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Distance-dependence in herbivory and foliar condition for juvenile *Shorea* trees in Bornean dipterocarp rain forest

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Abstract We assessed density- and distance-dependence in herbivore effects and juvenile condition for four species of *Shorea*, the most speciose genus in the dominant canopy family of southeast Asian rain forest trees (Dipterocarpaceae). Herbivore damage was quantified as partial leaf loss on young leaves, and whole plant foliar condition as the product of the fraction of leaf nodes containing leaves and the fraction of tissue remaining on extant leaves. Adults of the four species were centers of high total, as well as conspecific, density of juveniles (< 1 m tall). For two species, *S. hopeifolia* and *S. pinanga*, herbivore damage declined significantly with distance, decreasing by 40% and 51% respectively, between 5 m and 35 m from the parent. For the same two species, foliar condition improved significantly between 5 m and 35 m, increasing by 45% for *S. hopeifolia* and 24% for *S. pinanga*. If foliar condition influences juvenile survival and growth, more widely dispersed seeds of these species are more likely to recruit to the canopy. In contrast, there was no significant distance-dependence for *S. parvifolia* or *S. longisperma*. Among species, herbivore damage was greatest in those species with greatest local juvenile abundances, i.e., those with highest densities, leaf size, juvenile foliar mass and/ or foliar mass/m² ground area, but was unrelated to the toughness of mature leaves. However, distance was a better predictor of herbivore damage than was conspecific juvenile density, as evaluated by backward elimination regressions, for both *S. hopeifolia* and *S. pinanga*. For foliar condition, the best predictor was distance for *S. pinanga*, but conspecific density for *S. hopeifolia*, whose juveniles were smallest and occurred at the highest densities. Total juvenile density (all woody plants) was eliminated as a factor in all cases. The species-specificity of effects (i.e., their dependence on conspecific distance or density),

together with the marked differences among congeneric species, caution against generalizations regarding distance-dependent effects in diverse forests.

Key words Density dependence · Seedlings · Dipterocarpaceae · Foliar condition

Introduction

Density- and distance-dependent processes have been a major focus in ecological research on the seed and seedling stages of forest trees. This is because most seeds fall near parent trees, producing clumped distributions that may generate a number of density- or distance-dependent ecological processes. These processes can influence the performance and survival of progeny, and thus the distribution patterns of seeds, juveniles and adults (i.e., the spatial structure) of tree populations. For example, if the mortality (of either seeds or juvenile plants), or the growth (of juvenile plants), depends on distance from the parent, then the likelihood that individual progeny will recruit to the canopy will also be distance dependent.

Furthermore, in a community such as the tropical rain forest, seedlings of each species occur in a spatially complex understory community that is generated by the overlapping seed shadows of many co-occurring species. In this context, distance- or density-dependent factors affecting juveniles have been invoked as mechanisms promoting tree species coexistence.

Spacing of conspecific adults is not, by itself, sufficient to maintain the observed diversity of rain forest trees (Hubbell 1979, 1980). However, reducing the number of potential canopy recruits near conspecific adults (effective distance dependence) can, by increasing the spacing of conspecific trees, decrease the likelihood that common species will completely dominate the community (Janzen 1970; Connell 1971). Effective distance dependence can occur whether mechanisms re-

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spond directly to either distance or density, because of the generally strong correlation between distance from parent and progeny density. Similarly, effective density dependence at the seedling stage (measured as the effects of seedling density on progeny survival) can occur even if the underlying mechanisms respond to distance from parent, providing conspecific seed shadows overlap.

The original model of Janzen (1970) and Connell (1971) hypothesized negative density dependence (reduced performance of progeny at high densities) and/or positive distance dependence (better performance of progeny at greater distance from the parent). Clark and Clark (1984), in a review of 24 data sets on seeds or seedlings of tropical woody species, found that “most evidence indicates either density-dependence or distance-dependence in progeny mortality” (referring to trends in the directions predicted by Janzen and Connell). Density- or distance-dependent trends, also in the predicted directions, have since been reported by Becker and Wong (1985), Howe et al. (1985), Kjellson (1991), Howe (1993), Peres et al. (1997), Akashi et al. (1997), Fragoso (1997), Yamada and Suzuki (1997), and Cintra (1997). However, others have reported opposite trends, i.e., an improvement in the performance of progeny at high densities or nearer adults (Sarukhan 1978; Boucher 1981; De Steven and Putz 1984; Nilsson 1985; Sork 1987; Schupp 1988, 1992; Augspurger and Kitajima 1992; Howe 1993; Terborgh et al. 1993; Burkey 1994). Multi-species studies have found density- or distance-dependent trends in half or fewer of the species examined (Connell et al. 1984; Hubbell et al. 1990; Forget 1991; Condit et al. 1992, 1994; Terborgh et al. 1993). In summary, since the review of Clark and Clark (1984), recent work has produced mixed results. Distance- and/or density-dependent effects are clearly important, but the direction of effects may differ among tree species, and among the agents responsible for the effects on the progeny.

Janzen (1970) and Connell (1971) suggested that natural enemies were the most likely agents to respond to distance and/or density. Indeed, both pathogens (Augspurger 1983a,b, 1984; Augspurger and Kelly 1985; Gilbert et al. 1994) and seed predators (e.g., Forget 1991; Cintra 1997; Fragoso 1997; Peres et al. 1997) have been shown to respond to both distance and density. Yet, the response of seed predators has often been inverse-density dependent, favoring seed survival in areas of high density under parent crowns (Sarukhan 1978; Boucher 1981; De Steven and Putz 1984; Nilsson 1985; Sork 1987; Schupp 1988, 1992; Augspurger and Kitajima 1992; Howe 1993; Terborgh et al. 1993; Burkey 1994). Satiation of seed predators can allow seeds at high density to escape predation (Janzen 1974, 1976). In such cases, the potential for distance- and density-dependent mechanisms promoting coexistence shifts to the vegetative stage, i.e., to juvenile plants (Clark and Clark 1984). Recent analyses on juveniles of the most common species at Barro Colorado Island, Panama,

indicated negative effects of conspecific density on recruitment for 67 out of the 84 species examined (Wills et al. 1997).

However, surprisingly few studies have investigated the effects of herbivores on juveniles, even though Connell (1971) originally hypothesized that herbivores could be responsible for altering spatial patterns of recruitment. Janzen (1971), Denslow (1980) and Clark and Clark (1985) examined apical meristem damage and all found a decrease in damage with distance for woody seedlings. Augspurger and Kitajima (1992) found density dependence in mortality of tree seedlings due to mammalian herbivores, but not distance dependence. While these results suggest that distance- or density-dependent herbivory around parent trees might be common, inferences about the density or distance dependence of herbivore effects remain limited by data from just four single-species studies, based on seedlings around only 1–2 focal trees, and all in the Neotropics.

Furthermore, the “background” seedling community, i.e., the heterospecific seedlings that co-occur with the focal species, has been largely ignored. Yet it is plausible that herbivore damage to any species might depend on total juvenile density (heterospecific plus conspecific), rather than conspecific density alone. Thus, some potentially important questions remain unanswered. Are the juvenile shadows around parent trees superimposed on a more or less constant background community of juveniles? If so, then the total density of juveniles would vary in concert with conspecific (focal species) juvenile density, resulting in patches of high total density on the scale of individual tree crowns. In this case, density or distance dependence in juvenile performance could be due to processes responding to either total or conspecific juvenile densities. Alternatively, is total juvenile density more or less constant, with respect to distance from parent trees? If so, then heterospecific juvenile densities would be inversely related to the density of conspecifics, and conspecific density would not covary with total density.

In this paper, we examine herbivore effects on four species of *Shorea*, the most species-rich genus in the Dipterocarpaceae. This family dominates the canopy and provides almost all the timber harvested from large areas of southeast Asian rain forest. We chose four species from a single genus that cover a range of life history attributes (Table 1); the species differed in seed size, juvenile height, leaf size, the total amount of leaf tissue (biomass) per plant, and leaf toughness. Leaf toughness is an index of lignin content, a feeding deterrent (Coley 1983). We examine both conspecific and total juvenile densities, and assess herbivore damage and a leaf-based index of seedling condition, all as a function of distance from replicated parent trees.

Specifically, we address the following research questions:

- (i) How do conspecific and total juvenile density vary with respect to distance from parent tree?

- (ii) Does herbivore damage vary systematically with respect to distance from parent, or the conspecific or total density of juveniles?
- (iii) Is herbivore damage related to the species attributes that differ among the four congeners?

Materials and methods

Study site and species

Field research was conducted in lowland old-growth dipterocarp rain forest on sandstone-derived soils at the Cabang Panti Research Station, at the western end of the 900 km² Gunung Palung National Park (1.13°S, 110.7°E), in West Kalimantan, Indonesia, on the island of Borneo. Mean annual rainfall is 4.5 m, evenly

distributed throughout the year, except for a few weeks of lower rainfall, in July or August.

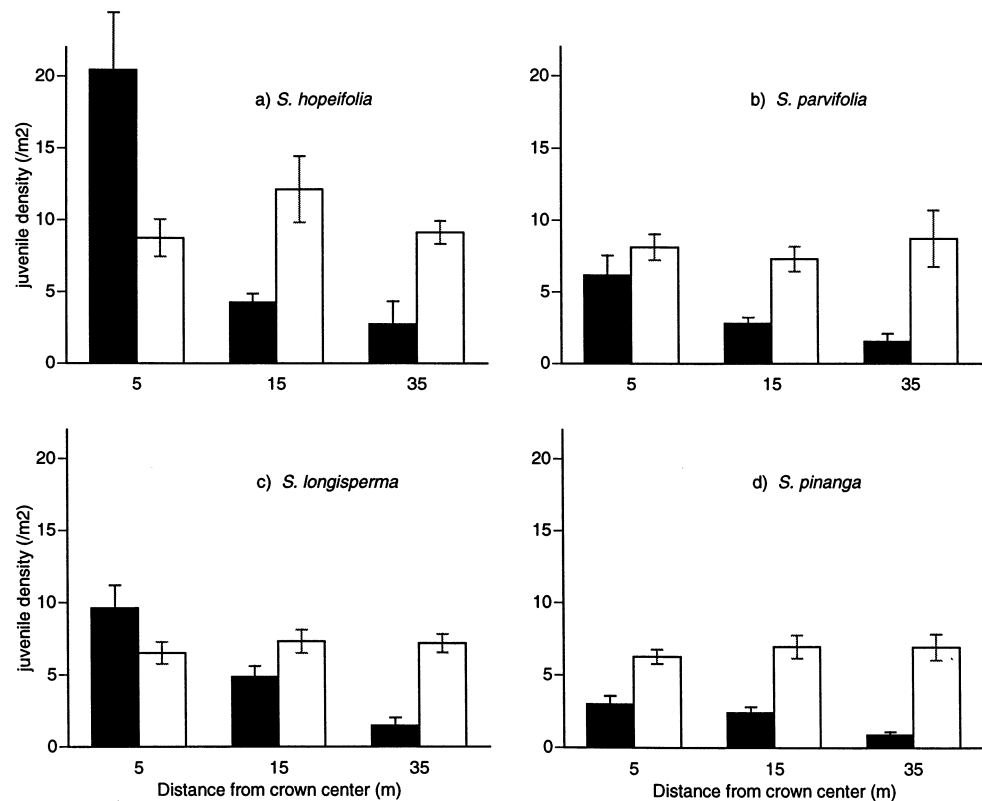
Dipterocarps comprise more than 80% of stems > 30 cm diameter at 1.37 m (dbh) at the study site (M. Leighton, unpublished data, C.O. Webb, unpublished data). Dipterocarp trees are wind dispersed, with the highest concentrations of seeds falling below the crown (Appanah and Rasol 1995). They have no seed bank and fruit only in community-wide synchronous “masts”, once every 3–5 years (Ashton 1989). Of the four *Shorea* species in this study, *S. pinanga* is least abundant at the adult stage, producing the largest seeds and the lowest densities of relatively large seedlings near adults. At the other extreme, *S. hopeifolia* is the most abundant at the adult stage, producing the smallest seeds and the highest densities of relatively small seedlings near adults (Table 1, Fig. 1). While all four species have a clumped spatial pattern as adults, *S. longisperma* adults are the most aggregated (Table 1); they tend to occur in stands near rivers (A. Blundell, personal observation). The seedling layer (up to 1 m tall) is dominated by seedlings of trees and lianas. Lianas grow vertically when young

Table 1 Characteristics of four *Shorea* species in lowland dipterocarp rain forest in Gunung Palung National Park, West Kalimantan, Indonesia. Adult density and spatial pattern are for trees > 30 cm dbh in 11.5 ha ($n = 45$ plots). The same plots were used to calculate Standardized Morisita's Index of Spatial Dispersion (Krebs 1989); values > |0.5| imply non-random spatial pattern ($P = 0.05$); -1 is uniform and 1 represents maximum ag-

gregation. See Materials and methods for details of focal trees; isolated trees are those without conspecifics > 50 cm dbh within 50 m. Leaf toughness, an index of leaf palatability, was measured as the loading necessary to penetrate the tissue of mature leaves ($n = 40$ leaves per species). Seed and adult data from L. Curran and M. Leighton (unpublished data)

Species	Adult density no./ha mean (SE)	Morisita's index of spatial pattern	No. of potential focal trees > 75 cm DBH (no. isolated)	Seed mass g	Juvenile height mean (SE; n) cm	Leaf toughness mean (SE) g
<i>S. hopeifolia</i> (Heim) Sym.	3.5 (4.3)	0.50	28 (9)	0.8	20.5 (0.58; 265)	194 (4)
<i>S. parvifolia</i> King	2.6 (4.1)	0.51	16 (7)	0.4	26.8 (0.69; 262)	268 (7)
<i>S. longisperma</i> Roxb.	0.48 (2.0)	0.64	11 (3)	2.0	29.1 (0.54; 286)	337 (9)
<i>S. pinanga</i> Scheff	1.8 (3.5)	0.51	11 (6)	9.9	49.7 (0.90; 285)	462 (18)

Fig. 1a–d Relationship between the density of juveniles (< 1 m tall; means \pm 1 SE) and distance from adults of four *Shorea* species in lowland dipterocarp rain forest in Gunung Palung National Park, West Kalimantan, Indonesia. For all four species, conspecific juvenile density (solid bars) decreased significantly with distance from parent's crown center (linear regression with log transformation; $P < 0.0001$ for all species). (a) *S. hopeifolia* $r^2 = 0.45$, $n = 60$ plots; (b) *S. parvifolia* $r^2 = 0.29$, $n = 60$; (c) *S. longisperma* $r^2 = 0.51$, $n = 60$; (d) *S. pinanga* $r^2 = 0.24$, $n = 72$. There was no relationship between the density of juveniles of other species (heterospecifics; open bars) and distance from focal adults (linear regression; $r^2 < 0.0010$, $P > 0.51$)



and can be distinguished from tree seedlings only by identification at the species level. Herbaceous plants and palms are very uncommon at this study site.

Overall sampling design

For each species, we measured the conspecific and heterospecific densities of juveniles (plants ≤ 1 m tall) in plots at 5, 15, and 35 m from the crown centers of isolated adult trees. At each distance, the condition of each juvenile plant in a random sample was measured as the overall proportion of leaf tissue retained, and herbivore damage on the youngest two extant leaves quantified as the percentage of leaf tissue loss attributable to herbivores. These data were analyzed to determine if juvenile condition and herbivore damage varied with distance from parent, or with conspecific or total juvenile density.

Selection of focal adults

The adult trees in the sample in Table 1 provided a list of prospective "focal" adults that were: (i) >75 cm dbh, to ensure a sufficient history of reproductive maturity to produce a substantial number of juveniles nearby, and (ii) isolated from reproductive conspecific adults, where possible. The latter was accomplished by reference to mapped populations of dipterocarps established at the site for another study (L. Curran and M. Leighton, unpublished data), so that focal trees had no conspecific neighbors >30 cm dbh within 50 m. We chose relatively isolated trees to reduce the influence of overlapping conspecific "seedling shadows" and to simplify interpretations of distance-dependent trends. From the acceptable lists, we randomly chose six adults of *S. pinanga* and five of each of the other three species. In the field, we then verified the absence of conspecific neighbors >50 cm dbh (the minimum observed size at reproduction; Curran and Leighton, unpublished data). An additional replicate tree of *S. pinanga* was included because of the low density of juveniles of this species (Fig. 1d). The only exception to the above criteria was *S. longisperma*, for which there were only three trees in the entire sample (see Table 1) that had no conspecific adults within 50 m, due to the species' very clumped dispersion pattern. Around the other two *S. longisperma* focals (in our sample of five), four juvenile plots were closer to another conspecific adult (>50 cm dbh) than to the focal tree. For these plots, the distance to the nearest conspecific adult was used as the independent variable.

Juvenile plots

For each focal adult, the longest dimension of the crown was first located and measured. Then, the crown center was defined as the intersection of this line with the widest perpendicular measurement, and projected onto the forest floor. The area around the crown center was divided into four equal (90°) sectors. Within each sector, we established a transect from the crown center along a random azimuth, and along each transect we sampled a 4 m^2 circular plot at distances 5 m, 15 m, and 35 m from the focal tree. If a plot location fell in a gap, on a large rock, or on a fallen bole, it was moved in 1 m increments along the transect to the nearest location free of these features. Because only 10% of the plots were thus moved, the farthest by 5 m (a 15 m plot moved to 20 m), data are presented in the original distance classes in Figs. 1 and 2, for simplicity. Actual distances were used in statistical analyses.

In each plot we measured the juvenile density of both the focal species and heterospecifics (all other non-palm woody species combined, including lianas that had not yet developed the climbing habit). As noted above, these species comprised almost all individuals and foliar biomass in the seedling layer; thus almost all individual plants were enumerated either as conspecifics or heterospecifics. We then selected the five conspecific juveniles nearest the plot center; if less than five juveniles were found, the plot was

expanded until five juveniles were encountered or a maximum plot size of 10 m^2 was reached.

Foliar status

For the five juveniles chosen in each plot, we measured height to the apical meristem and recorded the presence or absence of a leaf at each node, proceeding from the uppermost node (rank one) to the lowest and oldest node (maximum rank). For each node with a leaf present, we estimated the percentage of the leaf that was missing and attributable to herbivory (see below). The percentage of retained leaves was calculated as the number of retained leaves divided by the total number of nodes. In this paper juvenile "foliar condition" has two components: (i) the estimated fraction of tissue retained on extant leaves (partial leaf retention), averaged over all leaves on a plant, and (ii) the fraction of leaves retained on a plant (whole leaf retention). The product of these two components yielded the overall fraction of maximum leaf tissue retained, which we used as a whole plant measure of foliar status.

In analyses of juvenile condition as a function of distance or density, we used means over the five juveniles in each plot, because individuals could not be assumed independent within plots. Leaf retention percentages were arcsine-transformed, and juvenile density \ln -transformed, in order to meet assumptions of normality. To evaluate trends in herbivore damage and juvenile condition with distance, we tested each species separately using full and reduced regression models. In the full models, we tested the differences among conspecific focals in their relationship between condition (or herbivore damage) and distance (or density). Because the slopes of these relationships were not significantly different, we pooled the data for focal trees within each species, and tested the distance- (or density-) relationships in a simple linear regression (reduced) model, for the analyses reported in the Results.

Partial leaf loss; estimating herbivore damage

Although measures of herbivore damage at a single time cannot be used to estimate cumulative loss due to herbivores (Coley 1982; Lowman 1984; Phillip et al. 1995), they can be useful indices for comparing damage among plants and among species. Furthermore, we suggest that, in combination with measures of leaf retention (see above), estimates of partial leaf loss are more appropriate than estimates of total tissue loss (i.e., from longitudinal studies) for assessing the current foliar condition of plants.

Interspecific comparisons of herbivore damage using old leaves are complicated, because species differences might be expected in two confounding factors: leaf retention rates (in the absence of herbivory) and premature abscission of leaves partially damaged by herbivores (Bongers and Pompa 1990; Addicott 1991; Blundell and Peart, unpublished data). In addition, for most tropical plants examined, the youngest, fully expanded leaves have already experienced most of the loss to herbivores that will occur during their lifetimes ($>70\%$; Clark et al. 1992; Coley and Barone 1996). For these reasons, we used partial leaf loss on the youngest leaves to compare standing levels of herbivore damage among species.

We quantified partial leaf loss by visually estimating the percentage of foliar tissue lost from extant leaves (Kiew 1982). For consistency, all estimates were made by one of us (A.G.B.). We used percentage loss, rather than absolute area because percentages facilitate comparison among leaves of different sizes and species (Lowman 1992). All tissue that was clearly consumed (e.g., holes or removed drip tips), together with galls, mines, and non-fungal necrotic areas, was included in the category of herbivory (Coley 1983). Necrotic areas could result from chronic photoinhibition and/or lethal leaf temperature (Turner and Newton 1990), as well as the effects of herbivores that scrape leaf tissue. However, this type of damage was minor, i.e. $<5\%$ of all herbivory damage observed. Despite the occurrence of a diverse and apparently intact herbivore fauna at the study site (Blundell 1996), almost all partial

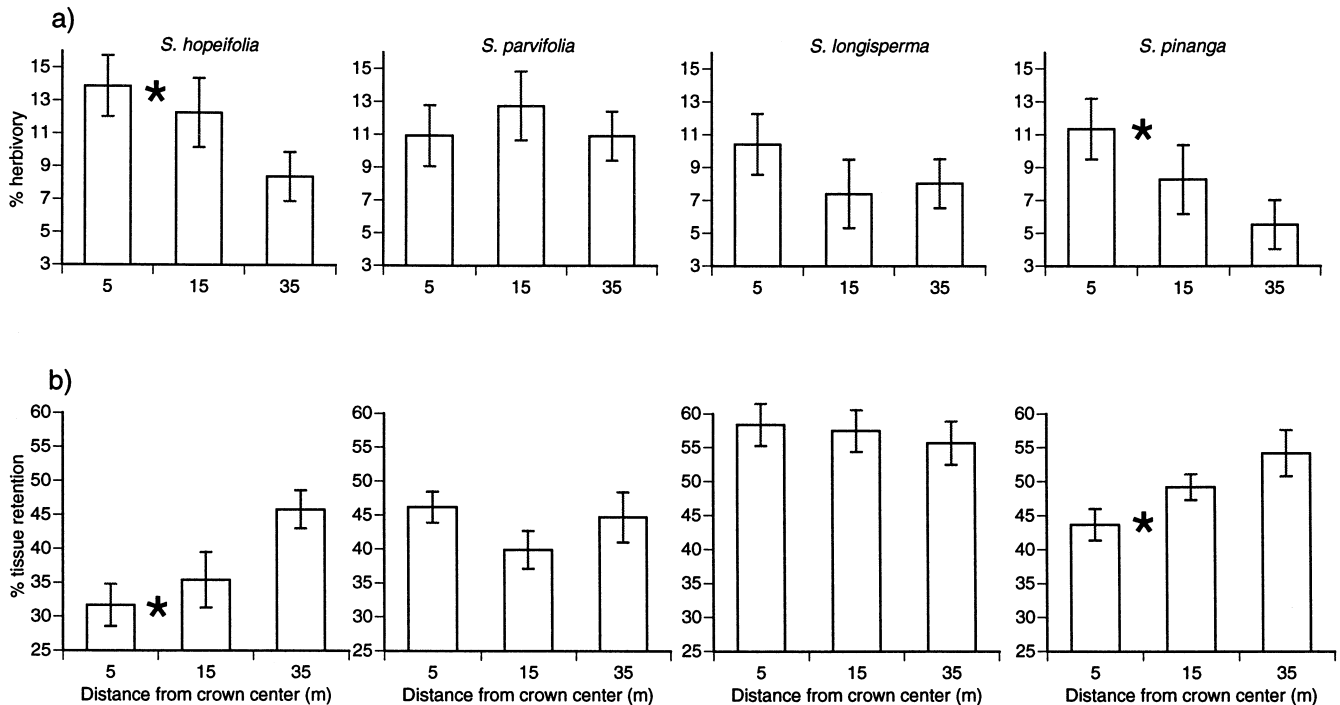


Fig. 2a,b Relationship between juvenile condition (means \pm 1 SE) and distance from adults of four *Shorea* species in lowland dipterocarp rain forest in Gunung Palung National Park, West Kalimantan, Indonesia. **(a)** Herbivore damage (percent partial leaf loss on youngest two leaves) on conspecific juveniles. There was a significant decline in herbivory with distance for *S. hopeifolia* ($r^2 = 0.070$, $n = 55$ plots, $P = 0.050$) and *S. pinanga* ($r^2 = 0.18$, $n = 62$, $P = 0.0006$), but not *S. parvifolia* ($r^2 = 0.020$, $n = 56$, $P = 0.32$) or *S. longisperma* ($r^2 = 0.014$, $n = 58$, $P = 0.38$). **(b)** Overall foliar condition, measured as the total percent tissue retention over whole plants (the product of partial leaf retention and whole leaf retention), increased significantly with distance for *S. hopeifolia* ($r^2 = 0.12$, $n = 55$, $P = 0.012$) and *S. pinanga* ($r^2 = 0.12$, $n = 62$, $P = 0.0064$), but not *S. parvifolia* ($r^2 = 0.003$, $n = 56$, $P = 0.69$) or *S. longisperma* ($r^2 = 0.0046$, $n = 58$, $P = 0.61$). Asterisks indicate significant relationships

indices were calculated. First, the mean percent tissue lost from the youngest two leaves (the two extant leaves of lowest rank), was used an index of herbivore damage, as described above. The second index was the mean percent tissue retention over all nodes, which was used as a measure of foliar condition.

Leaf toughness

For each of the four species, we measured an index of toughness on 40 mature leaves collected from juveniles on a 35 m transect from a randomly chosen conspecific focal adult. For each leaf, we used a "penetrometer" (Chatillon, N.Y. Gauge-R, Catl. 516-500; 3 mm diam.) and recorded the average of two measurements of the loading necessary to penetrate the leaf tissue.

Leaf and juvenile biomass

To determine whether foliar biomass (of individual leaves or whole plants) was associated with herbivore damage, we estimated leaf and individual plant biomass for each species. For each species, we collected 200 mature leaves (2 from each of 20 juveniles, randomly chosen within 35 m of each of five focal trees). We dried the leaves at 70°C for 5 days and weighed them in bundles of 50, to obtain mean leaf biomass. The total leaf biomass for each individual was estimated as its number of leaves times the mean leaf mass for that species.

Results

Density of juveniles around adults

Conspecific juvenile density declined strongly with distance from parent, (linear regression with ln-transformation, $P < 0.0001$ for all four species; *S. hopeifolia* $r^2 = 0.45$, $n = 60$ plots; *S. parvifolia* $r^2 = 0.29$,

tissue loss was apparently caused by insects. For each of the four *Shorea* species, <2% of juveniles showed evidence of chewed petioles or leaf damage consistent with vertebrate chewing.

To control accuracy, estimates of partial leaf loss were first calibrated outside the study plots, on the same species of dipterocarps, as follows. After recording visual estimates of herbivory for a leaf, the outline of the whole leaf (reconstructed based on the remaining tissue where margins were damaged) was traced to a transparent medium and the resulting leaf area measured using graph paper. A similar procedure was followed to obtain the leaf area remaining after herbivory, and the percentage of tissue lost on that leaf was then calculated. Visual estimates were practiced until estimated percentage loss was consistently within a range of $\pm 2\%$ of measured levels when the partial leaf loss was less than 20%, and within $\pm 5\%$ when more than 20% of the leaf was missing. Finally, within the study plots, a random sample of 5% of the leaves that had been assessed around each focal tree was collected. From these, 65 leaves were chosen randomly and measured as described above; these checks confirmed that accuracy in the actual field samples was within the ranges specified above. In a linear regression of estimated versus actual damage in the study plots, the r^2 value was 0.90 ($n = 65$; $P < 0.0001$).

We estimated partial leaf loss for all individual leaves on each of the five seedlings examined in each plot. From these data, two

$n = 60$; *S. longisperma* $r^2 = 0.51$, $n = 60$; *S. pinanga* $r^2 = 0.24$, $n = 72$; Fig. 1). The highest densities of juveniles measured for the focal species (at 5 m distance) ranged from approximately 20/m² for *S. hopeifolia* to 3/m² for *S. pinanga*. In contrast, the juvenile density of all other species combined did not vary significantly with distance from focal *Shorea* trees (heterospecific mean = 8/m²; linear regression with ln-transformation, $P > 0.51$, $r^2 < 0.0010$ for all four species; Fig. 1).

Herbivore damage on young leaves

Herbivore damage on the youngest two extant leaves declined significantly with distance from parent for two species, *S. hopeifolia* and *S. pinanga*, but not for *S. parvifolia* or *S. longisperma* (linear regression with arcsine-transformation; Fig. 2a). Tissue loss due to herbivory on young leaves was higher near the parent (at 5 m) than far away (at 35 m) by a factor of 1.7 for *S. hopeifolia* and 2.1 for *S. pinanga*. Mean partial leaf loss on young leaves (over species and distances) ranged from approximately 5–14%.

Juvenile foliar condition

For percent tissue retention on extant leaves, averaged over entire plants, there was no consistent trend with distance for any species ($r^2 < 0.08$; $P > 0.07$). Mean-tissue retention on all extant leaves ranged from approximately 83–91% for the four species and three distances measured.

The percentage of nodes with retained leaves increased significantly with distance for *S. hopeifolia* (linear regression with arcsine-transformation, $r^2 = 0.14$, $n = 55$ plots, $P = 0.006$) and *S. pinanga* ($r^2 = 0.063$, $n = 62$, $P = 0.045$) but not for *S. parvifolia* ($r^2 = 0.0003$, $n = 56$, $P = 0.88$) or *S. longisperma* ($r^2 = 0.022$, $n = 58$, $P = 0.27$). The proportional increase in whole leaf retention from near the parent (5 m) to far (35 m) was 33% for *S. hopeifolia* and 15% for *S. pinanga*.

Overall foliar condition, measured as the total percent tissue retention over whole plants (the product of partial leaf retention and whole leaf retention), increased significantly with distance for *S. hopeifolia* and *S. pinanga* but not for *S. parvifolia* or *S. longisperma* (linear regression with arcsine-transformation; Fig. 2b). Overall percent tissue retention at 35 m was 45% higher than at 5 m for *S. hopeifolia* and 24% higher for *S. pinanga*.

Leaf and juvenile biomass; leaf toughness

The mass of individual leaves differed significantly among species (ANOVA, $F = 83.2$, $P = 0.0005$), *S. hopeifolia* having the lowest biomass per leaf and *S. pinanga* the highest (Table 2). Results were similar for

the total foliar biomass of juveniles; total leaf biomass was lowest for *S. hopeifolia* juveniles and highest *S. pinanga* (ANOVA, $F = 122.6$, $df = 3$, $P < 0.0001$; Table 2).

When leaf mass was expressed on an areal basis (mg foliage per m² ground area) to assess the resource density available to foraging herbivores, mass per unit area declined significantly with distance for all species (linear regression, $r^2 < 0.20$, $P < 0.02$ for all species). In an ANCOVA of leaf biomass per area as a function of (a) species and (b) distance from parent, species differed significantly in juvenile leaf biomass density per unit area ($F = 11.1$, $P < 0.0001$; Table 3). *S. hopeifolia* had significantly less foliar mass/m² at all distances than *S. parvifolia* and both had less than either *S. longisperma* or *S. pinanga* (Tukey pairwise comparisons test, $P < 0.05$).

There was no significant relation between the toughness of mature leaves (Table 1) and mean herbivore damage over the four species (linear regression, $r^2 = 0.25$, $n = 4$, $P = 0.53$).

Density versus distance effects

Distance from focal trees, rather than juvenile density, was controlled in the sampling design. However, the main dependent variables (indices of herbivore damage and juvenile condition) could have been influenced

Table 2 Foliar biomass (dry weight) of single leaves and entire juvenile plants, for four *Shorea* species in lowland dipterocarp rain forest in Gunung Palung National Park, West Kalimantan, Indonesia. Leaf mass from dry weights of 4 bundles of 50 leaves for each species (see Materials and methods). Mean foliar mass per juvenile calculated as mean over juveniles of (no. leaves/plant × species-specific individual leaf mass). Values within columns followed by different superscripts (^a) indicate significant differences (Tukey Test, Means Comparison)

Species	Tissue mass per leaf mean (SE) mg	Leaf mass per juvenile mean (SE; n) mg
<i>S. hopeifolia</i>	54.8 ^a (7.8)	243 ^d (32; 265)
<i>S. parvifolia</i>	107 ^{ab} (8.5)	694 ^e (44; 262)
<i>S. longisperma</i>	169 ^b (0.7)	743 ^e (44; 286)
<i>S. pinanga</i>	350 ^c (38)	1680 ^f (81; 285)

Table 3 ANCOVA of differences in juvenile foliar biomass per m² among (i) species and (ii) distances from focal adult, for four *Shorea* species in lowland dipterocarp rain forest in Gunung Palung National Park, West Kalimantan, Indonesia. Conspecific foliar mass per m² declined with distance. Species differences in foliar mass per m² were *S. longisperma* = *S. pinanga* > *S. parvifolia* > *S. hopeifolia* (Tukey Test, Means Comparison)

Source	Sum of Squares	df	F	P
Species	225,838,431	3	5.014	0.0022
Distance	440,747,040	1	29.353	<0.0001

primarily by local juvenile density or distance from adult trees. Although conspecific and total (conspecific plus heterospecific) juvenile density both declined with distance from focals (Fig. 1), there was substantial variation in the relation between juvenile density and distance on the scale of 4 m² plots (Table 4). Distance explained only 24–51% of the variance in conspecific juvenile density and even less of the variance in total juvenile density.

To determine which of the independent variables (conspecific or total juvenile density, or distance from adult) explained most variation in the dependent variables, we used backward stepwise-elimination multiple regression tests (probability < 0.10 required to eliminate a variable). As a predictor of herbivore damage, distance explained more variance than juvenile density for both *S. hopeifolia* and *S. pinanga*. Distance was also the best predictor of foliar condition for *S. pinanga*, but not for *S. hopeifolia*, where the variation explained increased from 12% to 21% when conspecific density was used in place of distance (Table 5). Total juvenile density was eliminated as a factor in all backward elimination tests.

Table 4 Correlations (Spearman's rho) among distance from parent, conspecific juvenile density and total juvenile density for four *Shorea* species in lowland dipterocarp forest in Gunung Palung National Park, West Kalimantan, Indonesia

Species		Correlation coefficients	
		conspecific density	total density
<i>S. hopeifolia</i>	distance	-0.6107	-0.3744
	total density	0.7930	
<i>S. parvifolia</i>	distance	-0.5427	-0.2577
	total density	0.6736	
<i>S. longisperma</i>	distance	-0.6302	-0.3820
	total density	0.8105	
<i>S. pinanga</i>	distance	-0.4422	-0.1520
	total density	0.5852	

Table 5 Results of backward elimination stepwise multiple regression tests to determine which of the independent variables: conspecific juvenile density; total juvenile density; or distance from adult, explained most variance in (i) overall juvenile condition (total tissue retention after whole leaf loss and partial leaf loss; see text) or (ii) herbivore damage to young leaves for *Shorea hopeifolia* and *S. pinanga*

Dependent variable	Species	Remaining independent variable
Foliar condition	<i>S. hopeifolia</i> <i>S. pinanga</i>	conspecific density distance
% herbivory on youngest two leaves	<i>S. hopeifolia</i> <i>S. pinanga</i>	distance distance

Discussion

Spatial patterns in the density of juvenile plants

The consistent decline in juvenile density of conspecific *Shorea* spp. with distance from the parent was expected for wind-dispersed species. Less predictable was how these conspecific aggregations would affect spatial patterns in the total densities of juvenile plants. The adults of the four *Shorea* species we studied were centers of high total juvenile density, as well as high densities of conspecifics. Because the average density of other species remains more or less constant in space, one can visualize *Shorea* juvenile shadows as superimposed on a "background" of juveniles resulting from the overlapping shadows of the rest of the tree community, which is predominantly animal dispersed (Leighton 1990). Because dipterocarps share the general attribute of localized seed dispersal by wind, the pattern documented here for four *Shorea* species might be generalizable to the family level, i.e., the canopy emergent dipterocarp trees in southeast Asian rain forest may be foci of high total densities of juvenile trees on the forest floor. No significant effects of total density were found for the four species in this study. Nevertheless, dipterocarp-centered concentrations of juvenile densities could have important implications for any ecological processes in the understory of these forests that respond to total or congeneric density, e.g., herbivory, pathogen infection or seedling-seedling resource interactions.

Distance dependence in juvenile condition and herbivore damage

Both juvenile foliar condition and herbivore damage changed significantly with distance from parent for two of the four species examined. *S. hopeifolia* and *S. pinanga* juveniles were less damaged by herbivores (Fig. 2a) and had better overall foliage condition (Fig. 2b), farther from parent trees. However, additional measurements of juvenile performance over time would be required to determine whether these relatively small but statistically significant distance effects are associated with better juvenile growth and survival at greater distances from parents.

The trends in partial leaf loss on young leaves implicate insect herbivory in the distance dependence of whole leaf retention. Whole leaf loss may occur not only when mammals, such as deer, eat entire leaves, but also when leaves abscise prematurely due to damage by insect herbivores (Coley 1982; Lowman 1984; Filip et al. 1995; Blundell and Peart, unpublished data). Indeed, the lack of a significant distance-related trend when partial leaf loss was averaged over all the leaves of *S. hopeifolia* and *S. pinanga* juveniles may be due to earlier abscission of those leaves that experienced substantial tissue loss when young.

However, other factors could also contribute to the observed patterns of whole leaf loss. Litterfall from the canopy (Clark and Clark 1989), physical disturbance by vertebrates, pathogen infection and seedling-seedling competition may all plausibly be greater where the parent tree is closer and/or seedling densities are higher. Large, emergent dipterocarps in Borneo are known to produce disproportionately greater amounts of leaf litter than the rest of the tree community (Burghouts et al. 1994), which may result in greater physical damage to dipterocarp juveniles near parents. The concentrated seed fall beneath the *Shorea* adults may attract vertebrate seed predators (Curran 1994), e.g., bearded pigs (*Sus barbatus*), which may physically disturb juveniles, resulting in whole leaf loss. Pathogen infection, possibly hastening leaf abscission, may be more likely near parents and at high seedling densities (Augspurger 1983a,b, 1984; Augspurger and Kelly 1984; Gilbert et al. 1994), although we found little visible evidence of pathogen attack (Blundell, personal observation). Interactions among juveniles at high densities may also induce leaf loss, for example by mutual shading.

Although herbivory clearly contributes to the distance-related effects we observed, we have no evidence to distinguish among alternative hypotheses to explain why herbivore effects depend on distance. There are at least two possible causes for higher levels of herbivory near *Shorea* trees. First, specialist insect herbivores may aggregate, or have higher reproductive rates, in adult canopies or at high juvenile densities. This would result in greater damage near parents (Connell 1971), unless herbivores are satiated by the higher resource abundance there. Second, herbivores may exhibit switching behavior, preferring a species in areas where it is locally more abundant (Huntly 1991).

We have referred to the trends in herbivore damage and foliar condition as “distance-dependent” because distance was the factor controlled in the sampling design. We had limited power to determine from our results whether the agents responsible for the distance-dependent effects respond proximally to distance from adult, conspecific density or total juvenile density, all of which vary in concert. Yet, these factors were far from perfectly correlated (Table 4). There are plausible mechanisms by which conspecific or total juvenile densities could have been the factors generating the observed distance relationships. However, for the four species we examined, the backward elimination regressions provided only limited support for the importance of conspecific juvenile densities, and none for total juvenile densities (Table 5).

Differences among species; species-specific effects

Among species of tropical tree saplings in Panama, Coley (1983) found that the concentration of lignin, as measured by leaf toughness, was the best single predictor of herbivore damage on mature leaves. In this study, the

toughness of mature leaves of a species was unrelated to herbivory on the immature leaves, i.e., the stages where most herbivory on tropical woody species seems to occur (Coley and Barone 1996). Nor was there any consistent relation between herbivore damage and the mean size of seeds or juveniles, but the two species that demonstrated distance-dependent trends in herbivory were potentially the most “common” species to herbivores (*sensu* Feeny 1976; Rhoades and Cates 1976). *S. hopeifolia* was the most abundant and would be the most frequently encountered species, both as juveniles and adults. Individual *S. pinanga* juveniles were the largest of the four species, and also had the largest leaves and the greatest juvenile foliar biomass per unit area near adults.

Because the effects on herbivore damage and foliar condition shown for *S. hopeifolia* and *S. pinanga* were related to the proximity of the parent or the local density of conspecific juveniles, rather than total juvenile density, the mechanisms of those effects appear to act in a species-specific way. Such effects in one species would not necessarily imply their action in other, even closely related species. In spite of the marked decline in juvenile densities with distance from parent in the other two *Shorea* species examined, *S. parvifolia* and *S. longisperma*, distance-related effects on herbivory and foliar condition were either absent or too weak to be detectable in our samples. Both the species-specificity of the effects, and the differences in the trends we found, even among congeneric species, caution against generalizations about distance- or density-dependent effects on the juveniles of forest trees in diverse forests.

In conclusion, our results show that the distance- and density-related trends in forest tree regeneration that have been documented for several species in the Neotropics also occur in at least some species of the Dipterocarpaceae, the dominant family of trees in southeast Asian rain forests. Insect herbivory on juvenile plants appears responsible for at least part of the distance dependence we observed in partial leaf loss, and possibly for whole leaf loss as well. Because juvenile density is strongly correlated with distance from parent, distance-related trends would be generated whether the mechanisms actually respond to juvenile density or to distance; in either case, the outcome for tree populations and for the forest tree community would be similar. Specific inferences about population or community level effects are beyond the scope of this paper, requiring measures of individual performance as a function of distance and density over a substantial part of the life cycle. However, *S. hopeifolia* and *S. pinanga* juveniles distant from parent trees were in better condition and may, therefore, be more likely to survive and eventually recruit into the canopy than juveniles near parents.

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