Regeneration recruitment and survival in an Asian tropical rain forest: implications for sustainable management

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Abstract. Few studies have been published that focus on monitoring and investigating the long-term patterns of recruitment and survival of seedlings in the understories of tropical forests. Studies for mixed dipterocarp forest, the dominant tropical forest type for South and Southeast Asia, demonstrate seedlings in the existing forest understory (advance regeneration) play the most important role in forming a new forest after disturbance (e.g., logging, windstorms). Our study monitors the regeneration dynamic across a topographic gradient (ridge, mid-slope, and valley) of the understory for a mixed dipterocarp forest in the Sinharaja MAB reserve in southwest Sri Lanka. We recorded seedling recruitment, growth, and mortality by species in replicated plots on multiple forest understory sites over a ten-year period. Seedling density ranged from 26 to 31 m^2 with all of it categorized as advance regeneration of canopy tree species. Results show differences in seedling density per species across the topography and over time, with differences driven by changes in species composition from valley to ridge and in recruitment periodicity potentially related to supra-annual variations in climate. Seedling mortality was higher on ridges than valley and mid-slopes; and disproportionately higher seedling mortality occurs of relatively shade-intolerant late-successional trees species (70% mortality after 8 yr) compared with their more shade-tolerant associates (30% mortality after 8 yr). Our results contradict current selective logging prescriptions for tropical forests that comprise a single cutting cycle and minimum diameter felling for all commercial timber trees. Such harvests give no consideration to timing and manipulation of the forest canopy to favor release of advance regeneration. We recommend careful timing of timber harvests to occur in synchrony to the periodicity of seedling recruitment and silvicultural treatments that both insures their release and that accommodates to differences in seedling composition and density across topography.

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INTRODUCTION

Many studies have examined the role that different types of regeneration play within tropical rain forests after disturbance (Grubb 1977, Swaine and Whitmore 1988, Wright 2002). The reproductive phase of a forest is the window of time when forest composition has the ability to move and change with the establishment of seedlings in new growing spaces, particularly after canopy-level disturbance (Grubb 1977, Wright 2002).

Seedling studies of tropical rain forests have sought to explain patterns in composition and density through the role of niche differentiation in relation to non-random spatial distributions of tree species across topographies (Clark et al. 1998,

1999, Harms et al. 2001, Russo et al. 2005, Engelbrecht et al. 2007). Other studies have sought to understand how the frequency, type, and degree of disturbance play a role in promoting the mixing of early and late-successional tree species in what has been defined as the intermediate disturbance hypothesis (Davies et al. 1998, Schnitzer and Carson 2001). Still other studies have sought to investigate negative density dependence, whereby seedlings of a species have higher survival the further away from their parent trees (Harms et al. 2000, Comita and Hubbell 2009, Comita et al. 2010).

By far, the majority of seedling studies within wet tropical forests have been done at two places in the Neotropics—the Smithsonian's Barro Colorado Island, Panama and The Organization for Tropical Studies, La Selva, Costa Rica. And more generally, almost all the studies on tropical forest regeneration in the last twenty years have been focused on the Neotropics, providing a potentially biased perspective of our understanding on seedling regeneration dynamics within rain forests. Few studies originate in either the Asian or to an even more marked degree, the African tropics; two very different tropical biomes, both with very different biogeography.

Though there are many studies examining tropical forest regeneration at the seedling and sapling stage (as cited above), few studies have invested the time and energy into basic long-term monitoring of recruitment and mortality of regeneration in the forest understory. Yet understanding the long-term pattern of regeneration establishment and growth in forest understories of tropical wet forests has been demonstrated to be the critical factor in determining the future composition and structure of a new forest (Richards 1952, Gómez-Pompa et al. 1991, Chazdon 2003). Where such studies have been published, they have been conducted as a single survey or for only a few years, or some have been an intermittent census taken two-to-three times over a widely spaced period of years. Such studies in the Neotropics have demonstrated that the overall preponderance of seedlings in mature tropical forest understories comprises advance regeneration (Guariguata and Pinard 1998). Advance regeneration can be defined as seedlings of tree species that persist for some period of time (usually greater than one year) in the forest understory. A study by Comita

et al. (2007) showed that seedlings in a Panamanian rain forest comprised mostly shade-tolerant advance regeneration of late-successional canopy tree species, as compared to shade-intolerant canopy tree species or understory tree species. Their study also finds regeneration to be dominated by a few species that are in larger sapling size classes, suggesting either poor or low seed dispersal, low seed germination, or high initial seedling mortality.

Seedling studies examining tree species diversity in the Asian tropics have been limited almost exclusively to the major wet evergreen tropical forest type defined as mixed dipterocarp forest. This forest type is dominated in the canopy by one family of trees—Dipterocarpaceae—that is widespread throughout South and Southeast Asia. Like the Neotropics, studies have been primarily done at a few forests in Malaysian Borneo (Brown and Whitmore 1992, Whitmore and Brown 1996, Bebber et al. 2004, Palmiotto et al. 2004), the Malay Peninsula (Raich and Khoon 1990, Turner 1990a, b), or in southwest Sri Lanka (Ashton 1995, Gunatilleke et al. 1997, 1998). Studies in Borneo and Sri Lanka have shown that the regeneration of the dipterocarps in mixed dipterocarp forests strongly differentiates into a variety of habitat associations based upon aspect, slope position, and soil supporting the niche diversity hypothesis (Webb and Peart 2000, Russo et al. 2005, Gunatilleke et al. 2006, Paoli et al. 2006, Wiegand et al. 2007). Alternatively, Webb and Peart (2000) showed that about half the abundant mostly non-dipterocarp species in a mixed dipterocarp forest showed no trends or association; and other studies have demonstrated negative density dependence in these forests (Webb and Peart 1999, Peters 2003).

Though a few studies in mixed dipterocarp forest of tropical Asia are measuring forest regeneration, they chiefly record the spatial arrangement of regeneration in relation to each other at one point in time or over a short census period (e.g., 1–2 yr). These studies then correlate this to a variety of environmental factors in order to deduce regeneration pattern and process. Other studies cited above are strongly experimental using plantings and use of canopy openings to control for spatial variations in seedlings populations, age distribution among seedlings, and environmental variation in light and soil resources. Almost all of this work also only monitors seedling dynamics and growth for

only a short period of time (<2 yr). There has only been one investigation that we are aware of that has physically monitored seedling growth and development over a longer period of time (e.g., 10 yr; Delissio et al. 2002). Little is therefore known about the differential recruitment dynamics among tree species; differences in their survival, particularly advance regeneration; and how various environmental drivers may affect such processes within the forest understory. Where rain forest, such as mixed dipterocarp forest, has long periods of growth and development with only small intermittent disturbances to the forest canopy, understanding the nature of advance regeneration recruitment, survival, and growth is critical toward managing such forests for timber and non-timber forest products and for their restoration on lands where such conditions for advance regeneration do not exist. The study by Delissio et al. (2002) monitored seedlings in a mixed dipterocarp forest in Sarawak and showed that on average over 50% of seedlings survived longer than ten years. They found that seedlings can remain suppressed for long periods of time in the understory and can respond quickly to release when exposed to favorable conditions.

We designed our study to understand the pattern of recruitment, survival, and growth of advance regeneration in the understory of closed-canopy mixed dipterocarp forest. More specifically, we sought to record the nature of seedling recruitment frequencies, their survival, and growth as advance regeneration over multiple years in relation to topographic position. Surprisingly, very little work of this nature has been done on these factors for mixed dipterocarp forest. Yet this kind of information is vital for understanding basic forest dynamics and underlies the principles of forest management and restoration. In particular, understanding the recruitment periodicity and length of survival of advance regeneration of important timber tree species would facilitate more appropriate both timing and release of silvicultural treatments to insure their survival and growth to form the new forest after a timber harvest.

MATERIALS AND METHODS

Study site

Our study was done in wet evergreen rain forest of southwest Sri Lanka (Ashton and Gunatilleke 1987). The sites selected were in the western region of the Sinharaja World Heritage Site (6°45″ N, 80°30″ E). The topography is hilly, comprising ridges and valleys, and underlain by schist and gneiss metamorphic rocks (Cooray 1967). Elevations range between 250 and 600 m amsl. The soils are weathered in situ Ultisols (USDA 1975). They are deep and well drained in the valleys. On the ridges, soils are skeletal with an organic, dark-colored A horizon at the surface prone to erosion (Moorman and Panabokke 1961, Mapa et al. 1999). Rainfall is between 3500 and 6000 mm/yr with most coming over two monsoonal periods (April–July and October–December; Ashton 1992). Mean annual temperature is 24°C with little to no seasonal variation and greater diurnal variation that fluctuates between 18°C (night time) and 30°C (daytime; Ashton 1992, Gunatilleke et al. 1998).

The wet evergreen rain forest is a mixed dipterocarp forest, the dominant forest type of the high rainfall and per humid regions of Southeast and South Asia (Whitmore 1984). The forest type is dominated by a single family of canopy trees (Dipterocarpaceae); trees that have been widely selectively logged for their timber (Appanah and Weinland 1990).

Sampling design and measurements

Fifteen sample sites, at which both overstory vegetation and understory vegetation were sampled, were randomly selected from a stratified pool of closed-canopied mature forest conditions that represented valley ($n = 5$), mid-slope ($n = 5$), and ridge ($n = 5$) topographic positions within undisturbed primary rain forest of the western region of the 20,000 ha Sinharaja World Heritage Site. We demarcated a 20 × 20 m overstory plot (aligned east–west, north–south) at each site within which a 5 × 5 m grid was constructed with string and stakes (Ediriweera et al. 2008). We stem mapped all trees ≥5 dbh cm and measured their canopy projection area taken in N, S, E, and W dimensions using x-y coordinates. Heights to the top of the crown were also taken using a Suunto clinometer and 50 m distance tape. Mean canopy heights decreased from valley sites (25.5 m) to mid-slopes (21.0 m), and to ridges (17.8 m). Species were identified, and stem diameter was measured at diameter breast height (dbh), from which species basal areas were calculated. Basal areas increased on declining down from

ridge sites (18.7 m^2/ha) to mid-slopes (31.6 m^2/ha), and to valley sites (33.4 m^2/ha; see details of methods in Ediriweera et al. 2008; Table 1).

Four circular 1-m^2 seedling plots were placed within each overstory plot of the 15 sites. Regeneration plot centers were randomly selected from the 5 × 5 m intersections of the 20 × 20 m overstory plot. The plots were set up in 1998, and all seedlings identified to species and permanently tagged and then annually re-measured for height growth, leaf number, and survival for ten years running. Every year new recruits were identified, recorded, and tagged. Seedlings that were initially measured in the plots when they were set up were all individuals <1.37 m (dbh). In fact, given the nature of the rain forest understory almost all seedlings that were tagged were <30 cm in height. We first analyzed densities of new recruits and existing seedlings together and separately. However, seedlings that were used in the bulk of our data analysis were defined to only those individuals that germinated and recruited during the monitoring period. The rationale for restricting our

analysis to new recruits was to be able to control for seedling age and size in relation to survival, growth, and mortality.

Data analysis

Seedling density, mortality, and recruitment.—All analyses were performed in R version 3.1 (R Core Team 2014). All seedlings were used for preliminary analyses of seedling density. Subsequently analyses were conducted using data for the 1440 seedlings whose age is known because they germinated between 2000 and 2007. Data from the four plots per site were pooled and treated as subsamples for the purpose of the analysis. We used three-way repeated measures analyses of variance to evaluate the effect of topographic position, species (between-subjects factors), and year (within-subjects factor) on the density, mortality, and recruitment of seedlings using both univariate and multivariate approaches. Results were evaluated based on both methods, and where sphericity assumptions were violated, Huynh–Feldt adjusted *P*-values were used for

Table 1. Results of repeated measures analysis for seedling density, recruitment, and mortality on log transformed data.

Variable	Source	df	SS	F	Pr > F	H–F Adj. Pr > F	Wilks's Lambda
Density†,‡	Topo	2	9	0.167	0.846		0.8463
	spp.	28	2828	3.591	2.70×10^{-8}***		2.70×10^{-7}***
	spp. × topo	56	4073	2.586	2.28×10^{-7}***		2.28×10^{-7}***
	Time	8	15	3.435	0.017*	0.0168*	0.0178*
	Time × topo	16	6	0.673	0.672	0.6728	0.0403*
	Time × spp.	224	139	1.132	0.208	0.2077	0.0216*
	Time × spp. × topo	448	218	0.893	0.934	0.8170	0.9387
Recruitment†,§	Topo	2	9	0.861	0.425		0.4246
	spp.	16	100	1.265	0.226		0.2265
	spp. × topo	32	367	2.310	3.86×10^{-4}***		3.86×10^{-4}***
	Time	7	65	8.841	1.31×10^{-10}***	1.66×10^{-9}***	2.38×10^{-7}***
	Time × topo	14	42	2.858	3.05×10^{-4}***	6.58×10^{-4}***	1.49×10^{-3}***
	Time × spp.	112	190	1.614	1.21×10^{-4}***	3.02×10^{-4}***	1.40×10^{-4}***
	Time × spp. × topo	224	279	1.814	0.047*	5.88×10^{-2}**	0.0988
Mortality†,§	Topo	2	6	0.301	0.740		0.7404
	spp.	16	202	1.195	0.278		0.2780
	spp. × topo	32	890	2.638	4.20×10^{-5}***		4.20×10^{-5}***
	Time	7	13	1.800	0.083	0.0905	0.0600
	Time × topo	14	24	1.638	0.063	0.0701	0.2199
	Time × spp.	112	161	1.358	0.011*	0.0133*	0.0116*
	Time × spp. × topo	224	284	1.199	0.036*	0.0419*	0.0142*

Note: topo, topographic position; spp., species; SS, sums of squares; Pr, probability; H–F, Huynh–Feldt correction.
*P < 0.05, **P < 0.01, ***P < 0.001.
† Log +0.01 transformed data.
‡ Using data for species with nine or more individuals.
§ Using data for species with eight or more individuals.

the within-subjects effects (Algina and Kesselman 1997).

We use measures of seedling density of known age as the number of seedlings per plot. We use mortality density as a measure for analyzing the density of seedlings dying on an annual basis from September to September and recruitment density as a measure of the number of individuals that recruited on an annual basis again from September to September.

Seedling growth.—For growth analyses, we use leaves and heights of seedlings as measures. Mean change in the number of leaves is calculated as:

$$\frac{(\text{num.leaves}) - (\text{num.leaves } T\text{-1})}{T}$$

where, num.leaves = number of leaves for a seedling at time 2; and num.leaves T-1 = number of leaves for a seedling at time 1. T = time between the two, measured in years. Mean change in the number of leaves was calculated for each seedling per plot, and then, the mean change in the number of leaves for all seedlings per plot was evaluated.

We used mean relative height growth (RHT) from September of one year to September of the next year as a measure of performance in height growth.

$$\text{RHT} = \frac{\ln(\text{Ht}) - \ln(\text{Ht-1})}{T}$$

where Ht = height (in cm) time 2; Ht-1 = height in cm time 1; and T = time between the two. RHT was calculated for each seedling, and then, the mean change in height for all seedlings per plot was calculated.

We used two-way repeated measures analyses of variance to evaluate the effect of topographic position (between-subjects factor) and year (within-subjects factor) on the change in number of leaves per plot and RHT of seedlings using both univariate and multivariate approaches. Results were evaluated based on both methods using Huynh–Feldt adjusted *P*-values.

Seedling survival.—Survival analyses were conducted using data for the 1440 seedlings whose age is known because they germinated between 2000 and 2007, because the data are only right censored and therefore suitable for survival analysis. Analysis of survival was performed in R using a Cox proportional hazard model, a regression approach that evaluates time until failure (death; Cox and Oakes 1984) and correctly incorporates right-censored data (seedlings that were still surviving at the end of the experiment for which survival time is unknown). All analyses were conducted using the survival package (Therneau 2014) in R 3.1 (R Core Team 2014). We modeled the dependency of survival time on two predictor variables, topographic position with three levels (ridge, mid-slope, and valley), and species identity as well as the interaction between species and topographic position using the Cox proportional hazards regression for survival data (coxph function in R), which is the most common tool for studying the dependency of survival time on predictor variables (Fox and Weisberg 2011). Likelihood-ratio tests were then used to determine significant differences between species, topographic positions, and their interaction testing the null hypothesis that all of the βs (beta coefficients) are 0. We used the survfit function to estimate the distribution of survival times and the plot function to graph the estimated survival function.

RESULTS

Patterns in seedling density, recruitment, and mortality

Taking all seedlings into the analysis shows average densities in the forest understory to fluctuate between 26 and 31 seedlings/m^2 across the total period of the study. Seedling densities fluctuated across the topography with ridges showing high and low densities of 31 and 15 seedlings/m^2; mid-slopes 46 and 27 seedlings/m^2; and valleys 22 and 31 seedlings/m^2, respectively.

When analyzing only the 1440 seedlings whose age is known because they germinated between 2000 and 2007, a three-way analysis of variance interestingly shows that there was no difference in actual seedling densities across the topography (Table 1). Differences were apparent across time, among species, and in interaction between species and topography.

There were 30 species with sufficient seedling numbers to analyze for differences in density and seven showed differences in relation to topographic position (Table 2). Species more restricted to ridges were *Palaquium thwaitesii, Shorea affinis,* and *Shorea worthingtonii.* One species, *Shorea trapezifolia,* was dominant on mid-slopes, while *Mesua*

Table 2. Simple main effect of topographic position for each species that showed significant difference in seedling densities, recruitment between topographic position.

Species	N	Ridge	Mid-slope	Valley	$F_{2,9}$	Pr > F
Mean number of seedlings per m² (1998–2007)						
Cullenia ceylanica	473	0.041 b	1.798 a,b	1.444 a	7.219	0.0135*
Mesua ferrea	1368	0.312 b	0.257 b	8.930 a	8.744	0.0077**
Palaquium thwaitesii	438	2.653 a	0.388 a,b	0.000 b	4.923	0.0359*
Shorea affinis	623	3.951 a	0.284 b	0.090 b	7.692	0.0113*
Shorea megistophylla	746	0.000 b	0.187 b	4.993 a	8.150	0.0095**
Shorea trapezifolia	2307	0.000 b	15.625 a	0.396 b	4.489	0.0444*
Shorea worthingtonii	502	2.89 a	0.458 b	0.131 b	6.380	0.0188*
Mean recruitment of seedlings per m² per year						
Garcinia hermonii	13	0.062 a	0.023 a,b	0.000 b	3.733	0.066†
Mesua nagassarium	140	0.016 b	1.070 a	0.008 a,b	3.026	0.098†
P. thwaitesii	13	0.093 a	0.008 a,b	0.000 b	4.180	0.052†
S. affinis	59	0.391 a	0.055 a,b	0.016 b	3.420	0.078†
Shorea worthingtonii	49	0.359 a	0.016 b	0.008 b	6.645	0.016†

Notes: N is number of seedlings sampled for each species. Letters that are shared by different topographic positions signify no difference ($P < 0.05$). Letters that are not shared between topographic positions signify significant differences in densities for a given species.
  † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

ferrea and *Shorea megistophylla* showed a greater affinity to valley sites. *Cullenia ceylanica* was present on both valley and mid-slope sites. Seedling densities vary widely with certain species and by topographic positions (Appendix S1). Ridge sites were dominated by *Mesua nagassarium, Palaquium petiolare, P. thwaitesii, S. affinis, Shorea cordifolia*, and *S. worthingtonii*. Mid-slope sites were dominated by *S. trapezifolia* and *M. nagassarium,* while valleys had high numbers of *M. ferrea, Shorea disticha*, and *S. megistophylla*.

Seedling densities per species changed over the ten-year period of the study presumably because of fluctuations in annual seed production (Table 1, Fig. 1A). The high years of 2003 and 2004 were different from the low years of 1999, 2000, and 2007 with the intervening years (01, 02, 05, and 06) showing no difference between high or low years.

A three-way analysis of variance shows that there was no main effects of topographic position or species in seedling recruitment, but there was a difference over time, as to be expected, and also in interactions between species and topographic position, time and topographic position, and time and species (Table 1).

Comparing patterns in total recruitment over the study period, there were differences among species for each topographic position (ridge $F = 1.98$, $P = 0.03^*$; mid-slope $F = 1.97$, $P = 0.03^*$; valley

$F = 1.91$, $P = 0.04$). There were a total of 18 species with a sufficient number of recruits over the ten-year period to conduct an analysis to look for differences in recruitment in relation to topographic position for each species. Five species showed differences in seedling recruitment across the topography (Table 2). Most of these species were ridge specific with only one species recruiting to mid-slopes and no species recruiting preferentially to valley sites over the ten-year period. Total seedling recruitment also changed over time (Fig. 1B). The largest recruitment year was in 2001–2002, and the lowest years were 1999–2000 and 2005–2006.

A three-way analysis of variance shows that there was no difference in seedling mortality in relation to topographic position, species, or time, or in interactions between time and topographic position. But there were differences in interactions between species and time, species and topography, and among all three factors—time, species, and topography (Table 1). We focus on the three-way interaction given it was significant (Table 3). Only one year (1999–2000) showed no significance in mortality for the interaction of species × topography, whereas all other years did show differences. In these years, valleys always differed mostly because of higher rates of mortality from *M. ferrea* and sometimes *S. megistophylla* or *C. ceylanica* as compared to the other species. On occasion, ridges (years 2001–2002; 2004–2005;
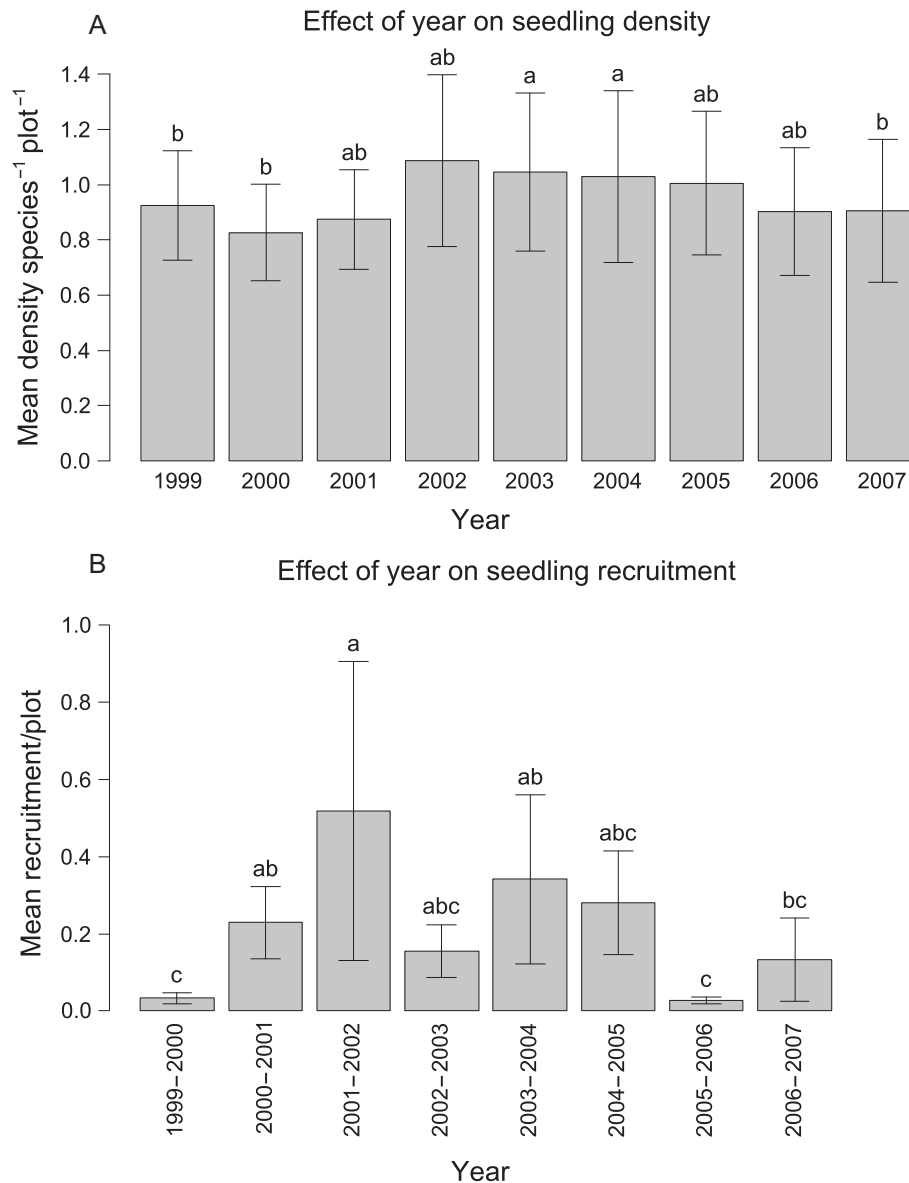
Fig. 1. (A) Mean seedling densities per species per m^2 (plot) pooled for all sites and topographic positions over years 1999–2007. (B) Mean annual seedling recruitment per m^2 (plot) pooled for all sites and topographic positions over years 1999–2007. Letters that are shared by different years signify no differences ($P < 0.06$). Letters that are not shared between years signify significant differences in densities of seedlings.

2006–2007) showed differences among species mostly attributed to the higher seedling mortality of *S. affinis* and *S. worthingtonii*. Mid-slopes showed a difference in only one year (2001–2002).

Seedling growth

Two-way analyses of variance showed that there was both a difference in the number of leaves per seedling at the different topographic positions and that leaf number changes over time (Table 4; Fig. 2A). Changes in leaf number with topography suggest changes in seedling morphology and growth phenology perhaps associated with changes resource availability. Seedlings in valley and mid-slope positions increased in leaf number, while seedlings on ridges decreased, and

Table 3. Main effects statistics showing significance for the interaction of species × topography for each time period.

Year (time)	F value	Pr > F	Position	F value	Pr > F
1999–2000		ns			
2000–2001	1.93	0.004**	Valley	4.31	3.27×10^{-5}**
2001–2002	3.00	3.4×10^{-6}***	Valley	3.22	7.66×10^{-4}***
			Mid-slope	2.11	0.022*
			Ridge	2.46	0.008*
2002–2003	1.72	0.016*	Valley	2.60	0.005**
2003–2004	2.03	0.002**	Valley	2.49	6.97×10^{-3}**
2004–2005	2.27	5.0×10^{-4}***	Valley	2.65	0.004**
			Ridge	2.67	0.004**
2005–2006	1.95	0.004**	Valley	1.96	0.036*
2006–2007	2.56	7.4×10^{-5}***	Valley	1.93	0.038*
			Ridge	3.05	0.001**

Note: When interaction was significant, showing the effect of species for each level of topographic position (if it was significant) on mortality density. ns, not significant.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

both mid-slope and valley were significantly different from ridges. Change in leaf number over time could be attributed to a number of factors such as variations in herbivory, wetness, and/or drought that can all influence patterns in species recruitment and mortality with low years being 2000–2001, 2001–2002, 2004–2005, and 2006–2007. High years were 1999–2000, 2003–2004, and 2005–2006 (Fig. 2B).

Mean RHT per plot differed over time (Fig. 2D) and in interaction between time and topographic position (Table 3). Differences across topography were not significant (Table 4). The interaction between topography and time indicates significant

changes in RHT over time for seedlings located on ridges and mid-slope positions, but not in the valleys (Table 5).

Survival of newly germinated seedlings

Cox proportional hazards regression on seedlings that germinated during the period of the study (1998–2007) revealed that effect of topographic position and species were both significant, but their interaction was not (Table 6).

Effect of topographic position.—To examine the effect of topographic position, we fit a Cox regression model to the data using topographic position as a covariate to estimate hazard of

Table 4. Two-way repeated measures analysis of variance testing topographic position, and time and interactions between time and topographic position, respectively, for two seedling growth measures (number of leaves, relative height growth [RHT]).

Source	df	SS	F	Pr > F	H–F Adj. Pr > F	Wilks's Lambda probability
Number of leaves						
Topo	2	15.19	5.02	0.034*		0.0343
Residuals	9	13.61				
Time	7	18.67	4.65	0.0003***	0.0025	0.1184
Time × topo	14	6.52	0.81	0.6537	0.6090	0.1824
Residuals	63	36.13				
Mean RHT per plot						
Topo	2	0.009	2.18	0.1690		0.1685
Residuals	9	0.018				
Time	7	0.042	4.21	0.0007***	0.0010	0.0867
Time × topo	14	0.039	1.97	0.0347*	0.0366	0.4868
Residuals	63	0.090				

Note: topo, topographic position; SS, sums of squares; Pr, probability; H–F, Huynh–Feldt correction.
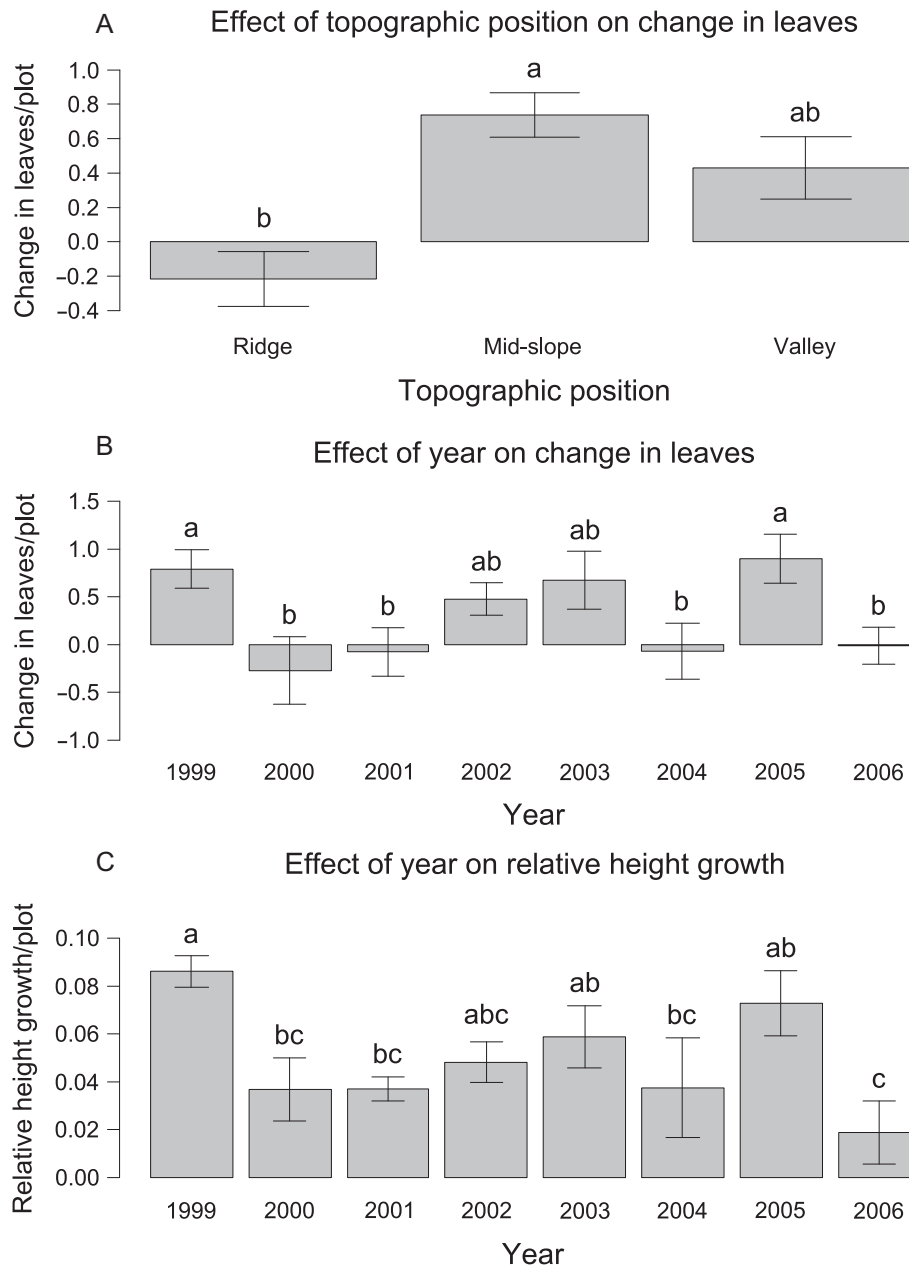*$P < 0.05$; **$P < 0.01$;***$P < 0.001$.

Fig. 2. (A) Change in leaves by topographic position; (B) change in leaves over years; and (C) relative height growth over time (m/yr). Letters that are shared by different topographic positions or years signify no differences ($P < 0.10$). Letters that are not shared between topographic positions or years signify significant differences in densities for a given species.

death, defined as the expected number of events per individual per unit of time. When we used the ridge as a reference (Table 7), we found that valley has a 66% decreased hazard of death compared to ridge and differences were significant, while mid-slope had a decreased hazard of death compared to ridge but differences were not significant. When using mid-slope as a reference, we found that valley has a 66% decreased hazard of death compared to mid-slope. This means that

Table 5. Simple main effects showing the effect of time on relative height growth for each topographic position.

Topo position	Source	df	SS	F	Pr > F
Ridge	Year	7	0.041	3.931	0.005**
	Residuals	24	0.036		
Mid-slope	Year	7	0.026	3.127	0.017*
	Residuals	24	0.029		
Valley	Year	7	0.014	1.101	0.394
	Residuals	24	0.043		

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 6. Dependency of the survival time of seedlings that germinated during the period of the study (1998–2007) on topographic position, species identity, and their interaction modeled using Cox proportional hazards regression, and evaluated using the chi-square statistic of the likelihood-ratio test.

Source	F value	df	P value
Topo	8.668	2	0.01312*
Spp.	140.09	16	2.2×10^{-16}***
Topo × spp.	27.24	22	0.20 ns

Note: The analysis is based on 1403 seedlings from 17 species that comprised at least 10 or more individuals per species.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 7. Dependency of the survival time of seedlings modeled using Cox proportional hazards regression for seedlings that germinated during the period of the study.

Position	Ridge	Mid-slope
Mid-slope	0.968 ns	
Valley	4.85×10^{-6}***	1.78×10^{-7}***

Notes: The analysis models hazard of seedling death and is interpretable as the expected number of events per individual per unit of time (yr). Beta coefficients show how much the percentage hazard of death is changed compared to the baseline; ridge data are used as a reference to compare with mid-slope and valley; and mid-slope as a comparison with valley.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

seedlings germinating and growing on valley sites were 66% less likely to die than those that germinate on ridges or mid-slopes.

Effect of species identity.—Survival functions and paired comparisons of species from seedling data pooled across topography demonstrate strong differences in survival between species (Fig. 3; Appendix S2). Species with low survival over time comprise *Litsea gardneri*, where only 12% of seedlings were expected to survive over an eight-
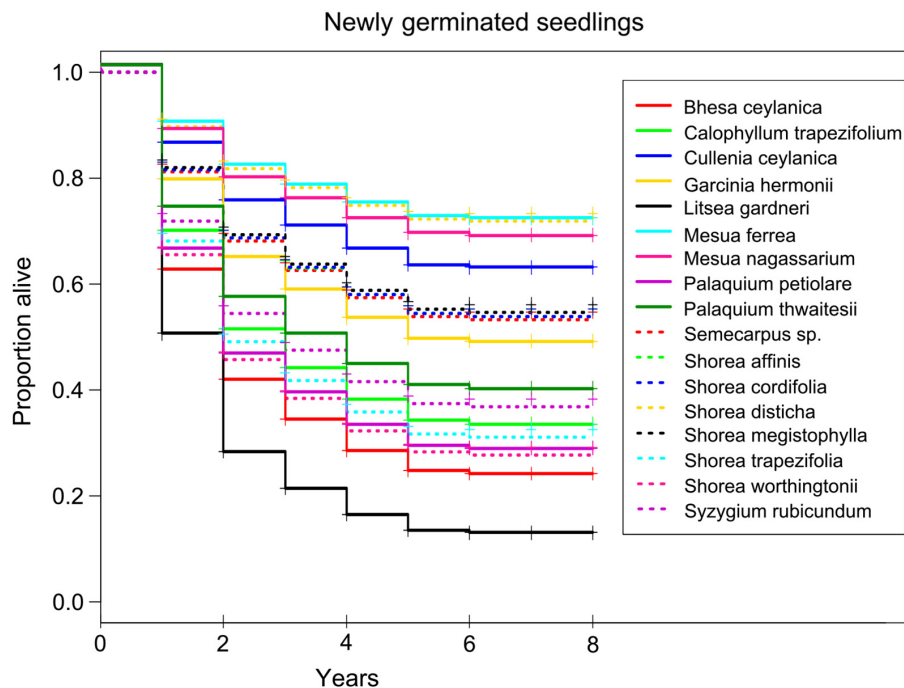

Fig. 3. An estimated survival function for the Cox regression of time to death for seedlings of species across all topographic positions that germinated over the period of the study. Data for each species survival function are based on at least 10 individuals.

year period, as well as *Bhesa ceylanica* (23%), *P. petiolare* (28%), *S. Worthingtonii* (28%), *S. trapezifolia* (31%), and *Calophyllum trapezifolium* (32%; Fig. 3; Appendix S2). Species that exhibited high survival over the eight-year period comprised *C. ceylanica* (62%), *S. disticha* (72%), and *M. ferrea* (71%).

Effect of species identity for each topographic position.—Log-likelihood tests on the effect of species identity for each topographic position (ridge, mid-slope, valley) were all significant (Table 8). Differences in species survival were apparent for each topographic position (Table 9). On ridges, *B. ceylanica* and *L. gardneri* showed low survival, while *Garcinia hermonii*, *S. affinis*, and *S. cordifolia* exhibited high survival. On mid-slopes, similar trends exist with low survival for *B. ceylanica* and higher survival for such species as *S. affinis*, *S. cordifolia*, and *C. ceylanica*. On valley sites, survival is highest for *S. disticha* and *M. ferrea* and lowest for *S. trapezifolia* and *C. ceylanica*.

Discussion

Patterns in seedling density, recruitment, and mortality

In our study, we recorded no pioneers, understory shrubs, or treelets of the 44 species we measured (Gunatilleke and Gunatilleke 1981, 1985, Ashton et al. 1997). The seedlings we measured were all considered species reliant upon advance regeneration of late-successional subcanopy and canopy trees. Such findings are reported for dipterocarp forests elsewhere (Raich and Khoon 1990, Brown and Whitmore 1992, Delissio et al.

Table 8. Dependency of the survival time of seedlings that germinated during the period of the study on species identity modeled separately for each of the three topographic positions using Cox proportional hazards regression, and evaluated using the chi-square statistic of the likelihood-ratio test.

Position	*F* value	df	*P* value
Ridge	16.42	8	0.03666*
Mid-slope	89.17	7	2.22×10^{-16}***
Valley	17.31	5	0.003994**

Notes: The analysis is based on seedlings from species that comprised at least five or more individuals per species: ridge (224 individuals from nine species); mid-slope (965 individuals from eight species); valley (175 individuals from six species).
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 9. Proportion of seedlings that survived by species for each topographic position for newly germinated seedlings.

Species	Ridge survival	Mid-slope survival	Valley survival
Bhesa ceylanica	0.14 b,c	0.22 d	–
Cullenia ceylanica	–	0.80 a,b	0.37 b
Garcinia hermonii	0.41 a,b,c	–	–
Litsea gardneri	0.08 d	–	–
Mesua ferrea	–	–	0.80 a
Mesua nagassarium	–	0.69 a,b	–
Palaquium petiolare	0.21 b,c	–	–
Palaquium trapezifolium	0.31 a,b,c	–	–
Semecarpus walkeri	–	0.79 a,b,c,d	0.45 a,b
Shorea affinis	0.46 a	0.85 a,b,c	–
Shorea cordifolia	0.41 a,b	0.88 a	–
Shorea disticha	–	–	0.74 a
Shorea megistophylla	–	–	0.56 a,b
Shorea trapezifolia	–	0.32 c,d	0.34 b
Shorea worthingtonii	0.18 c,d	–	–
Syzygium rubicundum	–	0.43 a,b	–

Notes: Letters denote statistical comparisons among species for each topographic position. Letters that are shared by different species signify no differences ($P < 0.05$). Letters that are not shared between species signify significant differences in survival. "–" signifies not present.

2002) and for other tropical forest types in Latin America (Comita et al. 2007) and Central Africa (Hall et al. 2003).

Our study did demonstrate the differences in species seedling distribution across the topographic positions. Species more restricted to ridges were *Palaquium thwaitesii*, *Shorea affinis*, and *Shorea worthingtonii*. Species that were strongly associated with mid-slopes was *Shorea trapezifolia*, while *Mesua ferrea* and *Shorea megistophylla* had a strong affinity to valley sites. *Cullenia ceylanica* was present on both valley and mid-slope sites.

Seedling densities also vary widely driven by certain species and topographic positions (Appendix S1). Ridge sites were dominated by *Mesua nagassarium*, *Palaquium petiolare*, *P. thwaitesii*, *S. affinis*, *Shorea cordifolia*, and *S. worthingtonii*. Mid-slope sites were dominated by *S. trapezifolia* and *M. nagassarium*, while valleys have high numbers of *M. ferrea*, *Shorea disticha*, and *S. megistophylla*. Interestingly, many of those species that exhibit affinity to particular topographic sites were also those species that dominate seedling densities for their respective site. These findings conform to results from experimental studies on seedling transplants of some of these tree species (*Shorea*

spp., *Mesua* spp.) that monitored survival across the same topographic gradient (Ashton et al. 1995) and to studies that characterized the demographic patterns of adult trees across the topography (Gunatilleke et al. 2004, 2006).

Seedling densities per species changed over the ten-year period of the study, but these changes were not very dramatic. In this forest type, we should expect to see marked changes because of fluctuations in annual seed production. This is because many of the trees are known masting species (e.g., Dipterocarpaceae; Curran and Webb 2000, Table 1, Fig. 1). The high years in species seedling densities of 2003 and 2004 (moderate El Niño years; https://www.esrl.noaa.gov/psd/enso/data.html) were different from the low years of 1999, 2000, and 2007 (moderate to strong La Niña years; https://www.esrl.noaa.gov/psd/enso/past_events.html) with the intervening years (01, 02, 05, and 06) showing no difference between high or low years. Flowering and fruiting of dipterocarps has been linked to El Niño years (Ashton et al. 1988) and is therefore a logical reason for these trends. Though there was no strong El Niño year during our study, there was a masting event recorded for the dipterocarps for 2004. This mast year did not result in a dramatic increase in recruitment. This suggests that even longer term studies are necessary to monitor recruitment patterns. Other studies on tropical wet evergreen forest show similar synchronous seedling recruitment periodicity, but they demonstrate more dramatic difference across years (e.g., Panama, De Steven 1994, Australia, Connell and Green 2000).

In regard to seedling mortality, all years except one (1999–2000) differed in the interaction of species with topography. In these years, valleys always differed mostly because of higher rates of mortality from *M. ferrea* and sometimes *S. megistophylla* or *C. ceylanica*, as compared to the other species. On occasion, ridges (years 2001–2002; 2004–2005; 2006–2007) showed differences among species mostly attributed to the higher proportional seedling mortality of *S. affinis* and *S. worthingtonii*. Mid-slopes showed a difference in only one year (2001–2002).

These findings, when taken together, suggest a core group of canopy trees belonging to species rich genera (e.g., *Shorea* spp., *Mesua* spp., *Palaquium* spp.) having a regeneration capacity that dominates the forest understory and that are weakly cohort driven. Seedlings of this core group also show strong species affinities to topographic position. There can be multiple reasons for this; but one that needs exploring is their adaptation through exposure to soil formation processes (e.g., topographic position) and to cyclical changes in climate (El Nino-La Nina) processes (Ediriweera et al. 2008) that have been ongoing for thousands, if not millions, of years (Ashton and Gunatilleke 1987). This biogeography, together with the structural and compositional domination of one tree family (Dipterocarpaceae), makes this forest type different from other wet evergreen tropical forests (e.g., Neotropics; Harms et al. 2000, Comita and Hubbell 2009, Comita et al. 2010). This supposition is supported by other demographic studies for these same tree species within the Sinharaja forest region (Gunatilleke et al. 2006, Wiegand et al. 2007); and for mixed dipterocarp forest elsewhere in Southeast Asia (Webb and Peart 2000, Russo et al. 2005, Paoli et al. 2006).

Seedling growth

Plots in valley and mid-slope positions increased in leaf number, while plots on ridges decreased, and both mid-slope and valley were significantly different from ridges. Change in leaf number over time could be attributed to a number of factors such as variations in herbivory (Fine et al. 2004), wetness and/or drought (Engelbrecht et al. 2007), and canopy disturbance and increased irradiance (Ashton 1995, Ashton et al. 1995, 2005, Singhakumara et al. 2003). All can influence patterns in species recruitment and mortality with low years in growth and leaf production being 2000–2001, 2001–2002, 2004–2005, and 2006–2007 (all weakly correlated to El Niño). High years are 1999–2000, 2003–2004, and 2005–2006 (weakly related to La Niña; https://www.esrl.noaa.gov/psd/enso/past_events.html). Further studies clearly need to be conducted to identify what factors are influencing seedling growth and leaf production in the forest understory.

The significant main effect of topographic position suggests that RHT mirrors the same trends in years and topography for change in leaf number of species (Fig. 2). The interaction between topography and time indicates significant changes in RHT over time for seedlings located on ridges and mid-slope positions, but not in the

valley. Findings are supported by both transplant studies across the same environmental gradient in the forest (Ashton et al. 1995) and in controlled shelters (Ashton 1995, Ashton et al. 2005). These results show seedling growth to be prone to soil drying and interannual droughts on ridges where soils are shallow and skeletal as compared to lower elevations where soils are deeper and with greater water storage (Ashton 1992, Ediriweera et al. 2008) or to differences in soil fertility where valley soils had lower calcium, potassium and pH, as compared to the more nutrient rich ridges (Gunatilleke et al. 1997, Ediriweera et al. 2008).

Overall trends of relative growth rates of seedlings in our study are much lower than comparative studies in other forest types. Relative growth rates of seedlings in our study varied on average between 2 and 8 cm/yr. This is corroborated by prior studies of dipterocarp seedlings grown in shelters simulating forest understory environments. In these environments, seedlings grew on average between 2 and 5 cm/yr depending upon species (Ashton 1995). Similar findings are reported for other mixed dipterocarp forests in Asia (Swaine 1996, Blundell and Peart 2001). In contrast, studies from other forests, in the Neotropics in particular, show height growth rates that are almost double to triple these numbers (Comita et al. 2007, 2010).

Survival of newly germinated seedlings

Seedlings growing on the valley sites had a 66% decreased likelihood of dying compared to ridges and mid-slopes. Mid-slopes also had a decreased likelihood of dying compared to ridges, but the differences were not significant. Tree species that show low survival over time (between 10% and 30% survival after 8 yr) comprise *Litsea gardneri*, *Bhesa ceylanica*, *P. petiolare*, *S. Worthingtonii,* and *S. trapezifolia*. Except for *S. worthingtonii*, all other species that exhibit high mortality have autecologies that make them shade-intermediate or shade-intolerant (Ashton and Berlyn 1992; K. Panditharathna, M. S. Ashton, and B. M. P. Singhakumara, *unpublished data*). Species that have high survival (between 60% and 70% survival after 8 yr) comprise *C. ceylanica*, *S. disticha*, and *M. ferrea*; all known to be shade-tolerant (Ashton and Berlyn 1992; Panditharathna et al., *unpublished data*).

Management application

We believe our study is one of the first longer term studies on the demographics and cohort dynamics of seedlings for mixed dipterocarp forest. Findings demonstrate that a very significant proportion of the seedlings are canopy trees that have strong topographic site affinity and have recruitment patterns that appear not to be strongly pulsed even though the forest is dominated by masting tree species in the forest canopy. Survival and growth appear both correlated to the periodicity of climate (but this needs further longer term monitoring and analysis); and to differences in topography; with species and floristic associations associated with topography having very different levels of persistence.

Our results suggest that current management of forests through selective timber harvesting that are defined by fixed cutting cycles of 30–40 yr and single minimum diameter limits set irrespective of commercial timber species (usually between 50 and 60 cm dbh) ignores the regeneration recruitment periodicity, differential persistence of advance regeneration, and differences in species composition across the topography. Yet this regeneration is the basis for the development of canopy forest regrowth and recovery post-logging. We suggest that if these forests are to be selectively logged guidelines should be adopted that regulates the harvesting of the canopy trees so as to more opportunistically take advantage of the periodicity of the establishment of regeneration. Cutting also needs to cater to the differences in seedling species composition and persistence across the topography by routinely conducting pre-harvest surveys of the amount and condition of advance regeneration by topographic position and species composition. This is particularly the case for the canopy tree species that have relatively more shade-intolerant seedlings with lower abilities to persist in shade. Such species need release from competition through cleanings and overhead shade of the original canopy through liberation (Smith et al. 1997). In circumstances where regeneration is inadequate for future stocking, cutting of the parent trees should be delayed until the understory is replenished by new recruits.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2098/full