

## Biotic and abiotic factors influencing the seedling dynamics of four dipterocarp species

Shiori Suzuki<sup>1,3</sup>, Michiko Inanaga<sup>2</sup> and Michiko Nakagawa<sup>1</sup>

<sup>1</sup> Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya, Japan

<sup>2</sup> Institute of Wood Technology, Akita Prefectural University, Noshiro, Japan

<sup>3</sup> Author for correspondence (e-mail: disrin.cokola@gmail.com)

**Abstract** Identification of the factors influencing seedling dynamics is crucial for improved understanding of the mechanisms underlying the coexistence of trees in species-rich tropical rainforests. Both biotic and abiotic factors are known drivers of tree seedling establishment; however, interspecific differences in seedling survival and growth responses to these factors have not been thoroughly investigated. We monitored 1,038 current-year seedlings of *Shorea laxa*, *Shorea beccariana*, *Dipterocarpus globosus*, and *Dryobalanops aromatica* for eight months in each of the 20-m grids in the 4-ha Crane Plot following a mast fruiting event in 2013–2014 in the Lambir Hills National Park, Sarawak, Malaysia. Biotic (initial height, conspecific seedling density, dipterocarp seedling density) and abiotic (canopy openness, soil water content) factors were measured during the 8-month monitoring period. The survival proportion and growth rate of current-year seedlings were significantly different among species. The survival proportion of *D. globosus* was 44.0 %; those of *S. laxa*, *S. beccariana*, and *D. aromatica* were > 55 % (56.9–69.5 %). The growth rate of *D. aromatica* was the lowest among the species. Our modeling analyses selected different biotic and abiotic drivers of seedling survival and growth among the species. We suggest that interspecific differences in the effects of biotic and abiotic factors influencing seedling dynamics may underlie the coexistence of tree species in this forest.

**Keywords** Dipterocarps, Seedling survival, Seedling growth

### Introduction

Lowland tropical rainforests in Southeast Asia are dominated by diverse species of the family Dipterocarpaceae, which consists of canopy or emergent trees (Ashton 1982; Ashton et al. 1988). Many of the species produce high quality timber. Information on the regeneration dynamics and coexistence mechanisms of these dipterocarp species is not only an interesting theme in the field of forestry and forest ecology but also important knowledge for biodiversity conservation and forest management.

General flowering (GF) occurs at irregular intervals of several years in the humid tropics

of Southeast Asia (Ashton et al. 1988; Sakai 2002). During these events, nearly all dipterocarp species, together with various species in other families, bloom (Ashton et al. 1988; Sakai 2002). Predator satiation has been widely proposed as a strategy that explains the GF phenomenon (Janzen 1974). According to this postulate, long and irregular intervals between reproductive events of forest plants cause food shortages among seed predators, whose populations are driven down to low densities. When GF occurs, the small remaining predator populations are swamped by the food resources that suddenly become available, and many seeds escape predation (Sun et al. 2007).

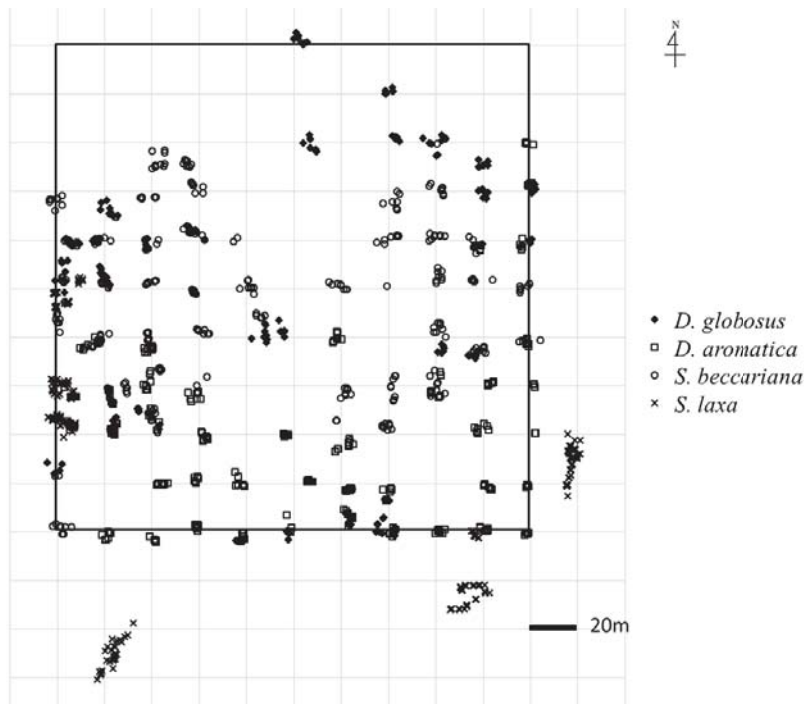
Species-specific differences in regeneration mechanisms and differences in regeneration niches are important for the maintenance of species richness in tropical rainforests (Grubb 1977). Seedling establishment and subsequent seedling survival determine the distribution of tree species because high mortality occurs at the seed/seedling stage (Connell and Green 2000). Hence, identification of the factors that drive seedling dynamics is crucial for improved understanding of the mechanisms by which tree species coexist in species-rich tropical rainforests. Both biotic and abiotic factors are drivers of seedling dynamics (Webb and Peart 2000; Maycock et al. 2005; Takeuchi et al. 2010). Regarding abiotic factors, seedling growth is strongly affected by light availability and soil water content (Hall et al. 2003; Montgomery and Chazdon 2002). Dipterocarp trees are generally shade-tolerant (Becker et al. 1998; Philipson et al. 2014), but increased light intensity often improves seedling survival and growth in some of the species, especially when light is limiting (Dent and Burslem 2009). Neighborhood density, a biotic factor, also influences seedling dynamics (Maycock et al. 2005; Takeuchi et al. 2010). Negative density dependency (density-dependent mortality) is expressed in forest sites as elevated seed and seedling survival rates where densities are low (Takeuchi et al. 2010; Oshima et al. 2015). Positive density dependency (predator satiation) occurs when seed predators are swamped by the abundance of food resources (Janzen 1971; Janzen 1974). Takeuchi et al. (2010) observed negative density dependency in the seedling survival of *Shorea laxa* (Dipterocarpaceae) during a 6-month monitoring period. The effects of abiotic factors (light availability, soil moisture and conspecific density) on sapling survival has been found to be different among dipterocarp species (Aiba and Nakashizuka 2007; Oshima et al. 2015). However, few comparative data are available on the responses of individual species to the drivers of seedling survival and growth.

In this study, we monitored the seedling dynamics (survival and height-growth of current-year seedlings) of four dipterocarp species in an old-growth Bornean tropical rain forest and concurrently examined the biotic and abiotic drivers of these dynamics. We specifically addressed the following questions: 1) What are the patterns of survival and growth, and habitat condition in each species? 2) Which factors affect the survival and growth of current-year seedlings? and 3) Are there interspecific differences in the seedling dynamics, habitat conditions, and biotic and abiotic drivers among the dipterocarps studied?

## **Materials and methods**

### *Study site and study species*

The study was carried out in a mixed dipterocarp lowland forest in the Lambir Hills National Park, Sarawak, Malaysia. We selected four species in Dipterocarpaceae: *Dipterocarpus globosus* Vesque, *Dryobalanops aromatica* Gaertn. f., *Shorea beccariana* Burck, and *Shorea laxa* Slooten, which are very abundant emergent trees in the park (Lee et al. 2002; Ashton 2004). The



**Fig. 1** Distribution map of numbered current-year seedlings of four dipterocarp species. The square bounded by a thick line encompasses the Crane Plot (CP).

wind-dispersed seeds of *D. globosus*, *S. beccariana*, and *D. aromatica* have two, three, and five long wings, respectively; *S. laxa* has wingless seeds.

From 2013 to 2014, the second largest GF during the last 14 years was observed (Nakagawa et al., unpublished data).

#### *Field survey*

In January 2014, immediately after their establishment, we numbered and mapped current-year seedlings of the four dipterocarps in each of the 20-m grids in the 4-ha Crane Plot (CP); up to eight individuals of each species were identified in this manner in each grid (Fig. 1). No current-year seedlings were found in some of the 20-m grids. Since few current-year seedlings of *S. laxa* occurred in the CP ( $N = 107$ ), we included *S. laxa* seedlings that were found outside the grids, but in the proximity of the CP. We monitored the survival and height-growth of the selected individuals for eight months (January–September 2014). Heights were measured to an accuracy of 1 mm.

In October 2014, we gridded the area in and around the CP to a mesh size of  $2.5 \times 2.5$  m, and measured canopy openness and soil water content in each mesh when at least one individual of the selected species grew there. To estimate canopy openness, we captured hemispherical images 1 m above the forest floor at a random point in each mesh using a COOL PIX 950 (Nikon, Tokyo, Japan) camera with a fisheye converter FC-E8 0.21 (Nikon, Tokyo, Japan). The images were analyzed with CanopOn2 software (ver. 2.03c; Takenaka 2009), which provided the percentage canopy openness. Soil water content (%) was measured at a depth of 10 cm in the ground at three randomly selected points in each mesh using an HH2 Moisture Meter (Delta-T Devices, Burwell, UK). The measurements in all meshes were taken within two consecutive days.

We confirmed that the values were closely similar between the first and the second day. The mean value of soil water content in each mesh was used for our analyses. Conspecific density (individuals m<sup>-2</sup>) and dipterocarp density (individuals m<sup>-2</sup>) were calculated by counting the initial number of conspecific current-year seedlings and dipterocarp current-year seedlings, respectively, within the 1-m squares in which each of the tagged current-year seedlings was located.

### *Statistical analysis*

We calculated survival proportion in each species and absolute height-growth using the following expressions:

$$\text{survival proportion (\%)} = \left( \frac{\text{the number of individuals in September}}{\text{the number of individuals in January}} \right) \times 100,$$

$$\text{absolute height-growth (cm)} = \text{height in September (cm)} - \text{height in January (cm)}.$$

We calculated absolute height-growth for each individual and then calculated the mean value for each species.

We used the Chi-squared test to examine differences in survival proportion among species; pairwise comparisons were then conducted with the Bonferroni correction. We applied nonparametric Kruskal-Wallis tests followed by Steel-Dwass nonparametric multiple comparisons tests on measures of absolute height-growth, canopy openness, soil water content, conspecific density and dipterocarp density.

Generalized linear mixed models (GLMMs) were used to predict the probability of current-year seedling survival (binomial distribution) and absolute height-growth (normal distribution) as a function of initial height (height in January), canopy openness, soil water content, conspecific density and dipterocarp density; mesh was treated as a random effect. Prior to the analyses, canopy openness, soil water content, conspecific density, dipterocarp density and initial height were standardized as the means and standard deviations. We determined the best model based on Akaike's Information Criterion (AIC, Akaike 1973). All analyses were performed using the 'lme4' and 'MuMIn' packages in R software (ver. 3.1.2; R Core Development Team 2014).

## **Results**

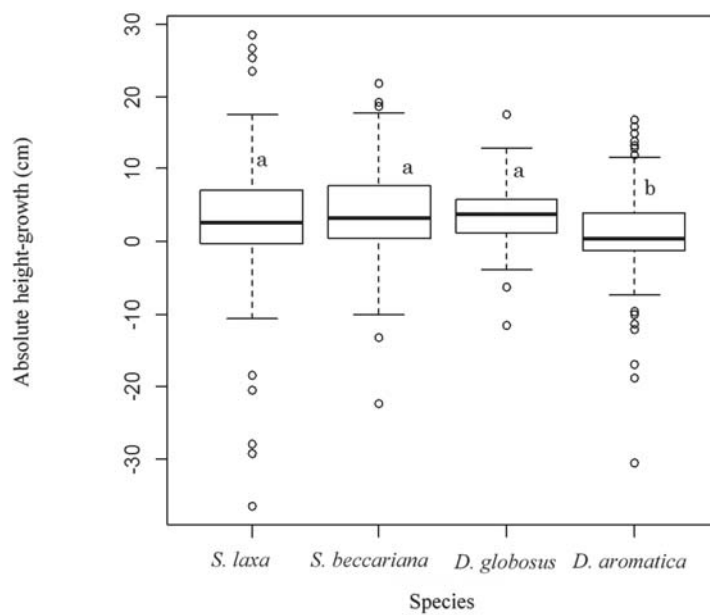
### *Current-year seedling dynamics and habitat conditions*

The proportions of current-year seedlings surviving through eight months were 69.5 %, 56.9 %, 44.0 %, and 61.6 % for *S. laxa*, *S. beccariana*, *D. globosus*, and *D. aromatica*, respectively (Table 1). The proportions differed significantly among species. Pairwise comparisons tests showed that *D. globosus* had a significantly lower survival proportion than the other species ( $P < 0.05$ ); the survival proportion of *S. laxa* was significantly higher than those of *S. beccariana* and *D. globosus* ( $P < 0.05$ ). Absolute height-growth also differed significantly among species ( $3.0 \pm 9.0$  cm,  $4.0 \pm 6.2$  cm,  $3.6 \pm 4.0$  cm, and  $1.2 \pm 5.9$  cm for *S. laxa*, *S. beccariana*, *D. globosus*, and *D. aromatica*, respectively; mean  $\pm$  SD). Pairwise comparisons tests showed that *D. aromatica* had a significantly lower absolute height-growth rate than the other species ( $P < 0.05$ , Fig. 2).

All habitat conditions (canopy openness, soil water content, conspecific density and dipterocarp density) at sites where current-year seedlings occurred differed significantly among species ( $P < 0.05$ ; Fig. 3). Seedlings of *D. aromatica* occurred in more open sites ( $5.9 \pm 2.4$  %, mean  $\pm$  SD) than other species; *S. laxa* seedlings occurred in sites that were more shaded than

**Table 1** Initial numbers and heights (mean  $\pm$  SD) of current-year seedlings (of four dipterocarp species) and their survival (%) over eight months. Different letters indicate significant differences in survival proportion between species.

Species	Initial N	Initial height (cm)	Survival proportion (%)
<i>S. laxa</i>	210	27.5 $\pm$ 6.8	69.5 a
<i>S. beccariana</i>	313	27.0 $\pm$ 6.7	56.9 b
<i>D. globosus</i>	223	18.5 $\pm$ 4.1	44.0 c
<i>D. aromatica</i>	292	30.7 $\pm$ 6.2	61.6 ab

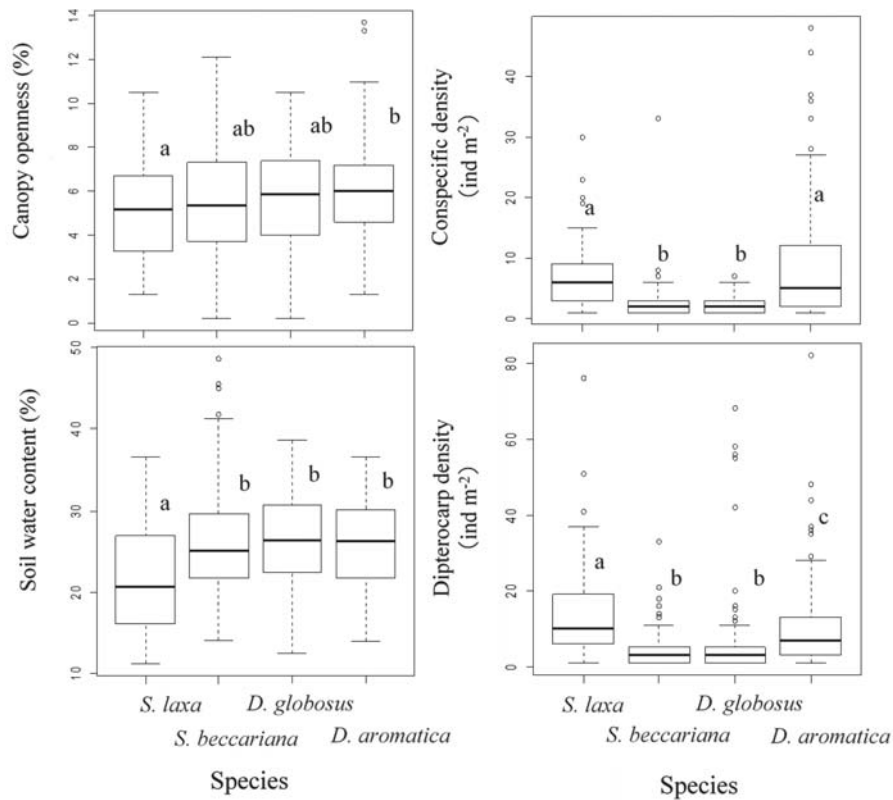


**Fig. 2** Absolute height-growth of current-year seedlings of four dipterocarp species over eight months. Different letters indicate significant differences between species ( $P < 0.05$ ).

those of other species ( $5.3 \pm 2.4$  %, mean  $\pm$  SD). Soil water content was lower in sites where *S. laxa* occurred ( $25.4 \pm 8.2$  %, mean  $\pm$  SD) than in sites containing other species. *Dryobalanops aromatica* and *S. laxa* had higher conspecific densities ( $7.2$ – $8.6$  ind.  $m^{-2}$ , mean  $\pm$  SD) than *D. globosus* and *S. beccariana* ( $1.9$ – $2.7$  ind.  $m^{-2}$ , mean  $\pm$  SD). Dipterocarp density was higher in sites containing *S. laxa* ( $13.8 \pm 10.3$  ind.  $m^{-2}$ , mean  $\pm$  SD) than in sites containing other species. Dipterocarp density was higher in sites containing *D. aromatica* ( $10.9 \pm 9.2$  ind.  $m^{-2}$ , mean  $\pm$  SD) than in sites containing *D. globosus* and *S. beccariana*.

#### *Biotic and abiotic factors affecting the dynamics of current-year seedlings*

The best performing models with the lowest AIC values are summarized for each dipterocarp species in Table 2. All of the best models included initial height as an explanatory factor for the survival of current-year seedlings; the effect of initial height was positive for all species. Canopy



**Fig. 3** Habitat conditions at locations where current-year seedlings of each dipterocarp species occurred. Different letters indicate significant differences between species ( $P < 0.05$ ).

**Table 2** Coefficients of generalized linear mixed models (GLMMs) analyses of the seedling dynamics of four dipterocarp species (upper: survival, lower: absolute height-growth). The best performing models with the lowest Akaike's Information Criterion (AIC) value are indicated. Bold values indicate significant differences ( $P < 0.05$ ).

Species	Canopy openness	Soil water content	Conspecific density	Dipterocarp density	Initial height
<b>Survival</b>					
<i>S. laxa</i>	<b>0.27</b>	0.33	<b>0.37</b>		<b>0.09</b>
<i>S. beccariana</i>				<b>0.68</b>	<b>0.06</b>
<i>D. globosus</i>					<b>0.22</b>
<i>D. aromatica</i>		<b>0.34</b>	<b>0.74</b>		<b>0.09</b>
<b>Absolute height-growth</b>					
<i>S. laxa</i>	-1.00	-0.75	<b>-1.46</b>		<b>-4.84</b>
<i>S. beccariana</i>	<b>1.31</b>				<b>-2.39</b>
<i>D. globosus</i>					<b>-1.54</b>
<i>D. aromatica</i>		<b>1.01</b>		<b>0.85</b>	<b>-1.47</b>

openness and soil water content positively influenced seedling survival in *S. laxa* and *D. aromatica*, respectively. Conspecific density had a positive effect on seedling survival in *S. laxa* and *D. aromatica*; dipterocarp density positively influenced seedling survival in *S. beccariana*.

Initial height was included in all of the best models as an explanatory factor for the absolute height-growth of current-year seedlings, but the effect was negative for all species (Table 2). A positive effect of canopy openness was detected for *S. beccariana*. Conspecific density negatively influenced the height-growth of *S. laxa* seedlings. Soil water content and dipterocarp density had positive effects on height-growth of *D. aromatica*.

## Discussion

### *Seedling dynamics and habitat conditions of current-year seedlings*

Previous studies reported *S. laxa* current-year seedling survival proportions (at our study site) of 62.8 % (six months) and 67.5 % (seven months) during the GF events in 2005 and 2009, respectively (Takeuchi et al. 2013; Oshima et al. 2015). We calculated a comparable survival proportion of 69.5 % (eight months) for the same species during the GF event in 2013. The consistency across years is likely related to the consistently high conspecific density of *S. laxa* seedlings during the three GF events. Seed dispersal via gravity will always lead to high seedling density, regardless of the intensity of the GF phenomenon. In contrast, current-year seedling survival in *S. beccariana* in 2009 (seven months, 68.6 %) was higher than that in 2013 (eight months, 56.9 %); this was also the case for *D. globosus* (61.8 % and 44.0 % in 2009 and 2013, respectively). The intensity of the GF event in 2009 was stronger than that in 2013 (Nakagawa et al. unpublished data); the higher seedling survival in 2009 may be indicative of predator satiation at the whole community level in that year. The current-year seedling survival of *D. aromatica* in 2013 was closely similar to that in 1991 (Itoh et al. 1995); however, we cannot compare these two GF intensities.

The low values of absolute height-growth in *D. aromatica* seedlings may have been related to their large initial heights. Itoh et al. (1995) reported that, after an initial rapid growth phase of one month, seedlings of *D. aromatica* in the understory grew little. It is also possible that intense resource competition among individuals at high-density reduced the growth rates of the seedlings in our study.

We detected differences in the habitat conditions of current-year seedlings among the four species. These differences may have reflected differences in seed dispersal patterns, the distributions of adult trees, and seed crop size. Indeed, current-year seedlings of *S. laxa*, which has wingless seeds, were established at drier and more shaded sites than those of other species. The adult trees of this species were located on dry ridges (Ashton 2004); hence, seeds falling under the influence of gravity (Takeuchi et al. 2005) and landing directly below the mother plant canopies would have encountered dry habitat conditions. Seed dispersal by gravity also created high conspecific densities below the crowns of the mother trees. Nevertheless, although we expected *D. aromatica* seeds with their five long wings to disperse far from the mother trees, the current-year seedlings of this species grew at high conspecific densities at sites where dipterocarp densities were also high, which may have been a reflection of the elevated adult tree (diameter at breast height > 30 cm) density in the study site (*D. globosus*: 2.3 ind. ha<sup>-1</sup>; *D. aromatica*: 6.5 ind. ha<sup>-1</sup>; *S. beccariana*: 6.5 ind. ha<sup>-1</sup>; *S. laxa*: 1.8 ind. ha<sup>-1</sup>) and the high level of seed production.

### *Factors affecting the dynamics of current-year seedlings*



We detected interspecific differences in the factors that influenced seedling survival. The effect of initial height, however, which was positive for all species, did not vary interspecifically. Initial size had strong effects on current-year seedling survival, in agreement with previous studies on dipterocarps and other tropical species (Comita et al. 2009; Jurinitz et al. 2013). The positive effect of canopy openness on *S. laxa* seedling survival may reflect the shadiness of sites in which it occurs. The survival of *D. aromatica* was positively influenced by soil water content, which may reflect the low drought tolerance traits of this species. The proportion of biomass allocated to roots in this species was lower than those of other species (*D. globosus*: 51.5 %; *D. aromatica*: 41.6 %; *S. beccariana*: 53.8 %; *S. laxa*: 45.6 %; Suzuki, unpublished data). Positive density dependency was probably indicative of predator satiation. Although the predator satiation hypothesis generally focuses on the seed stage of plant life histories, the mechanism may also operate at the initial stage of seedling establishment in the Dipterocarpaceae (Curran and Leighton 2000) because the seeds of this family have no dormant phase (Ashton 2004). The seedlings of *S. laxa* and *D. aromatica* occurred at high density, and their survival had a positive and stronger relation to conspecific density, but no or weaker relation to canopy openness and soil water content, suggesting that these species escape species-specific seed or seedling predation. Seedling survival in *S. beccariana* was positively related to dipterocarp density, suggesting that seedlings of this species escape the seed or seedling predation that was common across dipterocarp species. We found no negative density-dependency of seedling survival, in contrast to previous studies on dipterocarp seedlings (Takeuchi et al. 2010; Takeuchi et al. 2013; Oshima et al. 2015). This disparity among studies may be due to the low conspecific seedling densities in the studied quadrats that we measured by random sampling in 20-m grids. In most previous studies, seedling censuses were conducted within quadrats developed near the mother trees, where seedling densities were higher than those measured in our study (Takeuchi et al. 2013; Oshima et al. 2015).

We also detected interspecific differences in the factors that affected seedling growth. An exception was initial height, which negatively influenced height-growth across all species. *Shorea beccariana*, in which seedling growth is positively affected by canopy openness, is likely to be dependent on light availability. The seedling growth of *D. aromatica* was positively correlated with soil water content, which was also the case for seedling survival in this species, suggesting that *D. aromatica* is sensitive to water stress. The seedling growth of *S. laxa* was negatively influenced by conspecific density; this species occurred at high conspecific densities. Thus, seedlings of *S. laxa* likely experienced intense intraspecific competition for resources. In contrast, elongation growth is promoted by high seedling density in shade-tolerant species (Gilbert et al. 2001; Saito et al. 2012) because of the competition for light and space (Mithen et al. 1984; Canham et al. 2004). Competition among other species may explain the positive influence of dipterocarp density on *D. aromatica* seedling growth.

## **Conclusion**

Our results are consistent with previous studies showing that seedling dynamics and regeneration niches of dipterocarps differ among species (Grubb 1977; Turner 1990; Itoh 1995; Oshima et al. 2015). These observations suggest that a divergence of regeneration niches among species determines their distribution patterns and maintains species richness in the tropical rainforests of Southeast Asia (Itoh 1995; Connel and Green 2000). The factors affecting seedling dynamics would change as plants develop. Comita et al. (2009) observed changes in the relative importance



of abiotic and biotic factors for tropical tree species over time. Longer-term studies of the multiple factors affecting the dynamics of current-year seedlings and subsequent saplings will improve our understanding of the mechanisms by which species coexist in species-rich tropical rainforests.

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