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POPULATION ECOLOGY – ORIGINAL RESEARCH

Distance- and density-dependent leaf dynamics of seedlings of a tropical rainforest tree

Shinya Numata[1] · Naoki Kachi[2] · Toshinori Okuda[3] · N. Manokaran[4]

Abstract Parental distance and plant density dependence of seedling leaf turnover and survival was examined to investigate predictions of the Janzen–Connell hypothesis. The focal study species, *Shorea macroptera* is a canopy tree species in a lowland rain forest in peninsular Malaysia. We found that the peak of the distribution of plants shifted from 3–6 m to 6–9 m during the course of the change from seedling to sapling stage. The leaf demography of the seedlings was influenced by their distance from the adult tree and also by the seedling density. Although significant density- and distance dependence in leaf production was not detected, seedling leaf loss decreased with distance from the parent tree and with seedling density. Similarly, leaf damage was not found to be distance- or density-dependent, but net leaf gain of seedlings increased with distance from the parent tree. Although no significant distance- or density-dependence was evident in terms of leaf damage, significant distance dependence of the net leaf gain was found. Thus, we concluded that positive distance dependence in the leaf turnover of seedlings may gradually contribute to a shift in the distribution pattern of the progeny through reductions in growth and survivorship.

Keywords Dipterocarps · Janzen–Connell hypothesis · Leaf damage · Leaf turnover · Seedlings

Introduction

The Janzen–Connell hypothesis (J–C hypothesis) explains the mechanism of the maintenance of tropical diversity through parent-mediated distance- and density-dependent survival of progeny (Janzen 1970; Connell 1971). The hypothesis assumes that host-specific natural enemies such as seed predators, insect herbivores, and pathogens cause distance- and/or density dependence in seedling establishment. This hypothesis predicts negative density dependence (reduced growth and survivorship of progeny at high density) and positive distance dependence (better growth and survivorship of progeny at greater distance from the parent tree) in the regeneration of tree species. Several studies have suggested that the activity of pathogens and seed predators is both distance- and density dependent (e.g., Augspurger and Kelly 1984; Forget 1991; Gilbert et al. 1994). Clark and Clark (1984) reviewed both the density dependence and distance dependence of progeny mortality from 24 datasets of tropical woody plants, and found distance and/or density dependences in many trees. However, the direction of the dependence differed among species and among the different

✉ Shinya Numata
nmt@tmu.ac.jp

[1] Graduate School of Urban Environmental Sciences, Tokyo Metropolitan University, Minami-Osawa 1-1, Tokyo, Hachiouji 192-0397, Japan

[2] Graduate School of Science and Engineering, Tokyo Metropolitan University, 1-1 Minami-Osawa, Tokyo, Hachiouji 192-0397, Japan

[3] Graduate School of Integrated Arts and Sciences, Hiroshima University, 1-7-1 Higashi-Hiroshima, Hiroshima 739-8521, Japan

[4] Forestry Division, Forest Research Institute Malaysia, 52109 Kepong, Selangor, Malaysia

factors affecting the progeny. One meta-analysis provided no general support for the distance-dependence prediction of the J–C hypothesis (Hyatt et al. 2003), whereas a recent meta-analysis revealed fairly widespread support of distance- and density-dependent predictions (Comita et al. 2014).

It is clear that effective survival and growth of seedlings are crucial for the successful regeneration of tree species, and the growth of seedlings may be more sensitive than their survival when testing the predictions of the J–C hypothesis. Connell (1971) originally predicted that the distance effect should be stronger in seedlings than in seeds because seedlings would gradually decay due to herbivory and/or pathogen attacks. However, distance and density effects in slow-growing seedlings in the shaded understory are difficult to detect.

One way to integrate the joint effects of the myriad factors that covary with distance and density is to explicitly examine leaf dynamics of seedlings, including rates of leaf production, abscission, and longevity. The foliar condition of seedlings resulting from leaf population dynamics plays a crucial role in the survival and biomass production of plants (Bongers and Popma 1990). Leaf demographic parameters may be useful as an indicator of seedling growth in a shaded understory. Changes in the total leaf area of an individual plant are primarily determined by the patterns of production and leaf fall and by the longevity of leaves (Bazzaz and Harper 1977). Blundell and Peart (1998) found negative distance dependence in leaf herbivory and positive distance dependence in the foliar condition of dipterocarp saplings in Borneo. It was suggested that foliar herbivory is associated with a greater mortality of seedlings in Southeast Asian dipterocarps (Eichhorn et al. 2010). Therefore, the leaf dynamics of seedlings could be used to detect the distance- and/or density dependence of seedling performance through leaf herbivory and pathogen attacks.

This study examined on the distribution of 2-year-old seedlings and saplings over 10 years of an Asian dipterocarp species at a fine scale and on the leaf demography of seedlings near conspecific adult trees. In general, Asian dipterocarps participating in general flowering have cohorts of seedlings that continually replenish the seedling bank from successful mast years (Ashton 1988; Sakai et al. 2006). A comparison of the spatial distribution of different cohorts in the same population has been used previously to study the regeneration process of trees (Hubbell 1979; Yamada and Suzuki 1997). If distance dependence exists in dipterocarp seedlings, effects of mother tree distance on the leaf dynamics of seedlings and the distribution of progeny should differ among cohorts of different ages. Therefore, we first examined the spatial distribution of seedlings and saplings around conspecific adult trees to detect positive or negative density- and distance patterns. We hypothesized that, if any

distance and/or density dependence existed, the peak of the distribution should change from being near the adult to being at a distance from the adult. Second, we examined distance and density dependence in a cohort of seedlings from the perspective of leaf demography to consider physical (light availability) and/or biological (leaf herbivory and pathogens) factors that might affect seedling performance.

Methods

Study site

The study was conducted in a lowland rain forest at the Pasoh Forest Reserve, in Peninsular Malaysia (latitude 2°59′N, longitude 102°19′E, altitude 75–150 m). Field observations were made in a 6-ha plot of secondary forest (Okuda et al. 2004; Numata et al. 2006). The density of the adult trees (DBH > 30 cm) in the plot was higher (5.2 ha^{-1}) than that in the primary forest (2.0 ha^{-1}) (T. Okuda unpublished data). There are generally two weak dry seasons (in July and January) each year, and the annual rainfall averages approximately 2000 mm (Numata et al. 2003). During the study period, the mean monthly rainfall was 172.9 mm months^{-1}, varying from 21.0 mm months^{-1} (July 1999) to 293.7 mm months^{-1} (May 1999) (M. Tani and Abdul Rahim unpublished data).

Study species

Dipterocarp species (*Dipterocarpaceae*) are some of the best-known and most commercially important tropical trees. There are approximately 500 species of dipterocarps in Southeast Asia, and the Malaysian lowland rain forests contain more than 168 coexisting dipterocarp species (Symington et al. 2004). Asian dipterocarp species dominate both the lowland and hill tropical rain forests of Southeast Asia, where they can form both the canopy and the emergent layer. Most dipterocarp trees are usually weakly wind dispersed, with a high concentration of fruits falling beneath the crown (Appanah and Mohd. Rasol 1990; Naito et al. 2008). Therefore, many dipterocarp tree seedlings must survive in the shaded understory for long periods, and their seedlings die under the very low light regime of a closed forest canopy (Ashton 1995; Manokaran and Swaine 1994).

Shorea macroptera dyer is widely distributed in peninsular Malaysia, Sumatra, and north and west Borneo (Symington et al. 2004). The species produces timber classified as light hard wood, as well as an inferior variety of dammar (a triterpenoid resin). Among the coexisting *Shorea* species in the Pasoh Forest Reserve, *S. macroptera* is regarded as a relatively slow-growing species, with a low mortality rate and low relative growth rate (RGR) as measured by

diameter (Suzuki et al. 2009, 2012). Seedlings of the species may suffer from dieback of the leading shoot (Appanah and Weinland 1993). The species synchronizes flowering and fruiting at intervals of 1–10 years (mast fruiting), which results in synchronous germination of the species (Numata et al. 2003, 2012). Seedlings of the species can survive under shade conditions for many years, and a considerable number of seedlings are always found on the forest floor. The term "seedling" in this study refers to plants that emerged during general flowering in September 1996 and were 10–25 cm in height. The seedlings had 2–10 leaves in September 1998. The term "saplings" refers to individuals 50–200 cm in height, that likely emerged as seedlings during a major mast fruiting in 1985 or 1989 (Numata et al. 2003).

Selection of focal adults and sapling distribution

The study was conducted from September 1998 through March 2000 at a 6-ha plot in the Pasoh Forest Reserve. Three focal adult trees were chosen for the study (Fig. S1). The DBH of the focal adult trees was >30 cm, ensuring sufficient reproductive maturity to produce juveniles nearby. For each focal adult, the distance from the adult tree was measured for all saplings established before 1996 and growing within 20 m of the adult (Table S1). Density of each sapling was determined in terms of number of individuals per concentric ring area from adult (0–3, 3–6, 6–9, 9–12, 12–15 m). Saplings of the three focal trees were investigated in March 2000.

Seedling plots

In this study, 12 transect plots were used for a seedling census. For each adult tree, we established four 1×15-m transect plots from the bottom of the trunk of an adult tree along the azimuth of north, east, west, and south. All seedlings grown inside the transect plots were labeled using numbered aluminum tags and colored marking tape. In each transect plot, we measured the distances between individual seedlings and the focal adult tree. For the survey, the transect plot was divided into $1\ m \times 3\ m$ subplots in terms of distance class ($n = 60$), and the initial seedling density of each subplot was evaluated. Measurements began in April 1999.

Survivorship and growth were recorded every 2–3 months (60–94 days) from December 1998 through December 1999. For each adult tree, the survivorship of the seedlings was determined as the number of surviving seedlings in December 1999 against the initial number of seedlings in December 1998. The height of the seedlings was sequentially measured to the nearest 0.5 cm during the study. The relative growth rate was calculated as [ln (height at T_1 − ln (height at T_0)]/census interval for each period, where T_0 and T_1 are the beginning and end of a period. All leaves of each seedling

were sequentially numbered to determine leaf demography. Waterproof pens were used to inscribe small numbers on the axial surface of individual leaves. Newly developed leaves were also marked and monitored when they emerged. From the observations, the following parameters were derived: leaf production (number of newly developed leaves for each period), leaf loss (number of leaves lost for each period), and net leaf gain (number of leaves gained for each period).

To estimate the light availability of the habitat for seedlings, hemispherical photographs were taken at 1 m above the center of all subplots using a Nikon fisheye converter (FC-E8) mounted on a digital camera (Nikon Cool Pix 950, Nikon, Tokyo, Japan). We used Hemiview ver. 2.1 (Delta-T Devices Ltd., Cambridge, UK) software to determine the extent of the visible sky as a measure of canopy openness, i.e., the overall proportion of the sky hemisphere that is visible (Delta-T Devices 1999). The other indices of light availability (e.g., proportions of diffuse, direct, and global solar radiation reaching a given location) for each seedling displayed the same trend. The results at the nearest measurement point were used to estimate light availability to each seedling.

Leaf damage caused by herbivores and pathogens was visually estimated as proportion of the leaf damaged (Numata et al. 2004). Damage to individual leaves was assigned to one of four categories: no damage (<5%), light damage (5–30%), moderate damage (30–50%), heavy damage (>50%), and dead. Seedling level damage was calculated as the average of damage scored (for multiple leaves): no damage (0), light damage (22.5), moderate damage (37.5), heavy damage (75).

Statistical analysis

All statistical analyses were conducted using R v3.1.2 statistical software (R Foundation for Statistical Computing 2014). The survivorship of seedling was calculated for each adult tree. We compared the seedling survivorship among the classes of distance from adult tree (0–3, 3–6, 6–9, 9–12 and 12–15 m), and among the initial density classes (low, moderate and high) by one-way analysis of variance (ANOVA). To examine the density- and distance dependencies of seedlings, we used a generalized linear mixed model (GLMM); this was the lme4 package running the Laplace method in R (Bates et al. 2015). The density- and distance dependencies of the RGR in height, leaf production, leaf loss, and net leaf gain were examined using GLMMs with a Poisson error structure (leaf production and leaf loss); Gaussian error structure (RGR in height and net leaf gain); and a binomial error structure (leaf damage level) using the offset option of the survey interval (60–94 days). The fixed effects of initial density, distance from a conspecific adult, and canopy openness on leaf damage were also examined

using GLMMs. For these modules, we used seedling ID number and adult tree ID as the random effect. The level of significance was assessed by the Wald test.

Results

Distribution of seedlings and saplings around conspecific adults

The peak of the sapling cohort distribution around adult trees was at 6–9 m from the tree, whereas for the 2-year-old seedling cohort, it was at 3–6 m away (Fig. 1). The distance from conspecific adult tree was significantly greater for the saplings (mean = 9.7 m) than seedlings (mean = 5.1 m) (ANOVA: $F = 146.6$, $p < 0.0001$). The density of the saplings and seedlings showed ranges of 0.007–0.054 and 1.139–7.722 m^{-2}, respectively.

A total of 616 seedlings were monitored for the study (Fig. 2). The survival of the seedlings per adult tree from December 1998 to December 1999 ranged from 0.58 ± 0.02 (9–12 m; $n = 3$) to 0.75 (0–3 m; $n = 2$) by the distance classes, but there was no significant difference in survival of the seedlings among the distance classes (ANOVA, $F = 0.65$, $p = 0.64$). The average survival ranged from 0.55 ± 0.18 (low density) to 0.64 ± 0.16 (medium density) by the distance classes, but there was no significant
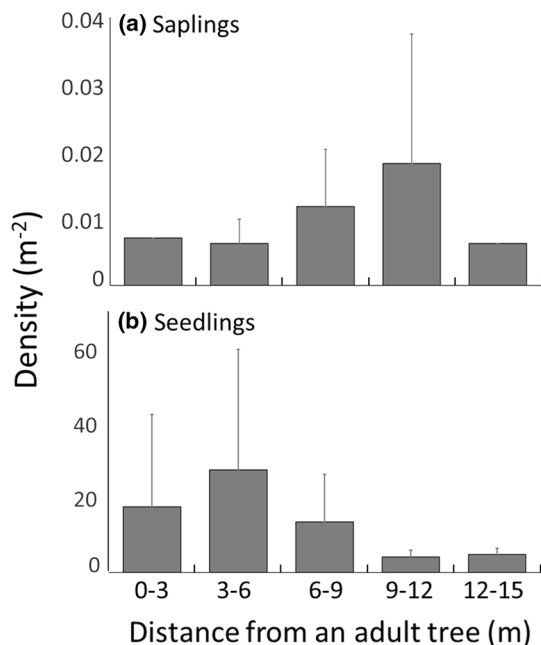
Fig. 1 Densities of (**a**) seedlings and (**b**) saplings in relation to distance from adult tree. Seedlings were measured in 1998; saplings were measured in February and July 1999 under three adults and presumed to be >10 years old because they were present in the plots when established in 1986. *Bars* are means + SD; $N = 3$ for all
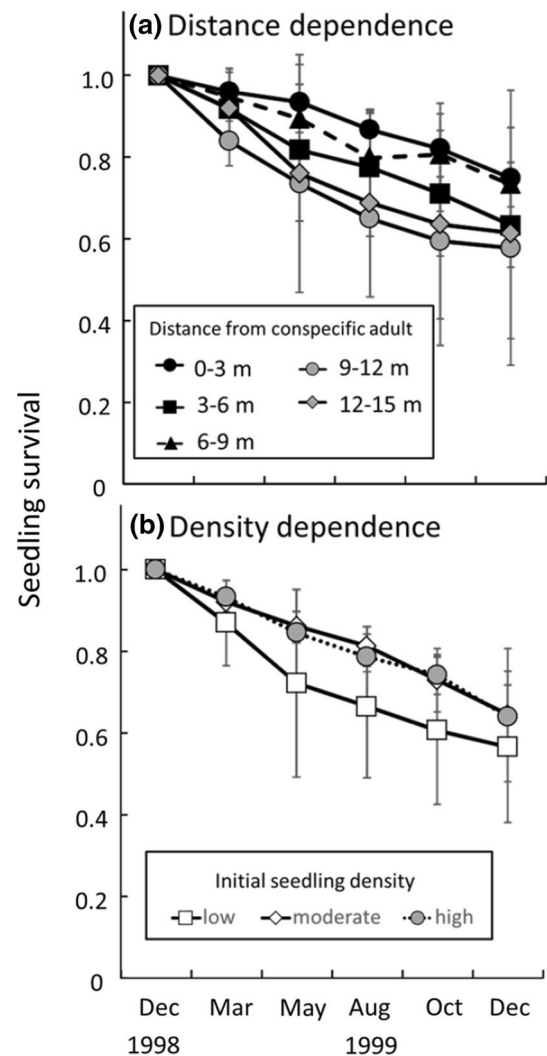
Fig. 2 Seedling survival (mean + SD, $n = 616$) of *Shorea macroptera* at **a** five distance classes and **b** three different initial seedling density classes

difference in survival of the seedlings among the distance classes (ANOVA, $F = 0.17$, $p = 0.85$).

Distance and density dependence in seedling growth

Overall averages of leaf production, leaf loss and net leaf gain of the seedlings were 0.101, 0.085, and 0.012 months^{-1}, respectively. The GLMM results suggested significant effects of distance and density on the leaf dynamics of the seedlings, but not on the RGR in height (Fig. 3; Table 1). The RGR in height of the seedlings was very low, and no significant effects of density or distance from adult trees were found in this study. Negative distance and density effects were evident in terms of leaf loss. Net leaf gain was significantly positively influenced by the distance from the adult tree.
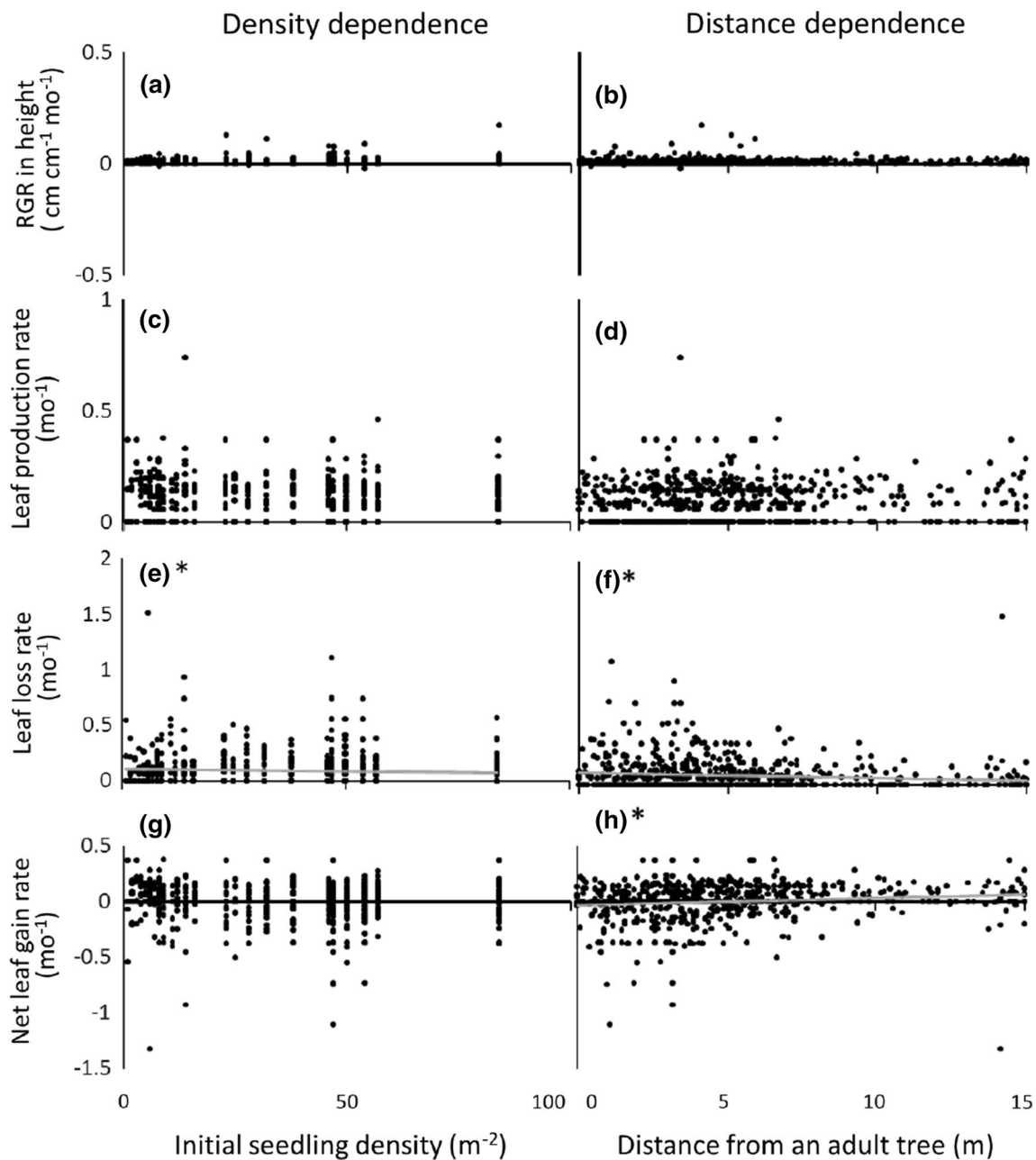
Fig. 3 Density-(**a**, **c**, **e**, and **g**) and distance-(**b**, **d**, **f**, and **h**) depend-ence in height growth rate and three leaf demographic parameters for *S. macroptera* seedlings. Relative growth rate was measured in terms of changes in height; leaf production rate as number of new leaves produced per month/individual; leaf loss rate as number of leaves lost per month/individual; and net leaf gain rate as net number of leaves gained per month/individual. The *asterisks* indicate statistically sig-nificant differences in density or distance dependence. *Regression lines* shown for significant density- and distance dependencies

Factors affecting the foliar condition of seedlings

Canopy openness around the adult trees was generally low, and there was no significant relationship between the dis-tance classes ($r = -0.12$, $p = 0.30$). No significant effect of canopy openness was evident in terms of height growth or leaf dynamics (Table 1).

Approximately 42% of leaves at the first observation were less than 5% damaged, and approximately 10% of leaves were damaged by more than 50% at the first obser-vation in all distance classes. There was no effect distance, density or canopy openness on leaf damage (Fisher's Exact Test: $p = 0.28$). GLMM analysis also indicated that the

Table 1 Results of generalized linear mixed models (GLMMs) examining the Poisson error structure (for leaf production and leaf loss) and the Gaussian error structure (for relative growth rate [RGR] in height and net leaf gain)

	RGR in height	Leaf production	Leaf loss	Net leaf gain
Intercept	<0.001	−5.60	−5.05	−4.45
Distance from an adult tree	<0.001	>−0.001	**>−0.001**	**<0.001**
Initial seedling density	>−0.001	−0.004	**−0.008**	<0.001
Canopy openness	<0.001	1.03	−5.11	1.04

Coefficients of intercepts and fixed effects are shown. Significant density- and/or distance dependencies of the leaf dynamics are shown in bold

leaf damage levels of seedlings were not significantly affected by distance, density, or canopy openness.

Discussion

We found that the peak of the distribution of plants shifted from 3–6 m to 6–9 m during the course of the change from seedling to sapling stage (Fig. 1). *Shorea macroptera* seedling survival from germination to 1 year later was approximately 20%, and the number of seedling surviving was highest at a distance 4 m from the parent tree (Miyamoto 1988). The radius of the crown of the focal adult trees was about 6 m (Numata personal observation). Therefore, it would be expected that the peak progeny distribution would change from beneath the parent tree to more outer areas during the course of tree regeneration. The change in the peaks of spatial distribution as plants grew from seedlings to saplings was evidence of distance dependence in the seedling establishment of the study species.

Although many studies showed distance- and density-dependent mortality of seedlings (e.g., Comita et al. 2014), significant distance- and density dependence in seedling survival was not found in this study. The primary reason may be due to short-term observation of seedlings in this study. During the observation, some of the seedlings were removed by wild pigs and pigtail macaques irrespective of the performance of seedlings. These attacks seemed to be concentrated on several seedlings with marked color tags. In this situation, such accidental disturbance could obscure distance- and density dependences even if density- and distance-dependent survival occurred.

Distance and density dependences in leaf dynamics

Both distance dependence and density dependence in the leaf demography of seedlings were found, and these were negative distance and negative density dependence in leaf loss. Leaf loss was a primary element in distance dependence in terms of seedling leaf demography. Consequently,

positive distance dependence in net leaf gain was observed as the result of the distance- and density-dependencies of leaf loss. However, the initial seedling density significantly negatively affected leaf loss, and this result is clearly inconsistent with prediction of J–C hypothesis. In addition, the density dependence of leaf production was not statistically significant since the negative density dependence of leaf production might occur due to competition with conspecific seedlings and/or due to pathogens (e.g., Tilman 1997; Watkinson 1997). This may be because the initial seedling density was not high when the present study began. In the present study, negative distance dependence in net leaf gain was not found. Therefore, the negative density dependence of leaf loss may not be strong enough to cause density-dependent leaf demography.

Herbivore damage causes the premature loss of leaves in juvenile trees (Blundell and Peart 2000). We found negative distance dependence in leaf loss, but the proportion of healthy leaves (non-damaged leaves) did not differ between the distance classes. Damaged leaves often shed more rapidly than undamaged ones, and the rate of abscission, therefore, increases as the damaged leaf area increases (Núñez-Farfán and Dirzo 1989; Pritchard and James 1984; Risley 1993). Thus, leaf damage by specific herbivores or pathogen infection likely did not account for the negative distance dependence in the leaf loss of seedlings.

Thus, we found no evidence of distance-dependent leaf damage caused by herbivores and/or pathogens. For small-sized seedlings, physical damage such as litterfall from the canopy may be one factor affecting the distance dependence of leaf loss of seedlings. Large emergent dipterocarps in Borneo are known to produce greater amounts of leaf litter than the rest of the tree community (Burghouts et al. 1994). Clark and Clark (1989, 1991) showed that 75–90% of seedlings were knocked over, flattened, or otherwise seriously damaged by litterfall during a single year. The average height of 2-year-old seedlings under a closed canopy was reported to be 13.8 cm (Numata 2001). Thus, litterfall may be involved in the distance dependence of our study species.

Concluding remarks and recommendations for further study

We confirmed that the distribution peak shifted from the seedling to the saplings stage. Our results also suggest positive distance dependence in the leaf dynamics of seedlings, including negative distance dependence in leaf loss. Therefore, we conclude that positive distance dependence in the leaf dynamics of seedlings may contribute to a shift in the distribution pattern of progeny through reduction in growth and survivorship. Our findings may answer why many studies fail to detect significant distance dependence in seedling performance; although significant positive distance dependence in seedling growth was identified, the growth may have been too small to detect. However, the mechanisms underlying the observed distance- and density dependencies remain unclear. Further research on factors affecting leaf production and leaf loss is needed to explore these mechanisms.

Author contribution statement SN and NK conceived and designed the experiments. SN conducted the measurements, and analyzed the data. SN wrote the manuscript, other authors provided editorial advice.

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