

Differences in Survival and Growth Among Tropical Rain Forest Pioneer Tree Seedlings in Relation to Canopy Openness and Herbivory

Uromi M. Goodale^{1,4}, Graeme P. Berlyn², Timothy G. Gregoire², Kushan U. Tennakoon³, and Mark S. Ashton²

¹ Key Laboratory of Tropical Forest Ecology, Chinese Academy of Sciences, Xishuangbanna Tropical Botanical Garden, Menglun, Mengla, Yunnan, 666303 China

² School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, U.S.A.

³ Institute for Biodiversity and Environmental Research (IBER) and Faculty of Science, Faculty of Science, Universiti of Brunei Darussalam, Jalan Tungku Link, Gadong BE 1410, Brunei, Darussalam

ABSTRACT

Although differences in canopy openness, herbivory and their interaction may promote species coexistence, how these factors affect pioneer tree species and potentially limit growth, and survival has been poorly studied, particularly in tropical South Asia. We monitored the effect of canopy openness and herbivore damage on seedling survival and growth of 960 individuals of six pioneer tree species: *Dillenia triquetra*, *Macaranga indica*, *Macaranga peltata*, *Schumacheria castaneifolia*, *Trema orientalis*, and *Wendlandia bicuspidata*. Seedlings were placed in four gap-understory positions—center, outer gap edge, inner forest edge, and understory—in four large, natural gaps within the Sinharaja World Heritage Reserve, Sri Lanka. Canopy openness positively affected survival probability beyond the 550-d experiment, while herbivory decreased survival and was highest in understory conditions. The relative order of species survival stayed fairly consistent between gap-understory positions and followed their known shade tolerance rankings. When averaged across all experimental conditions, *T. orientalis* had the lowest survival probability estimate beyond the 550-d experiment (0.05), but the greatest capacity for growth where it successfully established, while the species with highest averaged survival probability (0.79), *D. triquetra*, showed the lowest growth. One species, *W. bicuspidata*, responded positively to herbivory by re-sprouting. Coexistence of *D. triquetra*, *T. orientalis*, and *W. bicuspidata* can be explained by a trade-off among species in survival, growth, and response to herbivory. In addition to variation in canopy light environment, herbivory may be important in determining pioneer species distribution through fine-scale niche partitioning and should be carefully considered in reforestation efforts.

Abstract in Sinhala is available in the online version of this article.

Key words: Canopy gaps; *Dillenia* spp; growth-survival trade-off; *Macaranga* spp; regeneration niche; restoration; Sri Lanka; *Trema* spp.

THE ECOLOGICAL IMPORTANCE OF CANOPY OPENINGS created by fallen trees was described by the Finnish botanist, Pehr Kalm, in his journal entry on December 1748 in which he wrote, 'In this manner, the old trees die away continually and are succeeded by a young generation' (Kalm 1773, pp 324–327). Since then many studies have widely investigated the importance of canopy openings in tropical and temperate ecosystems resulting in a broader and deeper understanding of disturbance processes, and their effects on population and community processes (Frellich 2002, Johnson & Miyanishi 2007). Canopy gaps are complex and dynamic systems where environmental heterogeneity exists, within and between openings, and across spatial and temporal scales (Brokaw 1982, Putz 1983, Marthews *et al.* 2008).

Pioneers have traditionally been defined as being restricted to gaps, requiring high irradiance for establishment and growth (Swaine & Whitmore 1988). Pioneer species also show differences in distri-

bution in relation to canopy openness, with some species being more restricted to larger gaps and others being found more commonly in smaller tree fall gaps (*e.g.*, Pearson *et al.* 2002, Daws *et al.* 2008, Goodale *et al.* 2012). Canopy openings increase light, temperature fluctuation, and soil resources (nutrients, water) that change from gap center to understory (*e.g.*, Nicotra *et al.* 1999, Beckage & Clark 2003, Marthews *et al.* 2008). In the Neotropics, pioneer seed size variation correlate with differences in germination and seedling emergence and may explain the distribution of pioneer species in different gap sizes; smaller seeded pioneers can be stimulated to germinate with increased light, while larger seeded species will germinate with increased diurnal temperature variation (Dalling *et al.* 1998). Seedlings of tropical pioneer tree species have also been shown to differ in physiological, morphological, and biochemical adaptation to particular edge-gap positions within a canopy opening (*e.g.*, Pearson *et al.* 2002, Lambers & Poorter 2004, Daws *et al.* 2008).

Life-history trade-offs between high seedling survival and rapid growth are well recognized (Wright 2002, Leigh *et al.* 2004), and pioneers generally couple low survival with rapid growth (*e.g.*, Condit *et al.* 1996, Wright *et al.* 2003). This dichotomous charac-

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⁴Corresponding author; e-mail: ugoodale@xtbg.org.cn; uromi.goodale@gmail.com

terization is too simplistic; however, tropical tree species respond in different ways across resource gradients of irradiance and soil (Poorter *et al.* 2005), and across and within life-history stages (Kitajima 2002, Myers & Kitajima 2007). Others may show similarity in relative survival to growth trade-offs across regeneration classes (Wright *et al.* 2003, Gilbert *et al.* 2006).

The trade-off between survival and growth is inherently connected to species susceptibility to herbivory (Stowe *et al.* 2000). There is evidence that gap partitioning may result from a trade-off between seedling growth rate and the ability to resist herbivores and pathogens (*e.g.*, Coley 1983, Blundell & Peart 2001, Beckage & Clark 2005). Palatability tests have confirmed that shade leaves of understory environments are more prone to herbivory compared with sun leaves from the forest canopy (Lowman 1993, Coley & Barone 1996, Salgado-Luarte & Gianoli 2012). However, some studies have shown light conditions to have no overall effect on rates of herbivore damage suggesting that herbivory is a species-specific process coevolved between specific herbivores and their hosts (Eichhorn *et al.* 2007). Therefore, by implication, herbivory may not influence species distribution within gaps (Pearson *et al.* 2003).

Investigation of growth, survival and defence trade-offs together has not been previously conducted for co-occurring species in the pioneer guild. Using six pioneer species distributed along the shade tolerance spectrum from small tree fall gaps to large openings (Goodale *et al.* 2011), we investigated the influence of gap microenvironment position and herbivory, and the interaction between these factors, on seedling growth and survival for 550 d. The seedlings were transplanted and grown within different canopy gap positions. We tested the hypotheses that in these pioneer species: (1) seedling growth will be highest in the gap center, where light is less limiting compared with gap edge, forest edge or understory positions; (2) herbivore damage will be higher under shade compared with more open conditions; and (3) some species will outperform others in specific microenvironmental gap positions, as measured by seedling survival and growth, suggesting niche partitioning.

METHODS

SITE DESCRIPTION AND STUDY SPECIES.—This study was conducted in southwest Sri Lanka in the Sinharaja World Heritage Forest Reserve (6°21'–25' N and 80°21'–34' E) in an area selectively logged between 1973 and 1981 (IUCN 1993). Sinharaja is an aseasonal, mixed-dipterocarp forest with a *Shorea-Mesua* forest type (Gunatilleke *et al.* 2004). A perhumid climate with a mean annual precipitation of 3900 mm and day and night temperature variations of 25–32 °C and 18–23 °C, respectively (Ashton 1992) prevails on a landscape of parallel ridges and valleys lying along an east–west axis ranging between 300 m and 1170 m. The soils are ultisols with suborders *udults* and *humults* (USDA 1975) derived from gneiss and schist rock (Cooray 1988).

Six pioneer tree species that represent diverse life histories were used in this study: *Dillenia triquetra* (Rottb.) Gilg, *Macaranga indica* Wight, *Macaranga peltata* (Roxb.) Muell, *Schumacheria castaneifolia* Vahl, *Trema orientalis* (L.) Blume, and *Wendlandia bicuspidata* Wight and Arn (Table 1). Although *W. bicuspidata* is a tree, it resprouts after cutting the main stem resulting in a shrub-like appearance. None of the study species have compound leaves or defence structures (*e.g.*, spines, trichomes). All are common and sympatric at the landscape-level and have been shown to differentiate in distribution in relation to type and degree of disturbance (Singhakumara *et al.* 2000, Goodale *et al.* 2012).

EXPERIMENTAL DESIGN.—In May 2004, four canopy gaps resulting from convectional windstorms and monsoonal winds during May 2003 to May 2004 were selected from valley sites with elevations ranging between 489 and 522 m asl. In each location (LOC), four gap understory positions (GAP; Fig. 1; Brokaw 1982, Marthews *et al.* 2008) were identified along the north–south direction: gap center (GC), inside edge of the gap (GE), outside or forest edge of the gap (FE), and understory beneath closed forest canopy (FU; Table 2; Fig. 1). The innermost point reached by foliage from canopy trees that are more than 10 m in height was defined as GE. The first point, from the direction of the gap into the

TABLE 1. *Life-history characteristics of focal species.*

Species and family name	Proportion of visual sky in the 180° angle view above seedlings ^a	Comparative shade tolerance ranking	Seed size (mm)	Seed size (g)	Mature tree height (m) ^b	Dispersal agent ^c
<i>Trema orientalis</i> (L.) Blume., Ulmaceae	0.54 ± 0.17	4	3 × 2.5	0.29	11	Birds
<i>Macaranga peltata</i> (Roxb.) Muell, Euphorbiaceae	0.34 ± 0.19	3	5 × 4	3.25	11	Birds
<i>Macaranga indica</i> Wight, Euphorbiaceae	0.17 ± 0.07	2	4 × 3.7	0.93	16	Birds
<i>Dillenia triquetra</i> (Rottb.) Gilg, Dilleniaceae	0.17 ± 0.05	2	5 × 4	2.56	12	Ants, Birds
<i>Wendlandia bicuspidata</i> Wight & Arn, Rubiaceae	0.16 ± 0.06	2	0.4 × 0.05	<0.0001	13	Wind
<i>Schumacheria castaneifolia</i> Vahl, Dilleniaceae	0.11 ± 0.07	1	3.5 × 4	0.84	8	Ants

^aThe proportion visual sky in the 180° angle view above seedlings reported here is from seedlings naturally growing in and around the Sinharaja Forest Reserve and is from data published in Goodale *et al.* 2012.

^bData obtained from Goodale *et al.* 2011.

^cData from observations by E. Goodale and U. M. Goodale.

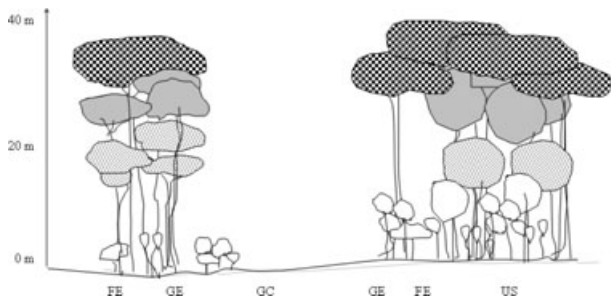


FIGURE 1. Crown map of valley gap site showing vertical profile running south north (left-right) indicating the center of the gap (GC), the inside edge of the gap (GE), outside or forest edge of the gap (FE), and the understory beneath the closed forest canopy (FU).

forest understory, at which a radius of 5 m contains trees taller than 10 m, was defined as FE.

The forest floor of each position was cleared, weeded, and demarcated into a 3.5 m × 5 m plots. Seedlings were germinated in 6 cm deep 30 × 46 cm trays beneath partial shade (50% shade cloth) at the Sinharaja nursery using seeds collected from January to July 2004. Trays were then taken to the gap sites, and seedlings were transplanted into 40 cm deep 24 cm diameter black polythene bags containing a mixture of forest valley topsoil from a single location and river sand (to improve drainage) in a 1:1 ratio (approx. 5.5 l [4.5 kg]; see protocol in Gunatilleke *et al.* 1996). Seedlings were maintained for two weeks under partial shade and moist soil conditions before being placed into a random predesigned location within a gap position.

In August 2004, seedlings were screened to exclude those with herbivore damage, and 960 healthy seedlings were randomly assigned places in 16 gap-understory plot positions. In each position, 10 seedlings each from the six species were placed using predetermined random assignments in a 6 row × 10 column rectangular arrangement with 30 cm distance between seedlings. Before placement, each seedling's number of leaves that were not cotyledons (NL), height to the tip of the apical shoot (H), and average of four crown radius measurements (ACR) was recorded using a digital caliper (Model 500-196-20, Mitutoyo America Corporation, IL, U.S.A.).

The seedling crown light environment of each gap-understory position was assessed at the beginning of the experiment using hemispherical photographs taken over the center and four corners of each plot using a Nikon 180° fisheye lens and a Nikon 990 camera (Nikon, Melville, NY, U.S.A.) mounted on a self-level with a compass at 1.0 m aboveground. We followed recommended protocol (Delta-T 1999) and obtained photographs at dawn and dusk or during times of evenly overcast sky. Images were analyzed using Hemiview v. 2.1 (Delta-T Devices Ltd. Cambridge, U.K.; Delta-T 1999). Crown light environment was quantified (Table 2) as the proportion of visual sky in the 180° angle view (VS) and 90° angle view (VS_{90°) with values ranging from 1 (open sky) to 0 (complete obstruction). Gap area was assessed considering any interconnected gaps as belonging to one gap site (Table 2; Brokaw 1982, Marthews *et al.* 2008).

In 2003, five seedlings, each of the six species, were grown in Sinharaja research center shade houses to assess the relationship between the percentage of leaves with herbivore damage and the percentage of photosynthetic tissue removed by herbivory in the same plant. Seedlings were grown under four shade conditions each replicated by four shade houses representing canopy openness conditions from forest understory to center of a large gap, in both total and quality of light (Table S1; Goodale 2009). After 22 mo, all leaves of each individual plant were marked as herbivore damaged or not, and photographed with a metric scale, and the removed photosynthetic area in each plant was calculated as a percentage using the digital images in Image J, 1.37v (NIH, Washington, DC). Percentage of leaves with herbivore damage for all pooled species and light conditions correlated well with percentage photosynthetic tissue that was removed from each seedling ($R^2 = 0.78$; Fig. S1 and Table S2).

Plants were re-measured in September and October 2004 and thereafter at two monthly intervals until December 2005. Based on above preliminary investigations, we used the percentage of leaves showing herbivore damage as a reliable index of the level of herbivore damage experienced by the species studied here. Therefore, our re-census measurements included the number of leaves showing herbivore damage during the census interval and a dead or alive score for each seedling. We tracked the number of leaves showing herbivore damage by marking all leaves, at each census, at the base of the petiole, from 1 to n

TABLE 2. Characteristics of the four gap-understory continuum positions – gap center (GC), gap edge (GE), forest edge (FE), and forest understory (FU) of the four locations.

Location	Gap area (m ²)	Proportion visual sky in the 90° angle view above each plot in canopy-understory positions				Proportion visual sky in the 180° angle view above each plot in canopy-understory positions				Cumulative value of the percentage leaves with herbivore damage			
		GC	GE	FE	FU	GC	GE	FE	FU	GC	GE	FE	FU
1	1534	0.62	0.35	0.17	0.06	0.44	0.25	0.22	0.11	12.3	14.8	41.9	36.8
2	1760	0.28	0.18	0.12	0.03	0.21	0.25	0.14	0.03	8.5	7.1	41.9	40.5
3	1245	0.48	0.33	0.16	0.04	0.41	0.33	0.22	0.07	8.4	15.8	40.1	23.2
4	890	0.41	0.23	0.14	0.05	0.38	0.28	0.17	0.10	31.3	44.0	42.5	34.0
Average	1375.25	0.45	0.27	0.15	0.04	0.36	0.28	0.19	0.08	15.1	20.4	41.6	33.6

(1 = the first leaf and n = total number of leaves produced during the experimental period). At the end of the experiment, we divided the number of herbivore-damaged leaves by the total leaves produced and multiplied the resulting value by 100 to obtain the cumulative percentage of herbivore damaged leaves for each seedling (LHD_{seedling}).

The average of LHD_{seedling} pooled for each gap position was calculated to represent the level of herbivore damage that plants experienced during the experimental period in each gap-understory position (LHD_{position}). Similarly, the average of LHD_{seedling} for each species pooled for all locations and gap positions was used to calculate the level of herbivore damage experienced by each species (LHD_{species}).

The experiment was concluded in 2007 after the rainy season by confirming dead or alive status of each plant.

DATA ANALYSIS.—Crown light environment (VS_{90°) and the level of herbivore damage (LHD_{position}) were compared in the four gap-understory positions using a one-way ANOVA, and the relationship between these factors was assessed using correlation analysis.

For the analysis of seedling survival and growth of experimentally planted seedlings, we used ‘survival analysis’ statistics employing both parametric methods that can assess the influence of explanatory variables and nonparametric methods that do not require distributional assumptions (see further details in Appendix S1).

Parametric analysis fitted the accelerated time models in the form:

$$Y = f(\text{seedling lifetime}) = \beta X + \sigma \varepsilon$$

where β is the vector of unknown regression parameters (includes the intercept term), X is the matrix covariates or independent variables, σ is a scale parameter, and ε is a vector of errors or deviations of Y from its expected value as given by βX .

Influence of eight predictor variables on the acceleration of time until death was assessed using SAS 9.1.3 - PROC LIFEREG procedure (SAS Institute Inc 2004). LOC, GAP, SPP, and their interaction terms were used as categorical predictors, while LHD_{seedling} , initial H, ACD, NL were added as continuous covariates. Plant position within each plot was considered as a random effect. From different classes of distributions, the Weibull probability density distribution with a natural log link was selected as the best fit for the random error distribution. Parameter selection for the fitted model was based on Akaike’s Information Criterion (AIC; Littell *et al.* 2006), and parameter estimates were presented in relation to the lowest level defined for a given explanatory variable.

For nonparametric analysis, we used the Kaplan–Meier estimator for the survival function $S(t)$, which is the probability of an individual seedling surviving at least until time t (*i.e.* $Pr [T > t]$ Where T is age at death and t is time since experiment began; Harrell 2001). We estimated $S(t)$ using SAS 9.1.3 - PROC LIFETEST procedure (SAS Institute Inc 2004), as:

$$S(t) = \prod_{i:t_i \leq t} (1 - d_i/n_i)$$

where i indexes the time interval, d_i is the number of deaths that occur in the interval t_i , and n_i is the number of seedlings that are alive at the end of the census interval t_i . Π is the product operator across all cases less than or equal to t .

The change in cumulative survival probability with time for populations of interest is presented using cumulative survival distribution function curves. Survival between strata and populations of interest (*e.g.*, plants in different gap positions) was compared using the log-rank test of equality (a lower value for the log-rank test indicates a higher ranking) over different levels of a given explanatory variable (Harrell 2001). VS , VS_{90° , LHD_{position} , LHD_{seedling} , and initial H, ACR, and NL were evaluated for their strength of association as covariates for comparing survival among seedlings. Using an automated forward stepwise selection procedure, variables that had a probability less than 0.0001 under the null hypothesis of ‘no effect’ were selected as having meaningful associations that can affect the outcome of the survival probability in the stratified populations.

The relative height growth rate (RHGR) of a seedling was calculated as:

$$RHGR = \log(H_k/H_0)/t$$

where H_k denotes the height of the seedling in the final, December 2005 census and H_0 denotes the initial height of the seedling in July 2004, and t is the elapsed time (d). Relative crown radius growth rate (RCGR) was similarly calculated as:

$$RCGR = \log(ACR_k/ACR_0)/t$$

where ACR_k is the final average crown radius, and ACR_0 , the initial measure. A general linear mixed model (SAS 9.1.3 - PROC MIXED procedure; SAS Institute Inc 2004) appropriate for unbalanced data (due to differential mortality among locations and gap positions) was fitted to RHGR and RCGR using the same variables and covariates in the survival analysis as fixed effects and plant position as a random effect. Within the context of the fitted model, single degree of freedom contrasts were calculated with the Tukey’s adjustment (Tukey 1953) to compare between levels of a categorical explanatory variable.

RESULTS

PIONEER SEEDLING SURVIVAL AND GROWTH RELATIVE TO GAP POSITION.—Canopy light environment was significantly different between gap positions (VS : $F_{3,12} = 16.83$, $P < 0.0001$; VS_{90° : $F_{3,12} = 17.90$, $P < 0.0001$). On average, measures of canopy openness assessed directly above the plot (in the 90° angle view) were 10 times greater in the gap center compared with the understory (Table 2). There were no significant correlations between gap size and canopy openness, both in the 90° and in the 180° angle views of canopy openness in each of the gap understory

positions ($R^2 \leq 0.29$). We found the highest seedling survival probability at the gap edge (0.42) followed by gap center (0.38) and forest edge (0.36). Pioneer survival was lowest in the understory (0.26; Fig. 2). Surprisingly, the relative height growth of pioneer seedlings was highest in the gap edge and not in the gap center ($P > 0.0001$; Fig. S2).

RELATIONSHIP OF HERBIVORY AND CANOPY OPENNESS.—Herbivore damage was also different among gap-understory positions ($F_{3,12} = 5.35$, $P < 0.0143$) with edge and understory positions showing on average a twofold increase compared with the plants that were grown in the center of the gap (Table 2). Herbivore damage at a given gap-understory position (LHD_{position}) was negatively correlated with canopy openness (VS_{90° ; Fig. 3).

EFFECT OF GAP POSITION AND HERBIVORY ON SEEDLING LIFETIME AND SURVIVAL.—Seedling survival probability beyond the 550-d experiment differed among species (Fig. S3) and between understory-gap positions (Fig. 2), but species rankings changed little among different understory-gap positions (Fig. 4). *Dillenia triquetra* had the highest survival probability beyond the 550-d experiment (0.79), followed by *S. castaneifolia*, *W. bicuspidata*, *M. indica*, *M. peltata*, and *T. orientalis* (see Fig. S3; 0.62, 0.40, 0.14, 0.07, and 0.05 respectively). *Dillenia triquetra* on average lived 410 d longer than *T. orientalis*. In the gap edge, forest edge and understory, seedling survival was lowest for *T. orientalis*, whereas in the gap center, the lowest surviving species was *M. peltata* (Fig. 4).

When all eight explanatory variables and their interaction terms were evaluated using parametric models, four factors had the largest effect on seedling lifetime: species (SPP), gap-under-

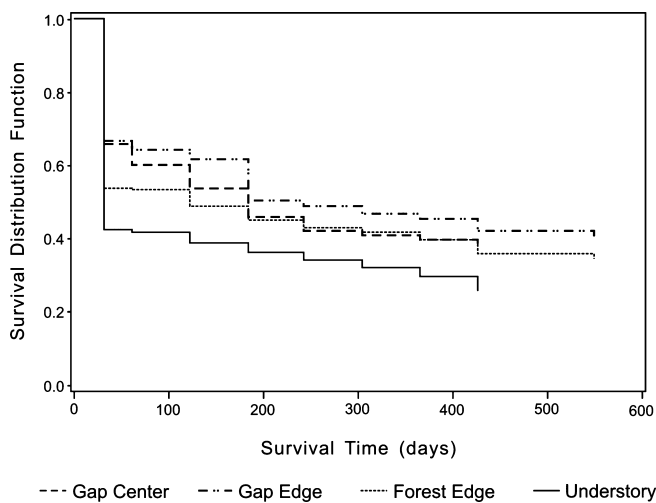


FIGURE 2. Seedling survival probability in the four gap-understory positions: gap center (GC), gap edge (GE), forest edge (FE), and forest understory (FU). Data pooled for all six species. The survival distribution function was calculated using the nonparametric Kaplan–Meier estimate. Note that the graph lines end when the survival probability does not change for a future census event.

story position (GAP), leaf herbivore damage at the seedling level (LHD_{seedling}) and interaction of $SPP \times LHD_{\text{seedling}}$ (Table 3; $P < 0.0001$ for these four variables). Model terms that had P values > 0.0001 and low χ^2 did not show significant differences between all levels of each variable. For example, although $P = 0.0003$ for location, the low χ^2 (18.6) was an indication that the parameter estimates of seedling lifetime were similar for some locations ($P > 0.0919$ for multiple comparisons between locations). Similarly, although the beginning height and number of leaves had a significant effect ($P = 0.0007$ and $P = 0.0056$ respectively), on seedling lifetime, the comparatively small χ^2 values (< 11.5) obtained for the assessment of height, average crown radius and leaf number indicated that plant size at the beginning of the experiment did not have a large effect on seedling lifetime. Therefore, consistent with the hypothesis being explored, the following full model was selected based on AIC as the best and most parsimonious model to further analyze the parameter effects on seedling lifetime:

$$\text{Log (seedling lifetime)} = \beta_0 + \beta_1 \text{SPP} + \beta_2 \text{GAP} + \beta_3 \text{SPP} \\ \times \text{LHD}_{\text{seedlings}} + \beta_4 \text{LHD}_{\text{seedlings}} + \sigma \varepsilon$$

Herbivory was the most influential factor determining seedling survival (Table 3). *Trema orientalis* was most negatively affected by herbivore damage, with three other species being less affected than *T. orientalis*. *W. bicuspidata*, had on average 1.45 times the seedling lifetime of *T. orientalis* with a unit increase in herbivory (Table 4).

Gap-understory position was the next most influential factor on seedling survival; in the gap center and gap edge, seedlings survived 6–7 times more than that they did in the understory (Table 3).

Seedling lifetime also differed between species (Table 3). The survival probability of *D. triquetra*, *S. castaneifolia*, and *W. bicuspidata*

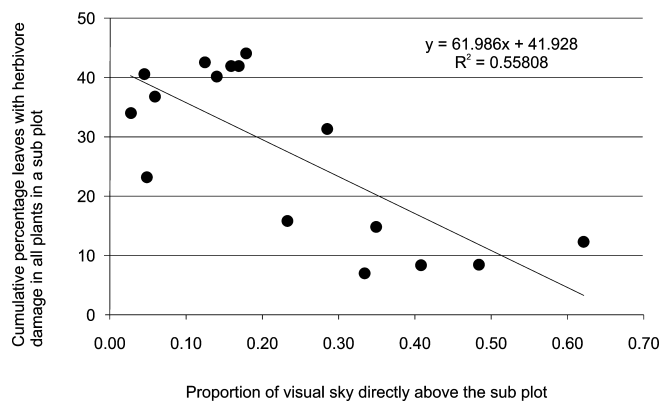


FIGURE 3. Percentage of leaves with herbivore damage in each subplot (gap-understory position) versus canopy openness directly above each gap-understory position in a 90° angle (VS_{90°) in each location. Herbivore damaged is averaged for all the plants of the six species for each plot. VS_{90° S is an average obtained for each plot from five photographs in the four corners and the middle of the plot before the experiment began.

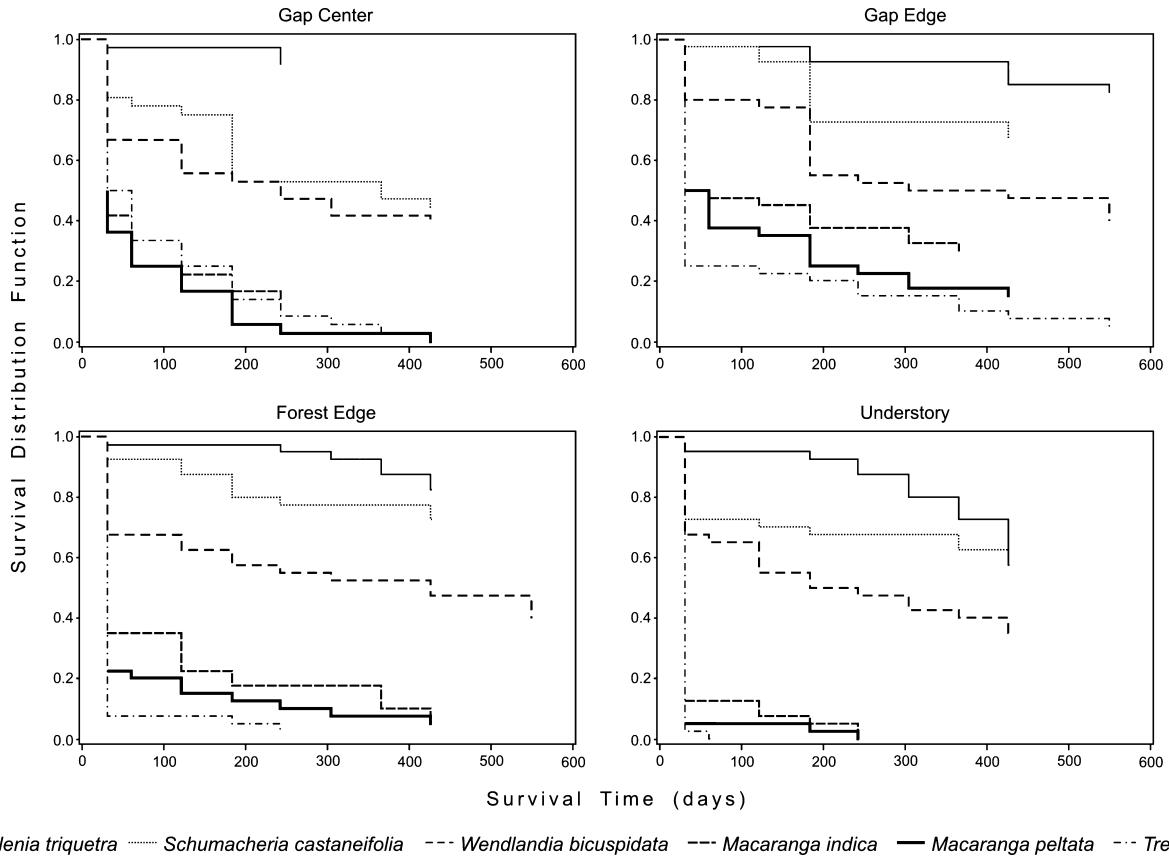


FIGURE 4. Seedling survival probability of *Dillenia triquetra* (DT), *Macaranga indica* (MI), *Macaranga peltata* (MP), *Schumacheria castaneifolia* (SC), *Trema orientalis* (TO), and *Wendlandia bicuspidata* (WB) in the four gap-understory positions: gap center (GC), gap edge (GE), forest edge (FE) and forest understory (FU). Small gap restricted species (DT, SC, WE) had higher probability of survival compared with the large gap restricted species (TO and MP). The survival distribution function was calculated using the nonparametric Kaplan–Meier estimate. Note that the graph lines end when the survival probability does not change for a future census event.

TABLE 3. ANOVA table for Weibull survival models for plot subplot interaction and covariance terms. Total number of seedlings in experiment was 960 and 333 lived beyond the experiment (right-censored) duration of 550 d. All plants were censored monthly for the first two months and every other month (interval-censored) thereafter. Model terms are arranged in increasing P values.

Model Term	Full Model			Final Model		
	df	Wald χ^2	$P > \chi^2$	df	Wald χ^2	$P > \chi^2$
Cumulative leaf herbivory for seedlings	1	197.9	<0.0001	1	241.6	<0.0001
Gap-understory position	3	142.3	<0.0001	3	183.9	<0.0001
Species	5	123.7	<0.0001	5	157.3	<0.0001
Species × cumulative leaf herbivory for seedlings	6	45.2	<0.0001	6	33.0	<0.0001
Location	3	18.6	0.0003			
Height	1	11.5	0.0007			
Location × gap-understory position	9	27.0	0.0014			
Number of leaves	1	7.7	0.0056			
Species × gap-understory position	15	28.0	0.0217			
Species × location	15	26.1	0.0368			
Average crown radius	1	3.3	0.0678			

ta was 46.9, 6.3, and 4.6 times greater than that of *T. orientalis* (Table 4). The survival probability for *M. indica* and *M. peltata* was similar to that of *T. orientalis* (1.57 and 1.17 time greater), although the difference between *M. indica* and *T. orientalis* was marginally significant (Table 4).

Nonparametric analysis results complemented the findings of the parametric analysis: seedling survival differed among species, location, and gap positions (Table S3). Survival was negatively associated with herbivory damage ($LHD_{seedling}$) for all these factors and positively associated with VS_{90° for location (Table S3).

CANOPY GAP POSITION AND HERBIVORY EFFECT ON SEEDLING HEIGHT GROWTH AND CROWN DIMENSIONS.—Relative height growth rate varied substantially among species (Table 5). Growth responses of *T. orientalis* contrasted with seedling survival probabilities assessed earlier: although it had the lowest survivorship, it had the fastest height growth rates across all positions (Fig. S2; Table 5). Although the species-level analysis of survival show that the three species that are more shade tolerant—*D. triquetra*, *S. castaneifolia*, and *W. bicuspidata*—are able to survive in the forest understory and the forest edge, they barely grew in height; average increase in height for the 16 mo duration of the experiment for the three species in the understory was about 4 cm. The test for significance of model terms (Table 5) and the parameter estimates for the final model (Table 6) for relative height growth rate showed that herbivore damage had a larger effect on height growth than the differences due to species and gap positions.

Further, the beginning height also affected the relative height growth rates observed at the end of the experiment (Table 5).

Average crown diameter at the end of the experiment did not show clear differences between gap-understory conditions (Fig. S4). Interestingly, however, the crown diameter growth had an opposite trend to the height growth rate for *T. orientalis*: height growth increased from gap center to gap edge to forest edge while the crown diameter decreased (Figs. S2 and S4).

DISCUSSION

We showed that although pioneer survival between gap center and gap edge were similar (Fig. 2), the height growth of these species was highest in the gap edge (Fig. S1), indicating that the species investigated here may have a physiological upper limit to growth under high irradiance, even though they are ‘pioneers’. Forest vegetation is known to increase light-use efficiency with increasing irradiance up to 30–50 percent full sun (Ruimy *et al.* 1996, Poorter 1999). Above this threshold of irradiance, the productivity of forest species generally plateaus (especially compared with crop species that continue to linearly increase productivity up to 2000 $\mu\text{mol}/\text{m}^2 \text{ s}$; Ruimy *et al.* 1996).

Only three of the six species studied here outperformed others through growth, survival, or resistance to herbivory, providing partial evidence for partitioning along the gap microenvironment. Many temperate and tropical studies have found similar results for niche partitioning or microhabitat specialization showing that only some of the study species outperform others (*e.g.*, Augspur-

TABLE 4. Parameter estimates for (full model) accelerated seedling lifetime with the model coefficients. Estimates are for the level of a given factor, *e.g.*, ‘Species: *Dillenia triquetra*’ is the level of the factor species for *Dillenia triquetra*. The data contained 960 seedlings with 333 surviving beyond the last census (right-censored). All plants were censored monthly for the first two months and every other month for the following year (interval-censored).

Model Term	Parameter coefficient	SE	Wald χ^2	$P > \chi^2$	Accelerated time
Intercept	2.30	0.19	127.75	<0.0001	9.97
Species (compared to <i>Trema orientalis</i>)					
<i>Dillenia triquetra</i>	3.85	0.39	94.8	<0.0001	46.99
<i>Schumacheria castaneifolia</i>	1.84	0.28	44.7	<0.0001	6.30
<i>Wendlandia bicuspidata</i>	1.53	0.22	46.8	<0.0001	4.62
<i>Macaranga indica</i>	0.45	0.21	4.7	0.0291	1.57
<i>Macaranga peltata</i>	0.16	0.21	0.6	0.4482	1.17
Gap-understory position (compared to understory)					
Gap center	1.97	0.18	122.06	<0.0001	7.17
Gap edge	1.88	0.18	110.0	<0.0001	6.55
Forest edge	0.43	0.18	5.0	0.0253	1.54
Cumulative leaf herbivory for seedlings ($LHD_{seedling}$) compared to <i>T. orientalis</i>	0.02	0.01	19.58	<0.0001	1.02
$LHD_{seedling} \times Dillenia triquetra$	0.004	0.01	0.33	0.5662	1.00
$LHD_{seedling} \times Schumacheria castaneifolia$	0.03	0.01	12.12	0.0005	1.03
$LHD_{seedling} \times Wendlandia bicuspidata$	0.38	0.01	17.47	<0.0001	1.46
$LHD_{seedling} \times Macaranga indica$	0.02	0.01	6.21	0.0127	1.02
$LHD_{seedling} \times Macaranga peltata$	0.002	0.01	0.07	0.7982	1.00

TABLE 5. ANOVA table for the relative height growth rate of seedlings that survived to the end of the experiment (550 d).

Model term	df	F value	$P > F$
Gap-understory position	3	13.1	<0.0001
Species	5	9.2	<0.0001
Gap-understory position × species	13	2.6	0.0092
Cumulative leaf herbivore damage for species	1	41.76	<0.0001
Average height for each species at the beginning of the experiment	1	6.36	<0.0154

TABLE 6. Parameter estimates for relative height growth rate (RHGR) with the model coefficients.

Model Term	Parameter coefficient	SE	t value	$P > t $
Intercept	0.00220	0.00010	12.38	<0.0001
Species (compared to <i>W. bicuspidata</i>)				
<i>Dillenia triquetra</i>	-0.00018	0.00016	-1.13	<0.2626
<i>Schumacheria castaneifolia</i>	-0.00015	0.00016	-0.93	0.3580
<i>Macaranga indica</i>	0.00016	0.00021	0.78	0.4371
<i>Macaranga peltata</i>	0.00017	0.00021	0.78	0.4371
<i>Trema orientalis</i>	0.00099	0.00019	5.30	<0.0001
Gap-understory position (compared to forest understory)				
Gap center	0.00029	0.00015	1.93	0.0601
Gap edge	0.00047	0.00015	3.03	0.0040
Forest edge	0.00049	0.00015	3.22	0.0024
Gap-understory position × species (compared to <i>W. bicuspidata</i>)				
FE × <i>Macaranga peltata</i>	-0.00068	0.00022	-2.41	0.0200
GC × <i>Schumacheria castaneifolia</i>	0.00059	0.00023	2.61	0.0124
GC × <i>Trema orientalis</i>	-0.00051	0.00025	-2.03	0.0484
Cumulative Leaf Herbivory for Seedlings	7.94E-6	1.22E-6	6.46	<0.0001
Height at the Beginning of the Experiment	0.1E-5	4.3E-6	-2.52	0.0154

ger 1984, van der Meer *et al.* 1998, Beckage & Clark 2003). Generally, researchers have offered two explanations for this: either (A) the species do partition resource axes that were not investigated (*e.g.*, Beckage & Clark 2003), or (B) there may be species-specific interactions with spatially variable biota such as soil microorganisms that limit species' distributions (*e.g.*, Klironomos 2002). Partial evidence for niche partitioning and consistency in species rankings for survival in different microenvironments has been demonstrated in other studies, even when a variety of

species and shade environments were investigated (Beckage & Clark 2003, Baraloto *et al.* 2005). We did, however, find that differences among species in their resilience to herbivory combined with differences in the amount of herbivory in different microhabitats, may explain the residual variability of species distributions and drive community composition (Klironomos 2002). In addition, the average of a species' response may be insufficient to recognize the importance of a few individuals surviving in extreme conditions and doing exceptionally well (Clark *et al.* 2010). On this last point, however, the species in our study that did not show obvious niche partitioning did not have higher individual variation than those species that did show partitioning. Our study supports the argument by Kitajima and Bolker (2003) that reversals of survival ranking occur infrequently with respect to microenvironmental position and by themselves do not significantly contribute to community organization in tropical forests.

The species survival probability rankings observed here closely followed the shade tolerance rankings observed for the same six species in our previous study (Goodale *et al.* 2012). The trade-off between survival in deep shade and growth in high light is also consistent with results from prior investigations, which focused mainly on late successional species (Kitajima 1994, Beckage & Clark 2003). For example, Beckage and Clark (2003) found that *Liriodendron tulipifera*, which had the lowest survival among the species they studied, outperformed the other species in growth when it did survive, similar to *T. orientalis* in our study. We found this trade-off with respect to relative height growth rate but not relative crown growth rate. Given that these are pioneer species, we expected the height growth to be driven by stem elongation, a well-documented shade avoidance strategy (Percy *et al.* 2005). The trade-off between survival and growth may also be related to fecundity: for example, Beckage and Clark (2003) found that the ranking of species survival was opposite to the observed fecundity among three species and argued that trade-offs between seedling performance and fecundity might promote a diverse assemblage of seedlings across the landscape. Low-surviving *T. orientalis* is known to produce large quantities of small seeds whereas high-surviving *D. triquetra* produces large seeds, though fewer in quantity per mature adult (Goodale *et al.* unpubl. data; Table 1). Hence, it is possible that *T. orientalis*, although it requires very specific high-light conditions to perform well, may find those conditions easily by having large numbers of seeds, ubiquitous in the soil seed bank and seed rain, and ready to germinate when suitable environmental conditions arise.

Herbivory may be an important component of species interactions that define species' microenvironments. In three species, *W. bicuspidata*, *S. castaneifolia*, and *M. indica*, herbivory showed positively affected survival probability compared with *T. orientalis* and *M. peltata* (Table 4). Although the full mechanisms behind this outcome for all three species are unclear, it was observed in *W. bicuspidata* that herbivory damage was followed by high rates of sprouting from the base of the seedling and that was followed by auxiliary stem growth. The ability to re-sprout after stem damage is known to strongly positively correlate with wood density, and underlies the growth-survival trade-off in Neotropical saplings

(Poorter *et al.* 2010). Indeed, among the six species studied here, *W. bicuspidata* has the highest stem density (Goodale *et al.* unpubl. data). Compared with the other slower growing species, *T. orientalis* may invest less in defence against herbivore damage because leaves can be quickly replaced in higher light conditions. This strategy could explain the rapid die-off of this species at the very beginning of the experiment in the understory and the forest edge positions (see Fig. 4). Similarly, a recent study demonstrated that greater herbivory in shade excludes the temperate pioneer species, *Embothrium coccineum*, from the forest understory because of inherent low physiological tolerance to shade (Salgado-Luarte & Gianoli 2012). However, in their study of three neotropical pioneers, Pearson *et al.* (2003) did not find herbivory to significantly influence the study species' distribution in different gap sizes. Finally, the negative relationship between canopy openness and herbivory (Fig. 3) might be due to differences between sun and shade leaf characteristics, as well as the favorability of the understory environments for foraging herbivores. Sun-adapted leaves are generally smaller, tougher and have higher phenolic contents and lamina thickness compared with shade leaves and thus may have reduced levels of herbivore damage (*e.g.*, Coley 1983, Lowman 1992, 1993).

This study has several limitations. First, we did not artificially implement different levels of herbivore treatments to assess the impact of herbivores on pioneer seedlings. Instead, we assessed herbivory individually for each plant as an observational measurement using the cumulative percentage of leaves with herbivore damage as a measure of herbivore impact. Furthermore, we did not identify each herbivore that damaged seedlings, although we did observe that the majority of the herbivores were crickets and caterpillars. Second, the study was conducted in naturally formed gaps in a previously logged area of the forest. It is possible that we would have found different results in a forest not so artificially disturbed. However, this area now has similar vertical structure to the nonlogged forest and exhibits canopy closure (Gunawardene *et al.* 2010, Kudavidanage *et al.* 2012). Third, the gaps used ranged in size from 890 to 1760 m², and gap size could influence seedling survival and growth. It would have been ideal to create new canopy gaps equal in size, but this is not possible in a forest of Sinharaja's conservation status. Fourth, we did not measure biomass growth of the study species, and hence, our interpretation of height growth differences might reflect patterns of allocation between above- and belowground components. We refrained from destructive sampling for biomass assessment because we needed to confirm, following a full growing season that plants scored as dead at the end of the experiment were correctly scored and not merely reflecting complete leaf senescence with belowground parts that were alive and capable of re-sprouting. We avoided another proxy of biomass, root basal area, which can be calculated from root collar diameter measurements, because the most reliable method of measuring this for live seedlings in an ongoing experiment, using a digital caliper at the soil surface, was damaging to the newly germinated seedlings and was not accurate compared with measurements made at the true root collar after washing uprooted plants.

Finally, the study period was 550 d, but defence allocation strategies may change ontogenetically (Boege & Marquis 2005, Boege *et al.* 2011). Studies that extend to mature tree stages and investigate possible switches in defence strategies are needed to gain a better understanding of the trade-offs between growth, survival, and defence.

In conclusion, species-specific tolerance to herbivory may allow pioneers to co-exist with species that outgrow them in high light conditions. Species that optimize growth at the expense of defence may be limited to high light and be excluded from shade because they do not have photosynthetic resources to offset herbivory. Despite the trade-off between low survival and high growth, these species may be ubiquitous among other pioneer species at the landscape level due to higher resource allocation at maturity toward reproduction. In the context of forest restoration and conservation, pioneer species have been considered as potential initial types of vegetation that can be planted in open sites with more than 60 percent of canopy openness to achieve reforestation (Ashton *et al.* 2001, Chazdon 2008), and the information gained from our investigation may be useful in implementing silvicultural treatments with the focal species. Finally, we show that some pioneer species may need protection from herbivory and some shade at the seedling stage. This undermines the idea that all pioneer species can be used to reforest large open areas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

APPENDIX S1. Justification for using both parametric and non-parametric forms of analysis and further explanation of analytical methods.

FIGURE S1. Percentage leaves with herbivore damage and % photosynthetic tissue area removed for the six pioneer species, *Dillenia triquetra*, *Macaranga indica*, *Macaranga peltata*, *Schumacheria castaneifolia*, *Trema orientalis*, and *Wendlandia bicuspidata*, grown under simulated gap understory conditions.

FIGURE S2. Relative height growth rate for the six species in each gap-understory position assessed from the plants that survived to the end of the experimental time period (550 days).

FIGURE S3. Seedling survival probability of the six pioneer species for pooled data for all gap-understory positions.

FIGURE S4. Relative crown diameter growth rate of for the six species in each gap-understory position assessed from the plants that survived to the end of the experimental time (550 days).

TABLE S1. Mean values and standard deviation of maximum measured photosynthetic photon flux densities (PPFD), between 1000 and 1600 h and R/FR ratio of the light treatments comparable to gap-canopy disturbance condition during the experimental period. Measurements represent every month of the calendar year and five sunny days per month and were obtained during the 22 month duration of the experiment.

TABLE S2. Percentage leaves observed with herbivore damage and % of photosynthetic tissue removed from each plant due to herbivore damage assessed using scaled digital photographs and ImageJ analysis software.

TABLE S3. Nonparametric estimate results for comparison of survival curves and the association of covariates with the survivor function using the Kaplan–Meier product limit estimator.

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