



Effect of microsite light on survival and growth of understory natural regeneration during restoration of seasonally dry tropical forest in upland northern Thailand

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ABSTRACT

The framework species method (FSM) of forest restoration involves planting mixtures of native forest trees to catalyze or complement natural regeneration and accelerate recovery of a diverse understory in tropical forests. Data on naturally regenerating tree seedlings, however, is sparse, and we lack an understanding of how environmental factors affect seedling persistence and growth. We investigated relationships between microsite light availability and two-year survival and growth of naturally-recruited tree seedlings in 11- to 14-year-old FSM trial plots, established to restore seasonally dry tropical forest (SDTF) in the highlands of northern Thailand. We also explored relationships among seedling survival, growth, successional guild and leaf habit. We sampled seedlings belonging to 13 tree species, representing various successional guilds (pioneer, intermediate and late-successional) and leafing habits (evergreen and deciduous). They included seedlings of “overstory species,” species planted to establish the plots, and “re-colonizing species,” species recruited into the plots by seed-dispersal from outside.

Seventy-two percent of sampled seedlings survived two years. Ten species had high two-year survival ($\geq 69\%$); however, three deciduous pioneer species had low survival ($< 50\%$). Deciduous pioneers had significantly lower probability of survival than any other combination of successional guild and leaf habit ($p < 0.001$). Mean microsite light availability was 11% of full sunlight. Survival was unrelated to microsite light, suggesting that most seedlings were tolerant of the range of understory light levels. Relative growth rates of height (RGR_H) and stem diameter (RGR_D) both increased significantly with microsite light level ($p < 0.001$). This indicated that seedlings were sensitive to increases in understory light and that light was an important factor that drove regeneration and community assembly in SDTF undergoing restoration. Still, neither model fully explained variability of either RGR_H ($R_m^2 = 0.230$) or RGR_D ($R_m^2 = 0.138$) suggesting that there are additional, unconsidered factors important to growth.

High two-year seedling survival indicated that within 14 years of implementing the FSM, the understory environment had become adequate for regeneration of a wide range of tree species. Regeneration of re-colonizing species confirmed previous reports that the FSM fosters regeneration of species-diverse tree communities. The results suggested that thinning or gap creation, to increase light levels, may accelerate seedling growth, but are not essential for regeneration of the studied species, and that enrichment planting or direct seeding of intermediate and late-successional species would help to accelerate ecosystem diversification. Introducing such species just before canopy closure and before planted overstory trees become reproductive may provide them with a competitive advantage over seedlings of overstory species.

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1. Introduction

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

The framework species method (FSM) of forest restoration involves planting mixtures of hardy, fast-growing, native forest tree species that are characteristic of the target forest ecosystem, to catalyze or complement natural regeneration. In northern Thailand, active forest restoration, using the FSM, can rapidly re-establish SDTF ecosystems on degraded sites (Elliott et al., 2003). Canopy closure can be achieved within four years after planting (Elliott et al., 2019, 2006). A few years thereafter, naturally-establishing tree seedlings grow up to form an understory. The forest canopy facilitates regeneration of tree seedlings in the understory by shading out herbaceous competitors and moderating the understory climate (Elliott et al., 2003; Goosem and Tucker, 1995; Lamb et al., 2005).

The FSM relies on natural seed-dispersal from intact forest to restore floristic composition and diversity. Ten-year-old restoration plots support species-diverse tree seedling communities that include naturally-recruited seedlings, belonging to both overstory and re-colonizing species (Sinhaseni, 2008). In this paper "overstory species" refers to the tree species planted to establish the plots, while "re-colonizing species" refers those that were absent at the time of plot establishment but later recruited through inward seed-dispersal from outside of the plots. The seedling communities are composed of species from various successional guilds and with various leaf and growth traits. The development of such communities provides evidence that restoration by the FSM initializes forest regeneration and re-establishes a successional trajectory towards mature forest, with rapidly increasing levels of structural complexity and biodiversity (Jantawong et al., 2017; Kavinchan et al., 2015a; Ratanapongsai, 2020; Sinhaseni, 2008; Toktang, 2005).

Recruitment of tree seedlings into the understory, however, is only the first step in the re-assembly of tropical forest ecosystems. Such seedlings have high mortality rates, compared with older saplings and trees (Harper, 1977). It is during the young seedling stage that the influence of habitat filtering (non-random survival of individuals as a result of habitat characteristics) is strongest (Baldeck et al., 2013). Habitat filtering is a dynamic process, which includes interacting abiotic (environmental) and biotic variables (e.g., competition and niche partitioning) that are challenging to tease apart (Kraft et al., 2015). Still, among abiotic factors, low understory light levels are known to limit seedling survival and growth in tropical forests (Delisio et al., 2002; Montgomery and Chazdon, 2002). This is based largely on research from aseasonal, moist, tropical forests, where light availability exerts a strong selective pressure on shade-intolerant species, while also inhibiting growth of shade-tolerant ones (Whitmore, 1996). Over time, selective-pressure and the repression of seedlings in the understory may be as consequential to the trajectory of forest succession as initial seedling establishment is.

In tropical forest, shade-tolerant species may persist for years in the understory and many do not mature without increased light from canopy gap formation (Denslow, 1987). In SDTFs, however, the role of light in understory regeneration is not as clear. In these forests, light may be less limiting, due to higher understory light levels that result from lower, less complex canopies, and higher proportions of deciduous trees (Murphy and Lugo, 1986). Moreover, seedling mortality in SDTFs is primarily attributed to moisture stress during the long dry seasons

(Khurana and Singh, 2001). Thus, in SDTFs light may be less important for limiting seedling establishment (Ferreira et al., 2015; Poorter and Markesteijn, 2008; Vieira and Scariot, 2006). In some cases, high light levels in SDTFs may actually kill forest seedlings by increasing water stress during the dry season (Lieberman and Li, 1992; McLaren and McDonald, 2003).

Given that seedling dynamics and interactions with understory light may play a crucial role in determining the trajectory of forest succession, an understanding of these processes during forest restoration projects is needed to evaluate the progress of ecosystem assembly and to determine whether additional interventions may be effective to achieve restoration objectives. In this observational study, we address this need by 1) characterizing seedling survival and growth over two years in the understory of 11- to 14-year-old forest restoration trial plots and by 2) investigating whether seedling survival and growth are related to variations in understory microsite light levels. The monitored seedlings included both re-colonizing seedlings and those derived from planted overstory trees. Because the seedlings spanned a range of successional guilds and leaf habits, we also incorporated these traits into our investigation, to explore whether they might be predictive of seedling survival or growth. Finally, we looked for patterns that might increase our understanding of regeneration strategies, used by trees in the restored forest and in SDTF more broadly. We discuss the potential management implications of our results and observations.

2. Study site

This study was conducted in 12 experimental forest restoration plots, covering a total of 3.84 ha, 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 (Fig. 1). Average annual precipitation at this elevation was 1,736 mm (as recorded by the Kog-Ma Watershed Research Station, the weather station nearest to the forest restoration plots at a similar altitude). Virtually all rainfall occurred during the six-month wet season (May to October). Precipitation averaged <100 mm per month during the dry season from November to April (Glomvinya et al., 2016). Temperature extremes ranged from a minimum of 4.5 °C in December to a maximum of 35.5 °C in March (Elliott et al., 2019).

The bedrock of the study site was granite and the soils consisted mostly of Acrisols and Cambisols (Elliott et al., 2019; Schuler, 2008). Prior to forest restoration planting, soil organic matter (SOM) in the plots (5.35%) was considerably lower than in nearby natural forest (8.45%). Eleven years after restoration, however, SOM in the plots had risen to 6.93% (Kavinchan et al., 2015b).

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 a threatened habitat in DSNP, since much of it has been cleared for agriculture and tourism infrastructure. The EGF on the sites of the forest restoration plots was cleared for farming more than two decades prior to restoration plantings. The land was later abandoned for both political and environmental reasons and became dominated by herbaceous weeds (Elliott et al., 2019).

At the time of this investigation, most of the slopes below the plots were still being intensively cultivated, as a main source of income for 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 north of the restoration plots (180°52'N, 98°51'E). The nearest remnant forest was Pah Dong Saeng, a patch of degraded primary EGF, located approximately 2–3 km east of the plots (Elliott et al., 2019).

Chiang Mai University's Forest Restoration and Research Unit (FORRU-CMU) began establishing replicated experimental forest restoration plots in 1997, to test and refine the Framework Species Method (FSM) for EGF restoration. Subsequently, plots were added to the system



Fig. 1. An aerial photograph showing the experimental forest restoration plots used in this investigation. Plots are identified with a code representing the year the plot was planted (i.e., “97” for 1997, “98” for 1998, and so on) followed by a number indicating which replicate the plot represented. Subplots labeled “C” are non-planted controls that were not included in this investigation.

annually until 2013. The FSM involves planting mixtures of 25–30 tree species that are characteristic of the target forest ecosystem, to catalyze natural forest regeneration. Although FORRU-CMU experimented with different species mixtures each year, the degree of species overlap among plots was high, because high-performing species were retained from year to year. In the species mixtures planted in 1997 to 2000, four species were included in all four years and 27 species overlapped at least two years.

Trees were planted at a density of approximately $3,125 \text{ trees ha}^{-1}$ (1.8 m apart on average) and canopy closure in the plots was complete within four years of planting (Elliott et al., 2019, 2006). Additional details regarding the planting, maintenance, and monitoring of the plots can be found in Elliott et al. (2019).

The study site consisted of 12 FSM restoration plots, each between 0.16 ha and 0.48 ha (total area = 3.84 ha, Fig. 1). Plots were established annually at the start of the rainy season from 1997 to 2000. When we started this investigation in 2011, the plots were 11 to 14 years old. We selected them because they were the oldest with the most developed forest. The oldest of the plots had already begun developing a dense two-layered canopy (Wydhayagarn et al., 2009). Four of the FSM plots shared no borders and were surrounded on at least three sides by other, younger, FSM plots or by regenerating secondary forest. We considered these four to be independent plots in our analyses. Eight of the sampled FSM plots, however were adjoining, or nearly so, forming a continuous stretch of forested land. Since these plots were not spatially independent, we grouped the eight plots into a single large plot for the analyses.

3. Methods

3.1. Species selection

Seedlings belonging to 13 tree species were monitored: nine overstory and four re-colonizers. These species were selected because they encompassed a range of successional guilds and leaf habits (Table 1). Furthermore, our criteria for species selection included availability of at least 100 seedlings of each species and that these seedlings occurred in at least three of the FSM plots. Assignment of successional type was based on FORRU-CMU’s database, Maxwell and Elliott (2001) and Gardner et al. (2000).

Most of the seedlings of overstory species were assumed to be the

offspring of the planted overstory trees, rather than the result of seed-dispersal from outside of the plots. This was based on our observation of mature, seed-bearing trees belonging to eight of the nine overstory species sampled as seedlings on the plots. *C. caudatum* was the only overstory species for which we did not observe a mature, seed-bearing individual on any of the restoration plots. Since seedlings of this species were also present across plots where it was not planted, it is possible that some or all of these seedlings were the result of seed dispersal from outside of the plots.

3.2. Seedling sampling

We sampled seedlings, defined here as juvenile trees <100 cm in height, across a representative range of understory microsite environments. For a species to be included in the investigation, at least 100 seedlings had to be available, across a minimum of at least three FSM plots. Seedlings of some species were more concentrated on some plots than others, likely due to the presence or proximity of seed-producing adults; however, seedlings were selected such that conspecifics were spread out as widely as possible across multiple plots, with no sampled seedling being closer than 1 m to the nearest conspecific seedling.

In January 2011, at least 100 seedlings of each species were tagged by encircling the stem of each seedling with an aluminum wire tie, indicating the seedling species and sample number. A flag, bearing a duplicate tag, was placed in the soil beside each seedling to facilitate re-location and re-identification.

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

3.3. Microsite light estimates

We estimated microsite light availability from hemispherical canopy photographs taken directly above each seedling in January and February 2011. We used hemispherical photographs rather than direct light

Table 1
Names and traits of the species used in this investigation.

Species	Family	Origin	Leaf Habit	Successional Guild ^b
<i>Archidendron clypearia</i> (Jack) I.C. Nielsen	Leguminosae	Overstory	Evergreen	Pioneer
<i>Artocarpus lakoocha</i> Roxb.	Moraceae	Re-colonizer	Deciduous	Late successional
<i>Bauhinia variegata</i> L.	Leguminosae	Overstory	Deciduous	Pioneer
<i>Castanopsis calathiformis</i> (Skan) Rehd. & Wils.	Fagaceae	Overstory	Evergreen	Late successional
<i>Cinnamomum caudatum</i> Nees	Lauraceae	Overstory ^a	Evergreen	Late/intermediate successional
<i>Erythrina subumbrans</i> (Hassk.) Merr.	Leguminosae	Overstory	Deciduous	Pioneer
<i>Ficus hirta</i> Vahl var. <i>hirta</i>	Moraceae	Re-colonizer	Evergreen	Pioneer
<i>Heynea trijuga</i> Roxb. ex Sims	Meliaceae	Overstory	Evergreen	Intermediate/late successional
<i>Litsea salicifolia</i> (Roxb. Ex Nees) Hook.f.	Lauraceae	Overstory ^a	Evergreen	Intermediate successional
<i>Prunus cerasoides</i> D. Don	Rosaceae	Overstory	Deciduous	Pioneer
<i>Rhus rhetsoides</i> Craib	Anacardiaceae	Overstory	Evergreen	Pioneer
<i>Schima wallichii</i> (DC.) Korth.	Theaceae	Re-colonizer	Evergreen	Intermediate/late successional
<i>Turpinia pomifera</i> (Roxb.) Wall. ex DC.	Staphyleaceae	Re-colonizer	Evergreen	Intermediate/late successional

^a These overstory species were included as part of the planting mixture for a single year; however, their seedlings were identified across plots of different ages. Thus, seedlings on different-aged plots likely originated from planted trees in adjacent plots, though we cannot rule out external seed sources.

^b The successional guild listed first for each species is the guild with which the species associates most strongly and is the guild to which the species is assigned in analyses.

measurements because obtaining direct measurements for each seedling was logistically impractical. Moreover, analysis of hemispherical canopy photographs is an efficient method for characterizing below canopy light environments (Fournier and Hall, 2017).

Photographs were taken during the dry season, because the absence of rain and mist allowed for clear canopy photographs. Attempts to take additional photographs during the 2011 rainy season, to provide a more complete estimate of microsite light throughout the year, were unsuccessful due to light diffusion caused by mist and droplets of water on the camera lens.

Microsite light estimates from the dry-season photographs were probably higher than the actual light received by seedlings throughout a year, because of seasonal changes in leaf cover and the presence of deciduous species among the canopy trees. Despite this, strong correlations between the light estimates and seedling growth indicated these estimates were sufficient to detect relationships between light and seedling dynamics in the understory.

Photographs were taken 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 as possible to the top of each seedling, but at a minimum height of approximately 40 cm above the ground. Photographs were taken throughout the day between approximately 10 am and 5 pm, when lighting was sufficient to create high contrast between the canopy and sky. To prevent errors due to

photograph under- or over-exposure, the autobracketing function of the camera was used to take three photographs for each seedling, one stop either side of the auto-exposure. The photograph with the best contrast between sky and canopy was manually selected for further analysis.

The HemiView Software package (Delta-T Devices, v. 2.1) was used to analyze photographs and estimate the Global Site Factor (GSF, described below) above each seedling. Prior to analysis, all photographs were classified with a programming script. This script converted the photographs from RGB to CIE color space. It then identified all blue and white hues as sky and all other hues as sky obstructions (i.e., canopy). Finally, the script converted the photographs to binary black and white images where the sky was white and the canopy black. Classifying photographs in this way minimized operator bias and streamlined processing and analysis of the photographs.

GSF is an index of the proportion of global radiation reaching a location relative to that of a location with no sky obstructions. In this study, GSF was converted 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 was analogous to the percentage of full sun available at each seedling microsite. 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 have been different from actual measurements, since measurements depended on conditions at any given point in time. GSF should therefore be viewed as an estimate of potential global radiation reaching a given location rather than a measurement. Henceforth we will refer to GSF as “microsite light”.

3.4. Data analysis

3.4.1. Relationships of survival to light and guild-habit

We analyzed the relationship between survival, microsite light, successional guild, and leaf habit, using a binomial generalized linear mixed model (GLMM) with a logit link. The model’s binary response was seedling survival or death by the end of the two-year investigation. We treated as fixed effects the estimated values of microsite light and the log of seedling height during the initial 2011 monitoring event ($\log(H_{\text{initial}})$). We included $\log(H_{\text{initial}})$ to take into account the expected positive correlation between survival and initial seedling size.

An exploratory initial analysis, investigating the relationship between survival and successional guild, found no statistical evidence of a relationship ($\chi^2_{2, 1232} = 4.2, p = 0.126$). Preliminary comparisons of survival by species, however, suggested a relationship between survival and a combination of successional guild and leaf habit. We were unable to include both variables in the model, though, because this study did not have every combination of the three successional guilds and two leaf habit types (i.e., no seedlings belonging to the intermediate guild were deciduous). Instead we combined the two variables into a single factor with five levels — guild-habit — and included this factor as a third fixed effect in the GLMM. We performed a test to determine whether survival of guild-habit levels varied by microsite light, but found no statistical evidence of an interaction ($\chi^2_{4, 1232} = 2.0, p = 0.739$). Therefore, we report only the simpler model here.

We treated both “species” and “plot” as random effects in the GLMM. As previously described in Section 2, for the analysis, the “plots” were comprised of four non-contiguous FSM trial plots and one large “plot”, formed by grouping eight adjoining FSM trial plots. Including “species” as a random effect made it possible for us to explore relationships with guild and guild-habit by including them as fixed effects. It also removed the need to make pairwise comparisons of slopes (odds of survival) among the large number of species. Prior to including species as a random effect, we tested whether the relationship between survival and light varied with species. We found no statistical evidence of an interaction ($\chi^2_{13, 1232} = 7.1, p = 0.870$).

Due to the logit link function of the GLMM, the estimated slopes of the relationships between survival and the fixed effects represent multiplicative changes. We expressed the relationship with light as a percent increase in odds of survival for a 1% increase in light. This increase represented an ecologically meaningful change, given the range of light in the understory. The GLMM also estimated the survival probability of each level of guild-habit. We expressed these as a proportion. To assess the statistical significance of the fixed effects, we used likelihood ratio Chi-squared tests. We used Tukey's method for pairwise comparisons of estimates for the five guild-habit levels.

3.4.2. Relationships of RGR_H and RGR_D to light

We analyzed the relationships between seedling growth, microsite light availability, and guild with two linear mixed models (LMMs). The relative growth rate of stem height [$RGR_H = 100 \times [\ln(\text{Height}_{2013}) - \ln(\text{Height}_{2011})]/(t_{2013} - t_{2011})$; units = % yr⁻¹] was the continuous response for the first LMM (RGR_H LMM) and the relative growth rate of stem diameter [$RGR_D = 100 \times [\ln(\text{Height}_{2013}) - \ln(\text{Height}_{2011})]/(t_{2013} - t_{2011})$; units = % yr⁻¹] was the continuous response for the second LMM (RGR_D LMM).

The LMMs included only seedlings alive during the entire two-year investigation period, with net positive height and diameter growth ($RGR_H > 0$ or $RGR_D > 0$); seedlings with net negative changes in height or diameter due to stem dieback were omitted.

We took into account expected negative correlations between initial seedling size and relative rates of seedling growth by including the log of initial height ($\log(H_{\text{initial}})$) as a fixed effect in the RGR_H LMM and the log of initial stem diameter ($\log(D_{\text{initial}})$) as a fixed effect in the RGR_D LMM.

We also treated "microsite light" and "guild" as fixed effects. We used successional guild rather than guild-habit because preliminary analysis of the relative growth rates did not suggest any relationship between guild-habit. Moreover, guild was more balanced, with each level including seedlings from at least three species. We initially tested whether relationships to light in the LMMs varied with guild. We did not find statistical evidence of an interaction in either the RGR_H LMM ($F_{2,787.5} = 0.6, p = 0.550$) or the RGR_D LMM ($F_{2,787.5} = 0.3, p = 0.804$). Consequently, we present the results of both models without the interaction.

We treated "species" and "plot" as random effects in both LMMs. As with the GLMMs, treating "species" as a random effect allowed us to treat "guild" as a fixed effect and removed the need for pairwise comparisons of slopes between species. Furthermore, it allowed us to include seedlings from species that might otherwise have been excluded, due to stem die back causing low survival and large numbers of seedlings experiencing net negative changes in height or diameter.

LMMs used Gaussian error distributions. The estimated slopes of the relationships with the fixed effects represent additive changes. We express the relationship with light as a percentage-point increase in RGR_H or RGR_D for a 1% increase in light. We used Satterthwaite-adjusted F tests to assess the statistical significance of the fixed effects. We used Tukey's method for pairwise comparisons of estimates for the three guild levels.

3.4.3. Data preparation and statistical packages

Prior to GLMM and LMM analyses, we excluded seedlings whose mortality could be clearly attributed to stochastic events such as falling debris, human foot traffic, or extensive damage to leaves or stems due to insect predation. We also excluded seedlings whose mortality could not be confirmed because identifying flags or tags were missing. Finally, we excluded seedlings that did not have microsite light estimates, due to technical errors in photography or human error.

We calculated summary statistics, marginal and conditional R^2 values (R_m^2 and R_c^2 , respectively) for each model, as described by Nakagawa and Schielzeth (2013), to quantify the amount of variance explained by each model, and to provide an absolute value describing

the model's goodness-of-fit.

We performed all analyses in the R 3.6.0 software environment (R Core Team, 2019). We fitted all mixed models using the lme4 statistical package (Bates et al., 2015). We obtained p -values for the GLMM using the afex statistical package (Singmann et al., 2020). We also calculated R_m^2 and R_c^2 with the MuMIn statistical package (Barton, 2020).

4. Results

4.1. Survival

At the start of the investigation, 1,339 seedlings were identified and tagged for repeated measurements, of which 107 were subsequently removed from the data set (for reasons explained in 3.4.3). Of the remaining 1,232 seedlings, 1,029 (83.5%) survived the first year and 887 (72.0%) of the initially sampled seedlings remained alive at the end of the second year (Table 2).

Annual seedling survival (irrespective of species) increased by 2.7% between the first and second year; however, changes in survival differed among species. Two-year mortality exceeded 50% for only three species, *E. subumbrans*, *P. cerasoides*, and *B. variegata*. These were the only deciduous pioneer species in the study. Interestingly, *F. hirta*, the species with the lowest mortality, was also a pioneer (but evergreen).

4.2. Height and diameter growth

All seedlings sampled were initially <100 cm tall. Mean initial height for 1,232 seedlings was 18.9 cm ($SD = 12.6$) and mean stem diameter was 3.0 mm ($SD = 1.5$). Heights and diameters differed by species (Fig. 2). Mean initial height by species ranged from a minimum of 7.8 cm ($SD = 5.9, n = 92$) for *T. pomifera* to a maximum of 37.4 cm ($SD = 16.8, n = 98$) for *S. wallichii*. Mean stem diameter by species ranged from a minimum of 1.7 mm ($SD = 0.5, n = 99$) for *P. cerasoides* to a maximum of 5.60mm ($SD = 1.0, n = 93$) for *E. subumbrans*.

Mean RGR_H for seedlings that survived the entire investigation period (irrespective of species) was 21.10% yr⁻¹ ($SD = 22.7, n = 887$; Fig. 3a). Between species, RGR_H ranged from 2.9% yr⁻¹ (*B. variegata*, $SD = 18.6, n = 48$) to 39.2% yr⁻¹ (*P. cerasoides*, $SD = 17.7, n = 28$).

Mean RGR_D for seedlings that survived the entire investigation period (irrespective of species) 14.2% yr⁻¹ ($SD = 15.2, n = 887$; Fig. 3b). Between species, RGR_D ranged from 2.9% yr⁻¹ (*B. variegata*, $SD = 12.4$,

Table 2

Seedling survival (%) over the entire two-year investigation and for each year of the investigation. The first row gives survival for all seedlings irrespective of species. Subsequent rows give survival percentages by species. From top to bottom species are arranged in order of highest to lowest overall survival. The last row gives the means and standard deviations across species.

Species	Initial Sample (n)	Survival (%)		
		Overall (2011–2013)	Year 1 (2011–2012)	Year 2 (2012–2013)
All seedlings	1,232	72.0	83.5	86.2
<i>F. hirta</i>	89	98.9	98.9	100
<i>S. wallichii</i>	98	93.9	96.9	96.8
<i>A. lakoocha</i>	99	93.9	94.9	98.9
<i>H. trijuga</i>	98	92.9	95.9	96.8
<i>L. salicifolia</i>	95	91.6	95.8	95.6
<i>C. calathiformis</i>	95	87.4	92.6	94.3
<i>A. clypearia</i>	87	75.9	93.1	81.5
<i>C. caudatum</i>	94	70.2	88.3	79.5
<i>R. rhesoides</i>	94	70.2	77.7	90.4
<i>T. pomifera</i>	92	67.4	73.9	91.2
<i>B. variegata</i>	99	48.5	80.8	60.0
<i>P. cerasoides</i>	99	28.3	55.6	50.9
<i>E. subumbrans</i>	93	18.3	41.9	43.6
Species means (SD)	94.7 (3.9)	72.1 (26.0)	83.6 (17.5)	83.1 (19.3)

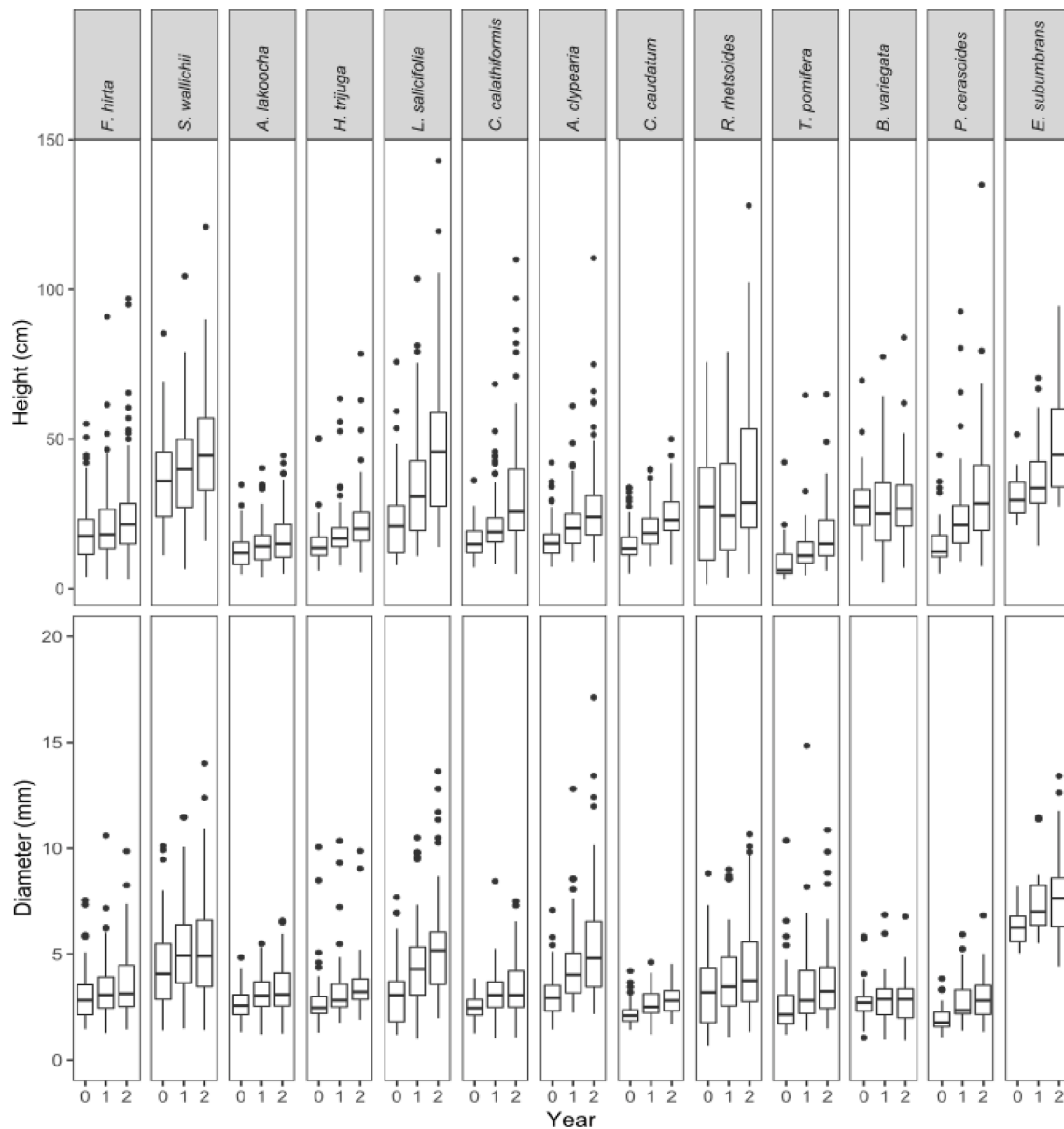


Fig. 2. Box plots illustrating absolute (a) height and (b) diameter measurements of seedlings that survived the entire investigation period, by species at each of the measurement events, held over course of the two-year investigation. From left to right, species are arranged in order of highest to lowest percent overall survival. 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.

$n = 48$) to $26.3\% \text{ yr}^{-1}$ (*L. salicifolia*, $SD = 12.0$, $n = 87$).

Among the seedlings that survived to the end of the investigation, stem dieback occurred frequently; however, re-growth usually resulted in net positive height and diameter growth by the end of the investigation. Some, though, had net negative changes, including 53 seedlings that had net negative height changes, 57 seedlings that had net negative diameter changes, and 38 seedlings that had both net negative height and diameter changes. All species had at least some dieback, but only one species, *B. variegata*, had >25% of surviving seedlings with net negative height or diameter changes. Fifty percent of surviving *B. variegata* had net negative changes in height and/or diameter.

4.3. Visual comparison of relative growth and survival

A visual comparison of the mean RGR_H and two-year survival by species showed no obvious relationship between RGR_H and survival (Fig. 4). RGR_H ranged widely among species and successional guilds,

irrespective of two-year survival.

4.4. Environmental factors

Microsite light (an index of % full sunlight reaching each seedling), ranged from 1.7% to 37.3%, with a mean of 11.0% ($SD = 5.2\%$, $n = 1,232$). >90% of the estimates were below 20% (Fig. 5).

4.5. Analyses

4.5.1. Relationships of survival to microsite light and guild-habit

Seedling survival was not significantly related to microsite light ($\chi^2_{1, 1232} = 0.6$, $p = 0.426$; Table 3). However, after accounting for $\log(H_{\text{initial}})$, seedling survival was significantly related to guild-habit ($\chi^2_{4, 1232} = 19.1$, $p < 0.001$, Table 3). This was primarily due to the estimated probability of survival of deciduous pioneer seedlings (0.26, CI [0.14 to 0.44], Table 4) being significantly lower than it was for all other guild-

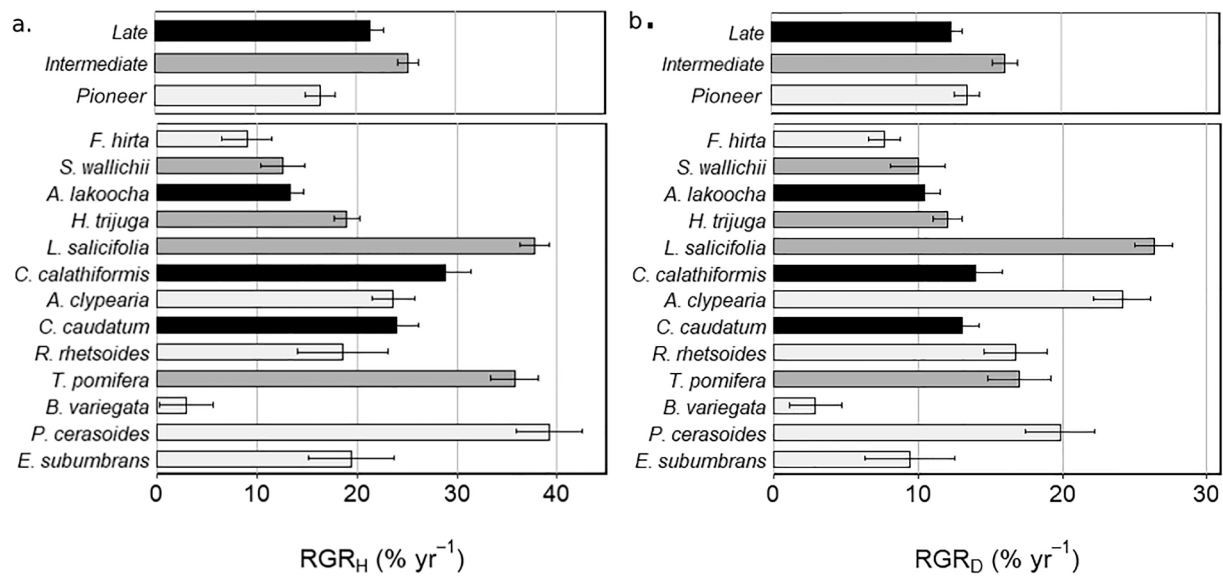


Fig. 3. (a) Mean RGR_H and (b) mean RGR_D for seedlings that survived the entire two-year investigation period, by successional guild and species. The top panels of each graph compare successional guilds. The bottom panels of each graph compare species. Species are arranged in order of highest to lowest percent overall survival. Error bars represent the standard error of the means. Late successional species are represented by black bars. Intermediate successional species are represented by dark grey bars. Pioneer species are represented by light grey bars.

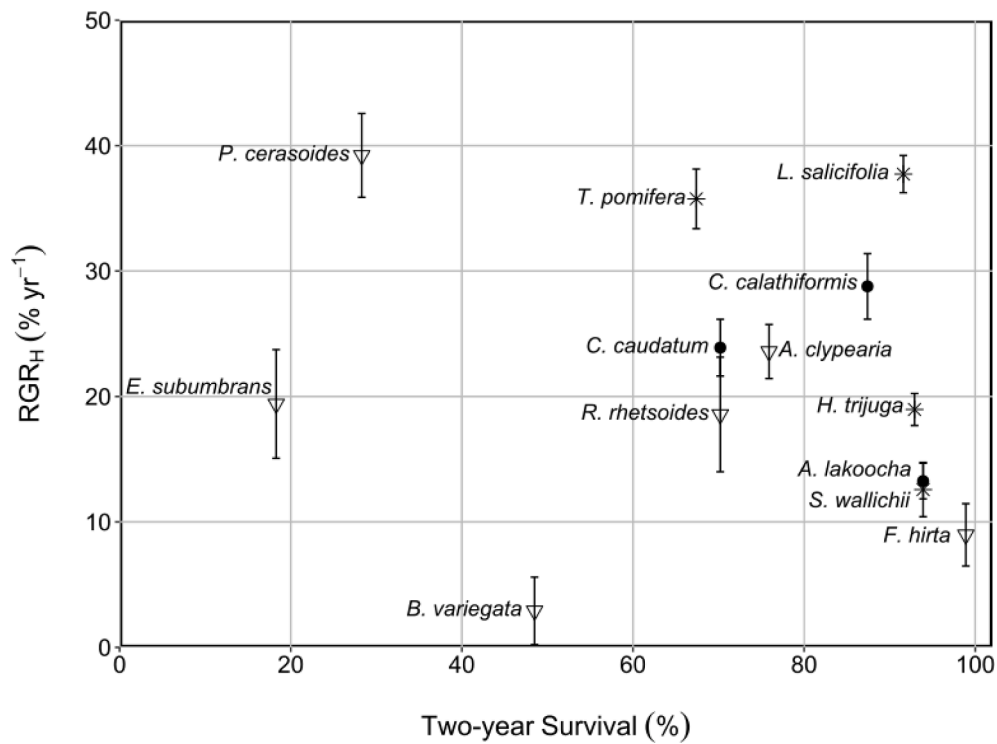


Fig. 4. Mean RGR_H by species versus two-year survival. Error bars represent the standard error of the means. Pioneer species are represented by white triangles. Intermediate successional species are represented by stars. Late successional species are represented by darkened circles.

habit combinations (p -values from all pairwise comparisons < 0.001 , Table 5).

Despite the statistical significance of the guild-habit relationship, GLMM fixed effects accounted for just 38.0% of variation in the model (R_m^2 , Table 3). Furthermore, the GLMM that included fixed and random effects explained only 45.2% of the variation (R_c^2), indicating that the model did not explain a substantial proportion of variation in seedling survival.

4.5.2. Relationships of relative growth rates to light and successional guild

An assessment of normality with residual plots of both LMMs indicated some right skew in the sampling distributions. However, given the large number of samples used in the LMMs ($n = 791$), the Central Limit Theorem justifies assumptions of normality for both models.

Relationships between microsite light and RGR_H ($F_{1,764.8} = 42.7, p < 0.001$) and between microsite light and RGR_D ($F_{1,721.0} = 46.4, p < 0.001$) were strong and positive, after accounting for $\log(H_{initial})$, $\log(D_{initial})$ and successional guild (Table 3).

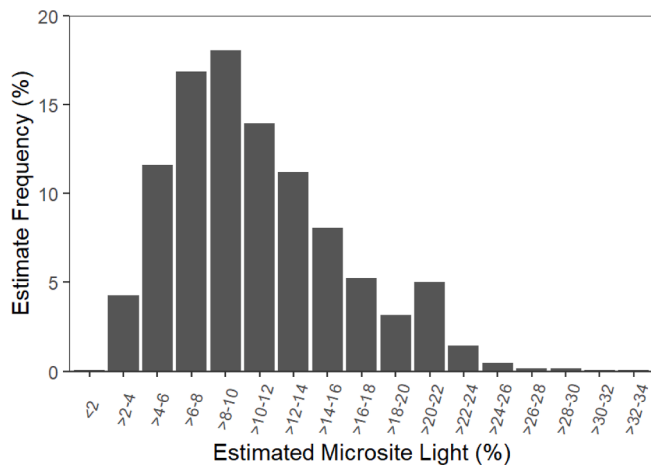


Fig. 5. Percent frequency of microsite light estimates in the trial forest restoration plots.

After accounting for the $\log(H_{initial})$ and successional guild, RGR_H was estimated to increase by 0.6 percentage points (95% CI [0.4 percentage points to 0.8 percentage points increase]) for every 1% increase in microsite light (Table 3). After accounting for $\log(D_{initial})$ and guild, RGR_D was estimated to increase by 0.5 percentage points (95% CI [0.4 percentage points to 0.7 percentage points increase]) for 1% in microsite light.

Note that the estimated increases for RGR_H and RGR_D are additive rather than multiplicative. For example, this means that for a seedling with $RGR_H = 10\%$ a 1% in microsite light will increase the RGR_H by 0.6 percentage-points so that $RGR_H = 10.6\%$. An additional 1% increase in light will increase the RGR_H by an additional 0.6 percentage points so that $RGR_H = 11.2\%$, and so on.

Guild was not significantly related to RGR_H ($F_{2, 13.0} = 0.3, p = 0.736$) or RGR_D ($F_{2, 13.0} = 0.7, p = 0.532$).

Despite statistical significance of the relationship between light and growth, fixed effects accounted for just 23.0% of variation in RGR_H and 13.8% of variation in RGR_D (R_m^2 , Table 3). Furthermore, R_c^2 -values indicated that even after accounting for random effects, >50% of variation in both models remained unexplained.

Table 3

Results of generalized and linear mixed models (GLMM and LMMs) relating survival probability, relative growth rate of seedling height (RGR_H ; % yr^{-1}) and stem diameter (RGR_D ; % yr^{-1}) to estimated microsite light availability (microsite light; %), successional guild (guild), a combination of successional guild and leaf habit (guild-habit) and log initial seedling height ($\log(H_{initial})$) and initial seedling diameter ($\log(D_{initial})$).

Response (model type)	Fixed effects	Est. slope (%)	95% CI		χ^2	F	df	p-value	R_m^2 ^a	R_c^2 ^b
			lower	upper						
Survival (GLMM)	$\log(H_{initial})$	3.3	2.4	1.04	65.1	-	1	<0.001	0.380	0.452
	microsite light	1.0	0.98	1.04	0.6	-	1	0.426		
	guild-habit	^c	-	-	19.1	-	4	<0.001		
RGR_H (LMM)	$\log(H_{initial})$	-12.8	-14.7	-10.9	-	184.5	1, 789.5	<0.001	0.230	0.405
	microsite light	0.6	0.4	0.8	-	42.7	1, 764.8	<0.001		
	guild	^c	-	-	-	0.3	2, 13.0	0.736		
RGR_D (LMM)	$\log(D_{initial})$	-9.2	-11.2	-7.3	-	86.1	1, 786.0	<0.001	0.138	0.325
	microsite light	0.5	0.4	0.7	-	46.4	1, 721.0	<0.001		
	guild	^c	-	-	-	0.7	2, 12.9	0.532		

Estimated slopes for the GLMM represents a multiplicative change (in percent) in odds of survival for a 1% increase in estimated microsite light availability. Estimated slopes for the LMMs represent an additive change (in percentage points) in relative growth rate of seedling for a 1% increase in understory microsite light availability. The p-values are for tests of the fixed effects based on likelihood ratio χ^2 tests (GLMM) and Satterthwaite adjusted F tests (LMMs).

^a R_m^2 (marginal) is the variation explained by the fixed effect.

^b R_c^2 (conditional) is the variation explained by both fixed and random effects.

^c Estimates for factor variables are given in Table 4.

5. Discussion

5.1. Overview

The objective of the Framework Species Method (FSM) of tropical forest restoration is to catalyze or complement natural forest regeneration by planting hardy, fast-growing trees, which create conditions conducive to regeneration of naturally-recruited trees. We characterized the persistence and growth of naturally-recruited tree seedlings in the understory of 11- to 14-year-old FSM trial forests and we investigated relationships between survival, growth, microsite light availability, and life history traits, such as successional guild and leaf habit.

Our results suggested that understory conditions in the FSM trial forests were sufficient not only for initial seedling recruitment, but also for long-term persistence of seedlings of a wide range of species and diverse life-history traits. Persistent species (with two-year survival > 70%) included both overstory and re-colonizing species – a strong indicator that FSM forests were fostering recovery of species-diversity in the regenerating tree communities.

We used microsite light levels to characterize understory light and to investigate relationships between light, seedling survival, and growth. We found no evidence of a relationship between estimated microsite light levels and survival, suggesting most seedlings were tolerant of the prevalent understory shade levels. Although they were persistent, seedlings in the understory grew relatively slowly and many seedlings experienced occasional stem die back. Despite this, we detected strong positive relationships between light and seedling height and diameter growth. This indicated that light was an important factor driving seedling regeneration and thus species assembly in restored seasonally dry tropical forest (SDTF). It also suggested that increased understory light levels could accelerate seedling growth and maturation (i.e., “release”) (for example due to the formation of natural canopy gaps or forest thinning).

Finally, we found that while no relationship between successional guild and growth was detected, deciduous pioneers exhibited significantly poorer survival than other combinations of guild and leaf habit, including evergreen pioneers. This suggested that physiological differences, inherent to this group, may have been responsible for their poor survival.

Table 4

Estimates of factors included as fixed effects in generalized and linear mixed models (GLMM and LMMs) relating survival probability, relative growth rate of seedling height (RGR_H; % yr⁻¹), and relative growth rate of seedling diameter (RGR_D; % yr⁻¹). Factors include successional guild (guild) and a combination of successional guild and leaf habit (guild-habit). See Table 3 for additional results of GLMM and LMMs.

Response (model type)	Fixed Effect (factor)	Levels	Estimates	95% CI	
				lower	upper
Survival (GLMM)	guild-habit ^a	pioneer-deciduous	0.26	0.14	0.44
		pioneer-evergreen	0.87	0.74	0.94
		intermediate-evergreen	0.91	0.82	0.95
		late-deciduous	0.96	0.85	0.99
		late-evergreen	0.83	0.64	0.93
RGR _H (LMM)	guild ^b	pioneer	27.8	20.3	35.2
		intermediate	27.9	19.0	36.8
		late	24.0	13.8	34.2
RGR _D (LMM)	guild ^b	pioneer	17.4	11.9	22.9
		intermediate	19.2	12.7	25.8
		late	14.5	7.0	22.1

Estimates for the five levels of the GLMM factor, guild-habit, represent the probability of survival for each level of the factor when all continuous variables in the model are fixed to their means. Estimates for the three levels of the LMM factor, guild, represent mean RGR_H or RGR_D when all continuous variables in the model are fixed to their means.

^a Pairwise comparisons of estimates are presented in Table 5.

^b Pairwise comparisons for guild levels are presented in Appendix A, Table A1.

5.2. Survival

Nearly three quarters of monitored tree seedlings persisted to the end of the two-year investigation. Overall seedling survival was substantially higher than that reported for other, comparable, SDTFs (Gerhardt, 1996; McLaren and McDonald, 2003), including lower-elevation Thai evergreen forest (Marod et al., 2002). Furthermore, survival remained relatively stable over both years of the investigation. Since seedling mortality in SDTFs is primarily attributed to dry-season moisture stress (Khurana and Singh, 2001), high seedling survival rates, found in the present study, may have been due to higher levels of precipitation. Rainfall levels at this site are considered to be at the moist end of the precipitation spectrum for SDTFs (Dirzo et al., 2011). Consequently, dynamics in the restored forest may have been more similar to that of humid tropical forest than to that of drier SDTFs. 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 (Montgomery and Chazdon,

2002; O'Brien et al., 2013; Welden et al., 1991).

The year we initiated the investigation, 2011, was an exceptionally cool and moist year (Thai Meteorological Department, 2012). It is possible that similarities in seedling survival between the restoration plots and more humid tropical forests are artifacts of this anomalous weather. However, if that were the case, we might expect mortality to increase in the second year, since 2012 was both warmer and drier (WorldWeatherOnline.com, 2020). Instead, annual seedling mortality decreased slightly and only three species experienced substantial increases in mortality in the 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 suggested that seedling survival was not substantially affected by 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.

The seedling selection method used in this study may have also favored persistent, 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, were the result of seedling accrual over multiple years. They may therefore have represented a pre-filtered population of seedlings that had already passed through one or more dry seasons.

5.3. Survival and guild-habit

Although overall survival was relatively high, survival differed among species groups. Ten species demonstrated high persistence in the understory (>67% survival over two years), while three survived relatively poorly (<50% survival over two years). These three species (*B. variegata*, *P. cerasoides*, and *E. subumbrans*) were all pioneers, which are deciduous as adults, although not as seedlings. When compared to other combinations of successional guild and leaf habit, the deciduous pioneers had significantly lower survival than any of the other combinations, including evergreen pioneers.

Aside from deciduous pioneers, survival rates of all guild-habit combinations were not statistically different from one another. This suggests that pioneers as a guild were not limited in the understory, but that physiological differences due to leaf habit may have played a role in survival differences between deciduous and evergreen pioneers. Shorter leaf life spans and higher growth rates are often linked in plants (Reich et al., 1992), but in limiting light, the cost of producing short-lived leaves may exceed their contribution to a plant's carbon balance (Givnish, 1988; King, 1994). Although the deciduous pioneer seedlings in our investigation retained at least a few leaves year-round, we observed that they tended to lose leaves as the dry season progressed and

Table 5

Tukey's method for pairwise comparisons of estimates for the five levels of guild-habit from the Survival GLMM. The number of species in the level is included in parentheses ().

Contrasts		Odds ratio	SE	p	95% CI	
guild-habit	guild-habit				lower	upper
pioneer - deciduous (3)	pioneer - evergreen*	0.053	0.032	<0.001	0.010	0.032
	intermediate - evergreen*	0.036	0.202	<0.001	0.008	0.020
	late - deciduous*	0.013	0.0117	<0.001	0.0116	0.0117
	late - evergreen (2)*	0.075	0.049	0.001	0.013	0.049
pioneer - evergreen (3)	intermediate - evergreen	0.683	0.393	0.964	0.142	0.393
	late - deciduous	0.248	0.223	0.528	0.0214	0.228
	late - evergreen	1.409	0.938	0.986	0.229	0.938
intermediate - evergreen (4)	late - deciduous	0.363	0.316	0.772	0.034	0.316
	late - evergreen	2.062	1.294	0.778	0.372	1.294
late - deciduous (1)	late - evergreen	5.619	5.303	0.338	0.446	5.303

The odds ratio for each pair of contrasts represents comparisons of estimated survival probabilities.

* The mean difference is significant at the 0.05 level, significant: P < 0.05.

flushed new leaves at the start of the rainy season. Therefore, higher production cost of their shorter-lived leaves may have contributed to their higher mortality in the lower-light of the understory. Note, however that comparison of survival and guild-habit was applied *post-hoc* to the investigation. Furthermore, comparisons were limited by unbalanced levels, due to an insufficient diversity of guild-habit among the sampled species. Consequently, we recommend additional research, to confirm and clarify these relationships.

5.4. Growth

Relative rates of height and diameter growth were comparable to those reported for tree seedlings in other tropical forests (Daisuke et al., 2013; Inman-Narahari et al., 2014). Although growth rates varied among species and stem die-back was common, mean relative growth rates were positive for surviving seedlings of all species. We also we found no evidence of a relationship between growth and successional guild. This suggested understory conditions were sufficient for growth of a range of naturally-establishing seedlings. Furthermore, individual seedlings of six species grew taller than 1 m, our cut-off height for differentiating seedlings from saplings. Most of these seedlings were of intermediate or late successional species, indicating conditions beneath the canopy of the forest restoration plots were able to support not only establishment and persistence of intermediate to late successional species, but also their eventual maturation.

5.5. Understory light availability

We estimated that seedlings received a median of approximately 11% of full sun with wide variation among microsites (1.7–37.3%). Although our estimates of light availability were limited to photographs taken during the dry season, when canopy openness was highest, these levels were comparable with reported levels in lower-elevation Thai mixed deciduous forests (Marod et al., 2004).

Seasonal changes in understory light availability are characteristic of SDTF, due to seasonal weather and the prevalence of deciduous canopy trees (Murphy and Lugo, 1986). Marod et al. (2004) found that in Thai mixed deciduous forest, light intensity in the rainy season was 80% lower in the understory and 20% lower beneath a large canopy gap, compared with the same niches in the dry season (estimated from hemispherical photos). 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. However, seasonal changes on the forest restoration plots in this investigation were likely to have been smaller than those in Thai mixed deciduous forest. This was because deciduous trees comprise nearly three-quarters of Thai mixed deciduous forest tree species (Maxwell and Elliott, 2001), but only 27% of species in Doi Suthep EGF (Elliott et al., 2006). Moreover, they comprised less than one third of the species that had been planted, to establish the restoration plots (FORRU, personal communication). Still, reliance on dry-season light availability estimates very likely led to overestimation of annual light availability in this investigation. Despite this, the strength of the relationship, between the microsite light estimates and relative rates of seedling height and diameter growth (discussed in 5.6), indicated that the estimates were adequate for gauging relative levels of microsite light availability.

5.6. Relationships of survival and growth to microsite light availability

Although understory light availability is a key limiting factor of both seedling survival and growth in tropical forests (Kobe, 1999; Montgomery and Chazdon, 2002; Whitmore, 1996), we were unable to detect a relationship between variations in microsite light and seedling survival. We should note that even the lowest light estimates in the restored forest plots were higher than those required for the long-term persistence of shade-tolerant seedlings in rainforest understory (Bloor and

Grubb, 2003; Montgomery and Chazdon, 2002). This suggested that light range in the understory was more than sufficient for persistence of most of the seedlings and therefore differences in survival were not detectable. The one exception to this might have been the deciduous pioneers, but we did not detect any indication of a relationship when we included an interaction between microsite light and guild-habit in the model of survival.

In contrast to seedling survival, relationships were strong and positive between microsite variations in light availability and relative rates of seedling height and diameter growth. After accounting for initial seedling height and diameter and successional guild, each 1% increase in microsite light added 0.63 percentage points to the RGR_H and 0.51 percentage points to the RGR_D .

Previous studies have shown that growth and carbon gain of tropical plants are highly responsive to microsite variations in light availability in the understory (Chazdon et al., 1996; Oberbauer et al., 1993). In tropical rainforests, the responsiveness of individuals and species to light variations in closed canopy microsites may determine their long-term persistence (Montgomery and Chazdon, 2002). Persistent species may pursue a regeneration strategy of “seedling banking,” in which understory accumulation of repressed or slowly growing seedlings persists for years, or even decades, until high light from canopy gaps releases them (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. In the restored forest, sensitive growth responses to light may have served a similar purpose, although higher light levels in the understory may have allowed some species to mature beyond the seedling stage, even in the absence of canopy gaps.

Although the relationship between growth and light was strong, large unexplained variance in both the height and diameter growth data suggested that additional factors, important to seedling growth, had been omitted from the investigation. These factors may have included soil moisture, which has been shown to increase mortality and limit growth during the dry season in SDTF (Khurana and Singh, 2001; McLaren and McDonald, 2003), and soil nutrients, which sometimes exert growth effects that rival that of understory irradiance in wet tropical forests (Holste et al., 2011).

5.7. Relationship of growth to successional guild

Although this study was not originally designed to test differences in growth between successional guilds, the sampling of seedlings belonging to all three guilds made it possible to do so. We were, however, unable to detect any statistically significant differences in growth. This may have been due to large variations in growth among species in the same guild (see 5.8 discussion concerning deciduous and evergreen pioneers), as well as an insufficient number of species for each guild. Guild was especially unbalanced for late and intermediate successional guilds, which were represented by just three and four species respectively.

5.8. Species observations

Surviving seedlings of two of the high-mortality deciduous pioneer species: *P. cerasoides* and *E. subumbrans*, had moderate to high relative growth rates. In full sun, both of these species have such high survival and rapid growth that FORRU-CMU has consistently included them in restoration planting mixtures to bring about rapid canopy closure (Elliott et al., 2003). In shade, however, their continued growth may have been due, in part, to etiolation or may indicate the existence of a few understory microsites that support both their survival and growth. It might also reflect natural selection for faster growth in light gaps, resulting in both high relative growth rates in both light and shade, but more rapid mortality in shade (Kitajima, 1994). Regardless, poor survival of these species, suggested that, while they had been planted to

achieve early canopy closure, they are unlikely to persist for long afterwards.

Many studies of both temperate and tropical seedlings and saplings have found evidence of trade-offs between high-light growth and low-light survival (Grubb et al., 1996; Kitajima, 1994; Kobe et al., 1995; Wright et al., 2010). Trade-offs occur because, unless plants have high physiological flexibility, high respiration rates needed to maintain rapid growth in high-light conditions can lead to an unfavorable carbon balance and starvation in low-light conditions (Bazzaz, 1979). Thus, we expected that fast-growing pioneer species in this investigation to have high mortality in the lower-light understory, compared with later successional species. While the deciduous pioneer species in this study met the expectation of such a trade-off, evergreen pioneers (*R. rhetsoides*, *A. clypearia* and *F. hirta*) survival and growth were similar to those of more shade-tolerant intermediate and late successional species. Yet, in trials, conducted by FORRU-CMU to test potential framework tree species, all three evergreen pioneers grew rapidly in open field (high-light) conditions. *F. hirta* and *A. clypearia* seedlings grew from initial heights of <40 cm to over 1.5 m in 16 months and *R. rhetsoides* seedlings grew from about 65 cm to an average height of 3.3 m in 15 months. The ability of these species to shift from rapid high-light growth to low-light persistence indicates high physiological plasticity. Their ability to facultatively adapt to shade may mean that they avoid much of the trade-off between growth and mortality. If so, this increases the likelihood that these pioneers will continue to be well-represented in the future restored forest community.

Intermediate and late successional species were able to both persist and grow in the understory. Of these, seedlings belonging to two overstory species, *L. salicifolia* and *C. calathiformis*, had high survival, high relative growth, and high final absolute height. This suggested that these two species were particularly well-suited to regenerating in the restored forest understory and that they were likely to continue to be members of the future forest community. This may be desirable, since one aim of the FSM is to “short circuit” succession by planting carefully selected intermediate and late successional tree species to plant alongside pioneers. In doing so, managers hope to more rapidly achieve the composition and structure of old-growth forest (Elliott et al., 2013). On the other hand, care should be taken to avoid planting species whose offspring may over-accumulate in the seed bank, since early-colonizing tree species sometimes inhibit, rather than facilitate, growth of late-arriving species by limiting access to key resources, particularly sunlight (Wunderle, 1997).

6. Management implications

The results of this investigation contributed to the growing body of research indicating that restoration, using mixed tree species indigenous to the target forest ecosystem, creates conditions that catalyze natural forest regeneration (Keenan et al., 1997; Lamb et al., 2005; Parrotta and Knowles, 2001). In this study, high survival and steady growth of intermediate and late-successional tree seedlings suggested that additional management interventions, to promote forest regeneration, are generally not necessary. On the other hand, the strong positive relationship between seedling growth and light availability did suggest that some thinning, to increase light levels, might hasten understory development and diversification. However, costs and benefits of thinning should be weighed against the likelihood that natural canopy gaps, occurring as a result of mortality of overstory pioneer and intermediate successional species, will gradually facilitate the release and maturation of seedlings from the seedling bank, without intervention. Furthermore, since light availability did not explain all the variance in seedling growth, we recommend additional investigation of other factors, such as soil moisture and nutrients.

Given that a wide range of seedling species persisted and grew without assistance, managers should focus limited resources on measures that accelerate re-assembly of species-diverse seedling communities, such as enrichment planting (direct seeding or planting of

seedlings of desired species). The high performance of intermediate- and late-successional tree species suggested that restoration plot understories are suitable for enrichment planting of similar species. This was further supported by high establishment rates of experimental plantings of large-seeded, intermediate- and late-successional species in the same restoration plots (Sangsupan et al., 2018). Such enrichment planting or direct seeding should be carried out just before complete canopy closure (in northern Thailand during the third rainy season after planting), since an incomplete forest canopy has light gaps that enable seedlings and saplings to mature more rapidly. For example, Bertacchi et al. (2016), attributed higher survival of enrichment planted seedlings in young Brazilian restoration plantations to greater light availability, compared with older plantations. Lastly, enrichment planting, before most of the planted overstory trees begin fruiting, might reduce competition between enrichment species and the offspring of overstory trees.

CRedit authorship contribution statement

Hathai A. Sangsupan: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft. **David E. Hibbs:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Bradford A. Withrow-Robinson:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Stephen Elliott:** Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119061>.

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