Zn, Mn, and Al) using linear mixed effects models (LMMs). Since plot was not the subject of the investigation, we controlled for these differences by including plot as a random effect in the LMMs. Although P was included in the soil nutrient measurements, we did not model the relationship between P and seedling growth because 72 samples had P levels at or below the minimum laboratory detection limit. Because models of the larger seedling population (described in Chapter 4 of this dissertation) indicated a strong relationship between seedling growth and light availability, we also included light availability as a fixed effect. We did not, however, test interactions between light availability and soil nutrients due to limited degrees of freedom.

4. Results

4.1 Overview

A summary of measured soil nutrients rates is included in Table B.1. A comparison between soil nutrient supply rates measured by Meason and Idol (2008) for Hawaiian soils is also included to provide a scale of reference. PRS probe analysis detected high variation in nutrient rates for nearly all measured nutrients. Several nutrients also exhibited high variation within plots, suggesting high microsite variation (Table B.2). Furthermore, N rates appeared to differ between species (Figure B.1).

4.2 Analysis

LMM analysis found a moderately strong relationship between Fe rates and height growth ($F_{1,156} = 4.19$, p =0.0424) and a strong relationship between K rates and diameter growth ($F_{1,154} = 7.63$, p =0.0064; Table B.3). Seedling height growth was also strongly related to interactions between Ca and species ($F_{8,156} = 4.19$, p =0.0013) and moderately related to interactions between N and species ($F_{8,156} = 2.10$, p =0.0392). Likewise, seedling diameter growth was strongly related to interactions between Ca and species ($F_{8,154} = 2.93$ p =0.0045) and moderately related to interactions between N and species ($F_{8,156} = 4.19$, p =0.0105).

Interactions between Species and Al ($F_{8,156} = 1.96$, p =0.056) and Species and Mg ($F_{8,156} =$ 1.96, p =0.055) were also nearly significant at $p < 0.05$.

Model based growth predictions (Tables B.4, B.5, and B.6) suggested that relationship between seedling growth and N, K, Ca, and Mg was positive while the relationship between Fe and growth was negative. However, the 95% confidence intervals for model predictions included 0 for most combinations of species and nutrients. This suggests that detectable LMMs were strongly influenced by interactions between nutrients and just a few species (*Arcl*, *Scwa, Tupo,* and *Fihi*). Furthermore, predictions for growth with N and Ca were negative for *Arcl*, but positive for *Scwa*. The only nutrient without conflicting species interactions was K, was the only tested nutrient with an overall predicted growth CI that did not include 0 and the only nutrient with just one species, *Fihi*, with a CI that did not include 0. Both predictions for K were positive.

Table B.1 A statistical summary of soil nutrient measurements in units of μg nutrient/10 cm^2 ion-exchange membrane/2 weeks (n=204). Where available, measurements reported by Meason and Idol (2008) for Hawaiian soil (Hawaii) are included for comparison.

Nutrient	Mean	Min – Max	Median	Std.Dev.	Std.Err.	Hawaii
Total Nitrogen (N)	43.6	2.7 - 308.9	22	52.9	3.7	377.0
Phosphorous (P)*	1.3	0 - 17.7	0.5	2.4	0.2	1.3
Potassium (K)	269.3	29.9 – 1,528.5	229.1	187.7	13.1	107.1
Sulfur (S)	34.7	11 – 100	31	14.8	1.0	-
Calcium (Ca)	190.2	12.6 – 927.9	143.9	159.3	11.2	1,650.3
Magnesium (Mg)	78.6	11.2 – 320.3	57.3	63.7	4.5	247.5
Aluminum (Al)	23.9	8 -121	18	16.5	1.2	-
Iron (Fe)	4.1	1.2 – 34.7	3	3.4	0.2	-
Manganese (Mn)	23.4	0.6 – 250.2	9.8	34.8	2.4	-
Zinc (Zn)	0.8	0.2 – 10.4	0.6	1.0	0.1	-

*72 samples were below the analytical detection limit for P.

Table B.2 A statistical summary of measured rates for N, K, Ca, Mg, and Fe by plot, in units of µg nutrient/10 cm^2 ion-exchange membrane/2 weeks.

Nutrient	Plot	n	Mean	Min – Max	Median	Std.Dev.	Std.Err.
N	1997	12	9.8	5.0 - 20.1	9.9	4.2	1.2
	1998-1	41	36.6	5.7 - 240.3	20.5	50.9	8.0
	1998-2	37	59.4	7.0 - 308.9	39.6	58.1	9.6
	1998-3	32	31.9	4.2 - 128.9	17.8	31.9	5.6
	1999-3	49	19.2	2.7 - 98.1	10.8	21.2	3.0
	2000	30	88.3	4.3 - 234.6	73.5	66.4	12.1
K	1997	12	226.2	61.0 - 587.2	209.5	136.8	39.5
	1998-1	41	288.5	126.2 - 757.1	221.2	124.5	24.1
	1998-2	37	234.5	29.9 - 1,528.5	130.0	297.2	48.9
	1998-3	32	225.5	59.4 - 495.1	213.0	85.5	15.1
	1999-3	49	223.2	44.3 - 478.4	195.8	123.2	17.6
	2000	30	412.9	105.3 - 899.9	403.6	173.3	31.7
Ca	1997	12	455.5	188.3 – 927.9	396.5	263.6	76.1
	1998-1	41	163.2	42.2 – 588.9	134.5	119.3	18.6
	1998-2	37	186.4	62.2 – 702.1	141.8	136.6	22.5
	1998-3	32	124.5	47.0 – 297.4	98.05	68.2	12.1
	1999-3	49	161.1	12.6 – 626.7	89.4	150.0	21.4
	2000	30	636.1	63.8 – 712.6	206.1	160.8	29.4

Table B.2 (Continued). A statistical summary of measured rates for N, K, Ca, Mg, and Fe by plot, in units of µg nutrient/10 cm^2 ion-exchange membrane/2 weeks.

Nutrient	Plot	n	Mean	Min – Max	Median	Std.Dev.	Std.Err.
Mg	1997	12	158.9	29.7 – 299.5	187.3	82.9	23.9
	1998-1	41	68.7	17.8 – 201.3	49.2	47.8	7.5
	1998-2	37	63.8	18.0 – 320.3	49.2	59.6	9.8
	1998-3	32	37.2	11.2 – 90.6	31.9	20.2	3.6
	1999-3	49	85.3	12.1 – 299.4	66.9	67.8	9.7
	2000	30	108.4	27.1 – 267.0	93.2	63.1	11.5
Fe	1997	12	2.2	1.5 – 4.5	2.0	0.8	0.2
	1998-1	41	5.0	1.5 – 34.7	3.2	5.5	0.9
	1998-2	37	2.5	1.2 – 5.7	2.3	1.0	0.2
	1998-3	32	4.1	2.5 – 8.8	3.8	1.4	0.3
	1999-3	49	4.1	1.9 – 12.2	3.1	2.3	0.3
	2000	30	5.6	1.7 – 20.0	3.5	4.4	0.8

Table B.3 Linear mixed model results testing the relationship between seedling height and diameter growth, soil nutrient levels, and species after taking into account the log of the initial dimension (height or diameter) and light availability (GSF). All *p*-values for Nutrients or Species*Nutrient interactions less than or equal to 0.05 are in bold.

Nutrient	Height Growth				Diameter Growth			
	Fixed effects	Statistic	*p*-value	R^2_{GLMM}	Fixed effects	Statistic	*p*-value	R^2_{GLMM}
N	Log Initial Height	$F_{1,156} = 23.19$	<0.0001	0.471	Log Initial Diameter	$F_{1,154} = 25.79$	<0.0001	0.449
	GSF	$F_{1,156} = 17.09$	0.0001		GSF	$F_{1,154} = 17.25$	0.0001	
	Species	$F_{8,156} = 7.43$	<0.0001		Species	$F_{8,154} = 5.77$	<0.0001	
	Total N	$F_{1,156} = 4.33$	0.0391		N	$F_{1,154} = 5.14$	0.0247	
	Species*N	$F_{8,156} = 2.10$	**0.0392**		Species*N	$F_{8,154} = 2.61$	**0.0105**	
K	Log Initial Height	$F_{1,156} = 20.19$	<0.0001	0.431	Log Initial Diameter	$F_{1,154} = 22.70$	<0.0001	0.431
	GSF	$F_{1,156} =17.96$	<0.0001		GSF	$F_{1,154} =17.70$	<0.0001	
	Species	$F_{8,156} = 8.91$	0.0120		Species	$F_{8,154} = 2.60$	0.0109	
	K	$F_{1,156} = 0.10$	0.7542		K	$F_{1,154} = 7.63$	**0.0064**	
	Species*K	$F_{8,156} = 0.49$	0.8604		Species*K	$F_{8,154} = 1.30$	0.2483	
S	Log Initial Height	$F_{1,156} = 17.98$	<0.0001	0.453	Log Initial Diameter	$F_{1,154} = 23.57$	<0.0001	0.427
	GSF	$F_{1,156} =17.36$	0.0001		GSF	$F_{1,154} =18.62$	<0.0001	
	Species	$F_{8,156} = 2.57$	0.0115		Species	$F_{8,154} = 3.61$	0.0007	
	S	$F_{1,156} = 0.0002$	0.9889		S	$F_{1,154} = 1.60$	0.2078	
	Species*S	$F_{8,156} = 1.45$	0.1780		Species*S	$F_{8,154} = 1.73$	0.0952	
Ca	Log Initial Height	$F_{1,156} = 21.55$	<0.0001	0.493	Log Initial Diameter	$F_{1,154} = 22.74$	<0.0001	0.459
	GSF	$F_{1,156} =14.44$	0.0002		GSF	$F_{1,154} =14.47$	0.0002	
	Species	$F_{8,156} = 3.29$	0.0017		Species	$F_{8,154} = 3.86$	0.0004	
	Ca	$F_{1,156} = 1.88$	0.1727		Ca	$F_{1,154} = 0.57$	0.4504	
	Species*Ca	$F_{8,156} = 3.39$	**0.0013**		Species*Ca	$F_{8,154} = 2.93$	**0.0045**	

Table B.3 (Continued) Linear mixed model results testing the relationship between seedling height and diameter growth, soil nutrient levels, and species after taking into account the log of the initial dimension (height or diameter) and light availability (GSF). All *p*-values for Nutrients or Species*Nutrient interactions less than or equal to 0.05 are in bold.

Nutrient	Height Growth				Diameter Growth			
	Fixed effects	Statistic	*p*-value	R^2_{GLMM}	Fixed effects	Statistic	*p*-value	R^2_{GLMM}
Mg	Log Initial Height	$F_{1,156} = 19.94$	<0.0001	0.456	Log Initial Diameter	$F_{1,154} = 23.10$	<0.0001	0.435
	GSF	$F_{1,156} = 14.70$	0.0002		GSF	$F_{1,154} = 14.03$	0.0003	
	Species	$F_{8,156} = 2.57$	0.0117		Species	$F_{8,154} = 3.24$	0.0020	
	Mg	$F_{1,156} = 0.37$	0.8481		Mg	$F_{1,154} = 0.22$	0.6395	
	Species*Mg	$F_{8,156} = 1.96$	0.0549		Species*Mg	$F_{8,154} = 2.10$	**0.0386**	
Fe	Log Initial Height	$F_{1,156} = 23.46$	<0.0001	0.460	Log Initial Diameter	$F_{1,154} = 25.44$	<0.0001	0.460
	GSF	$F_{1,156} = 18.00$	<0.0001		GSF	$F_{1,154} = 16.66$	<0.0001	
	Species	$F_{8,156} = 6.47$	<0.0001		Species	$F_{8,154} = 4.21$	<0.0001	
	Fe	$F_{1,156} = 4.19$	**0.0424**		Fe	$F_{1,154} = 1.09$	0.2986	
	Species*Fe	$F_{8,156} = 1.72$	0.0988		Species*Fe	$F_{8,154} = 0.70$	0.6939	
Zn	Log Initial Height	$F_{1,156} = 15.96$	0.0001	0.432	Log Initial Diameter	$F_{1,154} = 15.96$	<0.0001	0.400
	GSF	$F_{1,156} = 18.37$	<0.0001		GSF	$F_{1,154} = 18.37$	0.0001	
	Species	$F_{8,156} = 4.24$	0.0001		Species	$F_{8,154} = 4.24$	0.0001	
	Zn	$F_{1,156} = 0.30$	0.5841		Zn	$F_{1,154} = 0.30$	0.2986	
	Species*Zn	$F_{8,156} = 0.69$	0.6956		Species*Zn	$F_{8,154} = 0.69$	0.6939	
Mn	Log Initial Height	$F_{1,156} = 21.60$	<0.0001	0.442	Log Initial Diameter	$F_{1,154} = 25.73$	<0.0001	0.413
	GSF	$F_{1,156} = 14.80$	0.0002		GSF	$F_{1,154} = 17.31$	0.0001	
	Species	$F_{8,156} = 8.41$	<0.0001		Species	$F_{8,154} = 5.70$	<0.0001	
	Mn	$F_{1,156} = 2.11$	0.1479		Mn	$F_{1,154} = 0.97$	0.3260	
	Species*Mn	$F_{8,156} = 1.05$	0.4007		Species*Mn	$F_{8,154} = 1.07$	0.3897	

Table B.3 (Continued) Linear mixed model results testing the relationship between seedling height and diameter growth, soil nutrient levels, and species after taking into account the log of the initial dimension (height or diameter) and light availability (GSF). All *p*-values for Nutrients or Species*Nutrient interactions less than or equal to 0.05 are in bold.

Nutrient	Height Growth				Diameter Growth			
	Fixed effects	Statistic	*p*-value	R^2_{GLMM}	Fixed effects	Statistic	*p*-value	R^2_{GLMM}
Al	Log Initial Height	$F_{1,156}$ = 23.06	<0.0001	0.453	Log Initial Diameter	$F_{1,154}$ = 26.13	<0.0001	0.406
	GSF	$F_{1,156}$ =16.39	0.0001		GSF	$F_{1,154}$ =15.52	0.0001	
	Species	$F_{8,156}$ = 5.17	<0.0001		Species	$F_{8,154}$ = 3.20	0.0022	
	Al	$F_{1,156}$ = 0.086	0.7693		Al	$F_{1,154}$ = 0.21	0.6468	
	Species*Al	$F_{8,156}$ = 1.96	0.0555		Species*Al	$F_{8,154}$ = 1.01	0.4276	

Table B.4 Model predictions of percent change in median two-season height and diameter growth in response to each 1 µg N/10 cm^2 ion-exchange membrane/2 weeks by species and overall.

Species	Acronym	Δ Height growth (%)	df	95% CI		Δ Diameter growth (%)	df	95% CI	
				Lower	Upper			Lower	Upper
Archidendron clypearia	*Arcl*	-0.55	156	-0.96	-0.14	-0.57	154	-1.00	-0.14
Artocarpus lakoocha	*Arla*	0.17	156	-0.36	0.70	0.18	154	-0.36	0.72
Castanopsis calathiformis	*Caca*	-0.18	156	-1.03	0.66	-0.28	154	-1.15	0.61
Cinnamomum caudatum	*Cica*	0.24	156	-0.32	0.81	-0.13	154	-0.70	0.44
Ficus hirta	*Fihi*	0.21	156	-0.27	0.68	0.39	154	-0.10	0.88
Heynea trijuga	*Hetr*	0.18	156	-0.30	0.66	0.13	154	-0.37	0.63
Litsea salicifolia	*Lisa*	-0.01	156	-0.39	0.37	0.14	154	-0.25	0.53
Schima wallichii	*Scwa*	2.01	156	0.37	3.67	2.18	154	0.48	3.91
Turpinia pomifera	*Tupo*	0.46	156	-0.25	1.17	0.70	154	-0.04	1.44
	Overall	0.02	164	-0.17	0.20	0.06	162	-0.13	0.25

Table B.5 Model predictions of percent change in median two-season height and diameter growth in response to each 1 μg Ca/10 cm^2 ion-exchange membrane/2 weeks by species and overall. Species abbreviations are provided in Table B.4.

Species	Δ Height growth (%)	df	95% CI		Δ Diameter growth (%)	df	95% CI	
			Lower	Upper			Lower	Upper
Arcl	-0.27	156	-0.48	-0.06	-0.30	154	-0.52	-0.08
Arla	0.07	156	-0.23	0.37	0.08	154	-0.24	0.40
Caca	0.13	156	-0.12	0.38	0.06	154	-0.20	0.33
Cica	0.03	156	-0.12	0.19	0.02	154	-0.14	0.19
Fihi	0.01	156	-0.16	0.17	0.11	154	-0.07	0.29
Hetr	-0.11	156	-0.23	0.00	-0.13	154	-0.25	-0.02
Lisa	0.05	156	-0.11	0.21	0.00	154	-0.17	0.18
Scwa	0.33	156	0.12	0.54	0.22	154	-0.01	0.45
Tupo	0.18	156	0.04	0.31	0.18	154	0.04	0.32
Overall	0.03	164	-0.03	0.09	0.01	162	-0.05	0.07

Table B.6 Model predictions of percent change in median two-season height and diameter growth in response to each 1 μg Ca/10 cm2 ion-exchange membrane/2 weeks by species and overall. Species abbreviations are provided in Table B.4.

	Fe				K				Mg			
Species	Δ Height growth (%)	df	95% CI		Δ Diameter growth (%)	df	95% CI		Δ Diameter growth (%)	df	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
Arcl	-5.79	156	-13.44	2.52	0.09	154	-0.16	0.34	-0.60	154	1.13	-0.09
Arla	1.25	156	-10.00	13.90	-0.03	154	-0.27	0.20	0.15	154	-0.63	0.94
Caca	-7.62	156	-18.45	4.64	0.12	154	-0.10	0.34	0.21	154	-0.69	1.11
Cica	7.15	156	-3.60	19.10	0.14	154	-0.02	0.30	0.04	154	-0.41	0.50
Fihi	-1.43	156	-7.87	5.45	0.28	154	0.07	0.50	0.27	154	-0.25	0.79
Hetr	1.53	156	-2.28	5.50	-0.03	154	-0.22	0.16	-0.38	154	-0.72	-0.04
Lisa	-7.08	156	-17.84	5.08	0.00	154	-0.08	0.08	0.08	154	-0.40	0.56
Scwa	-7.93	156	-19.11	4.80	0.17	154	-0.04	0.38	0.28	154	-0.19	0.75
Tupo	-10.60	156	-18.48	-1.96	0.08	154	-0.08	0.23	0.36	154	-0.01	0.73
Overall	-1.36	164	-3.96	1.31	0.06	162	0.01	0.11	0.01	162	-0.15	0.18

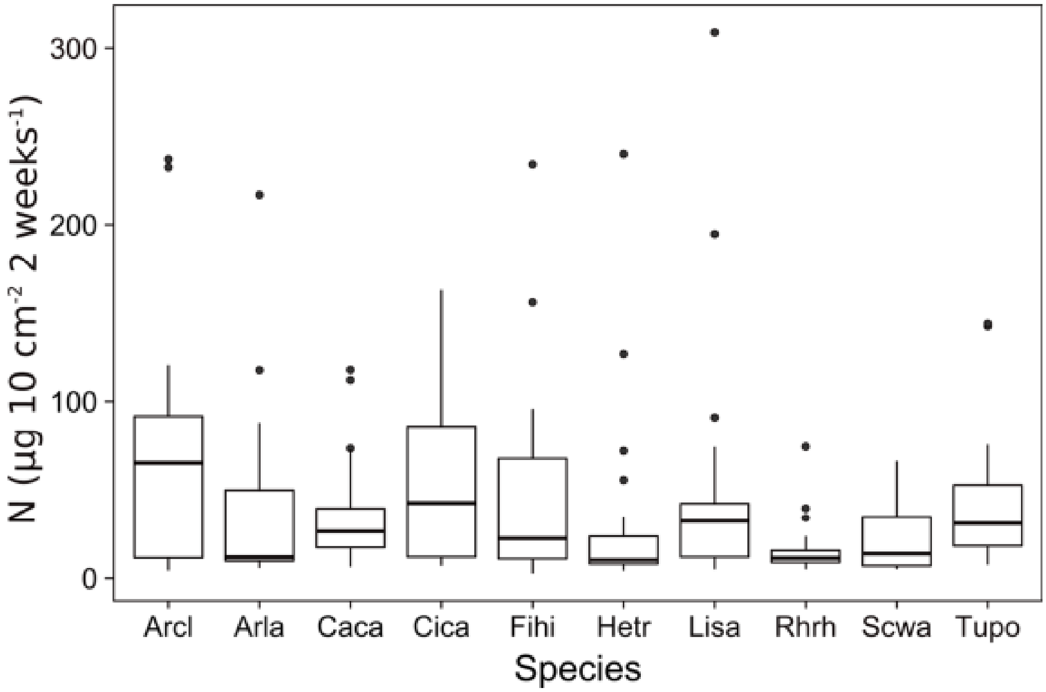

Figure B.1 Nitrogen (N) supply rates over the course of two weeks by species. Species abbreviations are provided in Table B.4.

5. Discussion

5.1 Limitations

Due to resource limitations, we were only able to sample a subset of the species and seedlings used in Chapter 4. Furthermore, the PRS probes could only be placed in the soil for two weeks. Meason and Idol (2008), found that for forest soils, a minimum of four weeks is optimal to allow for equilibrium of most nutrients. Given that the small sample size and the restricted time of sampling may have limited our ability to detect relationships between nutrients and growth, any relationships between soil nutrients and growth should be seen as suggestive, but not conclusive. Still it still appears that the research design was sufficient to suggest some potential research directions. In the future, research using these probes should allow for more time for probes to equilibrate and include more seedlings if possible.

5.2 Overview

Nutrient supply rates from similar soils were not available for comparison with the results of this investigation; however, Meason and Idol (2008) reported that nutrient supply rates for a Hawaiian forest soil suggests that rates measured at our study site were within a reasonable range. Compared to the soil at our study site, the Hawaiian soil is young due to its volcanic origins. This likely explains why Ca and Mg supply were substantially higher. Furthermore, the Hawaiian soil has a high concentration of silt, suggesting a higher cation exchange capacity, which may explain higher N, Ca, and Mg.

5.3 Nutrient Variations Among and Within Plots

Apparent differences in nutrient rates between plots may be the result of topographical or geological differences, since several plots are disconnected from one another and separated by as much as half a kilometer. Furthermore, duration and intensity of past land use may also differ from plot to plot, creating variation in soil nutrient dynamics. Agricultural practices may impact soil nutrient dynamics even decades after succession has begun (Markewitz et al. 2004, MacDonald et al. 2012).

The results of this investigation suggest that there are species differences in microsite soil N rates. *Arcl*, the only member of the Leguminosae family among the sampled species, has the highest median N rate. Since symbiotic nitrogen fixation is common among leguminous tropical trees (Sprent 2005), elevated soil N is likely the result of N-fixation from symbiotic rhizobium. Interestingly, *Cica*, a member of the Lauraceae family, also appears to have elevated N rates, though not as high as *Arcl*. To the best of my knowledge, however, no lauraceous trees are known to fix N. Additional research may clarify whether N in soil surrounding *Cica* seedlings is actually significantly higher than other seedlings, or whether our observations are due to other factors such as seedling location.

Differences in N may also represent differences in species composition since the number of leguminous species differed from year to year (FORRU). There was also high variance within plots, however, not just of N, but also of K and Ca. This suggests the possibility of the existence of microsite nutrient hotspots on the forest floor. Hotspots may be the result of microsite topographical heterogeneity. Roy and Singh (1994) reported higher C, N, and P concentrations in depressions on the forest floor. They attributed this to the decomposition of litter that had accumulated within the troughs. Although we did not quantify topographical heterogeneity within or among plots, we observed troughs due to plant roots as well as slopes of varying degrees throughout the plots.

We also observed a high level of variation in the effort required to insert the soil moisture and PRS probes into the soil beside seedlings, even for seedlings that were within just a few meters of each another. This appeared to be due primarily to microsite differences in soil structure and density as well as the concentration of roots in the soil surrounding the seedlings. Trenching experiments in tropical forests have demonstrated that root competition for soil nutrients significantly limits survival and growth of seedlings (Lewis and Tanner 2000), and high observed root density suggests that competition may be similarly limiting in the Thai restoration plantations. Root densities appeared to be particularly high near bamboo patches due to the presence of bamboo root mats near the soil surface. Dense bamboo clusters are a characteristic of secondary and degraded forests in Northern Thailand (Maxwell and Elliott 2001) and may be a key factor that determines the structure and dynamics of Thailand's SDTF (Marod et al. 1999). Although Griscom and Ashton (2003) reported that bamboo root competition for moisture may increase seedling mortality and contribute to arrested forest succession, we know of no studies that consider the impact of bamboo roots on soil nutrient limitations. Future research may consider whether competition for soil nutrients by bamboo and other species may further limit seedling regeneration SDTF forest restoration.

5.4 Nutrients and Seedling Growth

Model results were conflicting. Although models found that seedling growth was significantly related to K and Fe rates as well as interactions between species and N, Ca, and Mg rates. The majority of 95% CI included 0, and of those few that did not, interactions between species and nutrients were sometimes opposite for the same nutrient. This suggests that any detected relationships were weak and influenced by a small number of species with detectable relationships. The only unambiguously positive relationship appeared to be the relationship between K and with Fihi diameter growth. The weak results may have been due to the small sample size and the limited testing time discussed previously.

Putting 95% CIs aside, though model based predictions indicate the relationships between growth and N, K, Ca, and Mg were largely positive. By contrast, however, the relationship between Fe and growth was negative. Highly weathered tropical soils are often characterized by high concentrations of iron-rich minerals (Brady and Weil 1999). Moreover, in the humid tropics, precipitation leaches out much of the base-forming cations such as K, Ca, and Mg. As the soil becomes more acidic, P begins to form oxides with Fe and Al. These compounds are hypothesized to be the primary mechanism responsible for P limitations of net primary productivity in tropical forests (Chacon et al. 2006). In our research, exchangeable P was below detectable limits in more than a third of all samples. Although this precluded statistical analysis of P and growth, very low levels provide further evidence that exchangeable P is a key limiting factor in seedling growth.

5.5 Research and Management Implications

The results of this investigation suggest that microsite variations in N, P, K, Ca, and Mg may affect the growth of seedlings in the understory of Thai SDTF plantation, but given the limitations of this investigation and the weakness of the results, the findings are far from conclusive. Additional research should be conducted to clarify the relationships between soil nutrients, growth, and species.

One way to explicitly test the relationships would be to fertilize seedlings and measure growth response. This may also provide information as to whether fertilization can be used as a relatively simple and affordable strategy for accelerating the growth of desirable understory seedlings. Furthermore, the negative impact of Fe on growth suggests that strategies to increase microsite soil pH, such as the application of lime, may assist in alleviating P deficiency due to formation of Fe and Al oxides while simultaneously increasing exchangeable Ca and Mg. Future research should explicitly test this to determine the degree to which nutrients and soil pH limit seedling growth in the understory as well as the type and ratios of fertilizers and liming agents required to obtain the most efficient seedling growth.

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