

Habitat differences between two congeneric canopy trees, *Pterospermum javanicum* and *P. diversifolium* (Sterculiaceae) in an Indonesian floodplain forest

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ABSTRACT A comparison of tree architectures and allometries between two congeneric, light-demanding species, *Pterospermum diversifolium* and *P. javanicum* (Sterculiaceae), revealed that *P. diversifolium* is favored over *P. javanicum* at high light levels, but that the opposite is true at low light levels. Therefore, the abundance of these species within a landscape is likely to depend largely on habitat heterogeneities in understory light conditions. To verify this prediction, we compared the abundances and population size structures of these species among three 1-ha plots established on a ridge, a slope, and a flat plain within a tropical floodplain forest in East Kalimantan, Indonesia. We found a significant difference in understory light conditions among the plots: ridge > slope = flat plain. The abundances and size distributions of *P. javanicum* within the plots indicate that this species has a wide habitat range in the study area, from flat plains to slopes and ridges. We found no *P. diversifolium* in the flat plot; the habitat of this species may thus be restricted to ridges and slopes. Differences in the population size structures between the ridge and slope plots suggest that *P. diversifolium* regenerates more abundantly on ridges than on slopes. We discuss differences among plots in the abundance and size structure of *P. diversifolium* from the viewpoints of habitat heterogeneities in terms of differences in understory light and soil water conditions.

Key words: coexistence, competition, dispersal limitation, habitat, regeneration niche, tropical forest, understory light conditions

INTRODUCTION

According to the competitive-exclusion principle,

competition limits the diversity of woody species when superior competitors increase in abundance until other species are excluded from their niche (Wright, 2002). Nevertheless, it is possible to find hundreds of woody species within even a single hectare in diverse environments such as those in the tropics (e.g., Kohyama et al. 2001). Numerous mechanisms that delay or prevent competitive exclusion have been proposed from the viewpoints of equilibrium and what Hubbell (2001) described as “neutral phenomena”. The former include deterministic factors such as those included in the niche-differentiation hypothesis (Ashton, 1969), and the latter include random or stochastic historical factors, most notably restrictions imposed by the means of seed dispersal (Hubbell et al. 1999).

Yamada et al. (2005) analyzed interspecific differences in the allometry and architecture of two sympatric congeneric species, *P. diversifolium* Bl. and *P. javanicum* Jungh., in an Indonesian floodplain forest and concluded that the sapling growth strategy of *P. diversifolium* appears to be dynamic, emphasizing the opportunistic use of light following a disturbance, whereas that of *P. javanicum* appears to be static, with an emphasis on optimizing leaf display for current light conditions. Because the relative advantages offered by these phenotypes depend on the environmental context, it was hypothesized that these two species coexist by adopting different regeneration niches (Grubb, 1977) based on different understory light conditions; *P. diversifolium* is favored over *P. javanicum* at high light levels, but the opposite is true at low light levels (hereafter “the hypothesis of Yamada et al.”). Yamada et al. (2006) compared light requirements and growth rates of these species in relation to understory light conditions and showed that the distribution of *P. diversifolium* was significantly more skewed towards brighter microsites than that of *P. javanicum*. Stem elongation by *P. diversifolium* in bright microsites was also significantly

higher than that of *P. javanicum*. Because these results met the premise underling the hypothesis of Yamada *et al.*, the authors concluded that *Pterospermum* species coexist as a result of the diversification of regeneration niches with respect to understory light conditions. At the same time, we predicted that the abundance of these species within a landscape may change greatly in accordance with habitat heterogeneities, such as the understory light regimes and frequency of canopy gap formation in the stands. To verify this prediction, we compared the population structures of these species in three 1-ha plots established in different topographic environments with a range of understory light conditions. We addressed two main questions: (1) Do the population size structures and abundances of these species differ among the plots? (2) Do any observed differences in population size structures and abundances relate to aspects of the physical environment, such as understory light conditions?

MATERIALS AND METHODS

Our study was conducted in an equatorial floodplain forest in Labanan (Berau, East Kalimantan, Indonesia; 1° 52'30"N, 117°12'00"E). We established three 1-ha plots within the forest in 2002 and 2003; one was along a ridge (hereafter, the "ridge plot"), another was on a slope (the "slope plot"), and the other was on a flat plain (the "flat plot"). All three plots represented untouched natural primary forest. The ridge plot ran 500 m along the main ridge, was 20 m wide and was divided into 100 quadrats, each ca. 10×10 m². The slope and flat plots were 100×100 m² in area and were divided into 100 quadrats of 10×10 m². The differences in elevation between the highest and lowest points within the plot were 10, 19, and 8 m for the ridge, slope, and flat plots, respectively. The location of the plots is shown in Fig. 1. All trees with a dbh greater than 4.8 cm have been censused in the slope and flat plots (E. Suzuki, unpublished data). The density of trees was 1360 ha⁻¹ in the slope plot and 1029 ha⁻¹ in the flat plot. The total BA (basal area) was 28.8 m² ha⁻¹ in the slope plot and 33.0 m² ha⁻¹ in the flat plot. 140 and 169 tree species were recorded in the slope and flat plots, respectively. Both plots were dominated by *Endertia spectabilis* Steenis & de Wit of the Fabaceae (Caesalpinioideae). Numerous species belonging to the Euphorbiaceae, Ebenaceae, Annonaceae, Sapindaceae, and many other families formed the main continuous canopy at a height of about 30 m. Since only *Pterospermum* trees were censused in the ridge plot, we cannot show the forest physiognomy

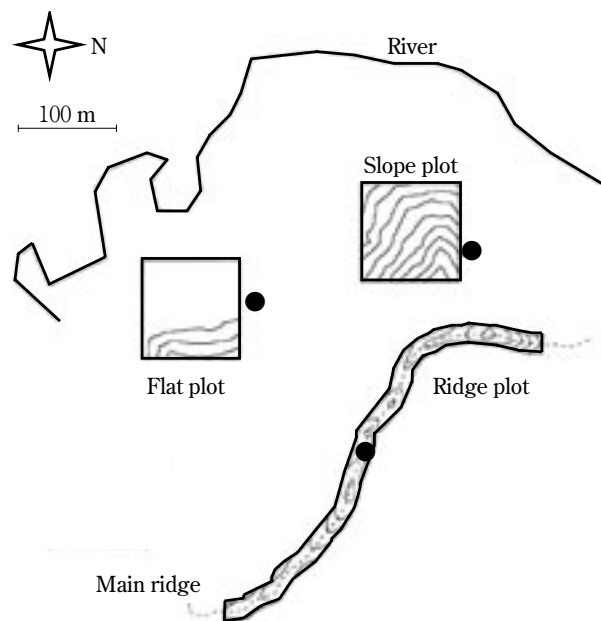


Fig. 1. Diagram of the Labanan study site (Berau, East Kalimantan, Indonesia), showing the three 1-ha plots. The contour interval within a plot is 2 m. The soil sampling sites (•) are also shown.

dimensions of this plot.

Our study focused on *P. javanicum* and *P. diversifolium*. Both are light-demanding trees (Kochummen, 1972), but both can also be found under the closed canopy at our research site (Yamada *et al.* 2006) and form part of a continuous canopy at about 30 m above the ground (Yamada *et al.* 2005). We measured the diameter at breast height (dbh, at 130 cm) and mapped the position of all *Pterospermum* trees with a dbh greater than 1 cm.

We measured the light conditions at 1 m above the ground in the plots by means of hemispherical fish-eye photographs taken in August 2003. We used a digital camera (Coolpix 950, Nikon, Japan) with a fish-eye lens (Nikon FC-E8 fisheye lens) mounted on a pole. The camera was kept in a horizontal position using a leveling device. We analyzed the digital images with an image-processing program (Gap Light Analyzer, GLA, ver. 2; Frazer *et al.* 1999). The basic model of light transmission in canopy gaps that is used by GLA is similar to the gap light index (Canham, 1988) and estimates the percentage of transmitted total (direct plus diffuse) radiation reaching the position at which the photograph was taken. Details of the calculation procedure of GLA are provided by Frazer *et al.* (1999). In the ridge plot, we took pictures every 10 m along the midline (500 m long) of the plot, for a total of 51 photographs. For the slope plot, we measured

light conditions at every corner of a quadrat (i.e., at 121 points). In the flat plot, we measured the light conditions at 30 randomly chosen corners of the quadrats. We statistically analyzed differences in light conditions among the plots using the Kruskal–Wallis test because their variances were heterogeneous (Levene's test, $P < 0.05$). When the Kruskal–Wallis test revealed a significant difference, we performed multiple comparisons for every combination of plots using the Mann–Whitney U -test with sequential Bonferroni correction (Rice, 1989).

Within each site, we collected soil samples at one point (Fig. 1) at depths of 10 to 15 cm (soil₁₀) and 30 to 35 cm (soil₃₀). We brought the soil samples to Japan for analysis of their textural class using by means of wet-sieving.

RESULTS

The abundances of *P. javanicum* were similar among the three plots: 69, 82, and 61 trees in the ridge, slope, and flat plots, respectively. However, the abundance of *P. diversifolium* differed greatly among the plots: 97, 37, and 0 trees in the ridge, slope, and flat plots, respectively. It was particularly noteworthy that we found no *P. diversifolium* in the flat plot.

The understory light conditions in the ridge plot were brighter than in the other plots (Fig. 2; Mann–Whitney U -test with sequential Bonferroni correction, $P < 0.05$). The light conditions did not differ significantly between the slope and flat plots ($P > 0.05$). Particle-size distributions differed little among the plots at both soil depths (Fig. 3). There were no visual differences in understory community structures between the slope and flat plots although we do not have quantitative data on it.

The observed maximum dbh values for *P. javanicum* and *P. diversifolium* in this study were 31 and 130 cm, respectively (Fig. 4); *P. javanicum* thus seems to be smaller than its counterpart congener. However, we encountered one *P. javanicum* tree with a dbh larger than 90 cm near the slope plot (Yamada et al. 2005).

The frequency distributions of *P. javanicum* were reverse J-shaped in all three plots (Fig. 4). The frequency distributions of *P. diversifolium* in the ridge and slope plots were also reverse J-shaped. However, the distribution in the ridge plot was more right-skewed than that in the slope plot; we found some trees larger than 50 cm in dbh in the ridge plot but no trees larger than 15 cm in dbh in the slope plot.

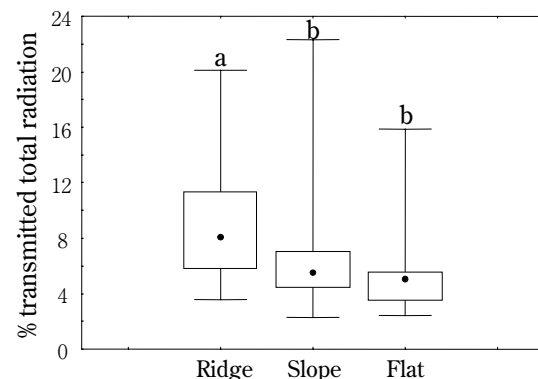


Fig. 2. Transmitted total (direct plus diffuse) radiation at a height of 1 m in the ridge plot ($n = 51$), the slope plot ($n = 121$), and the flat plot ($n = 30$). Box plots show the median (•), interquartile range (box), and range (whiskers). The plots differed significantly ($P < 0.00005$, Kruskal–Wallis test). Boxes labeled with different letters differ significantly ($P < 0.05$, multiple comparisons with Mann–Whitney U test, sequential Bonferroni correction).

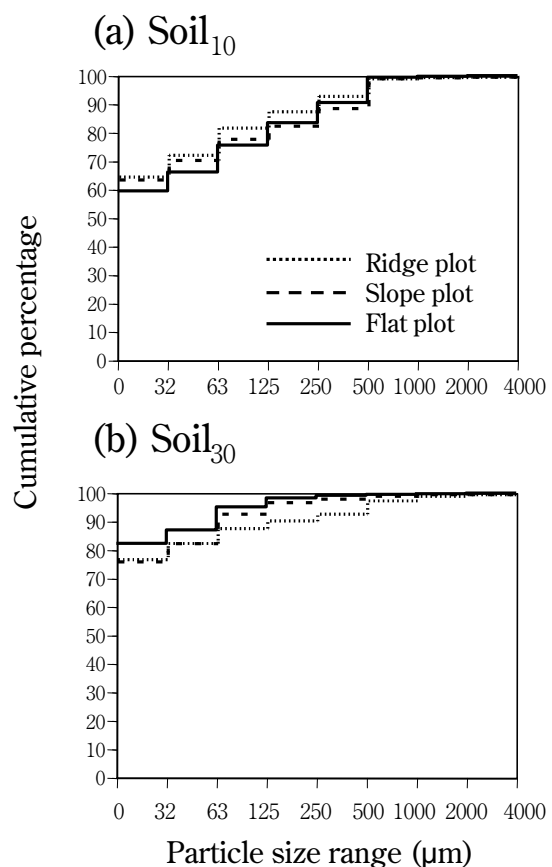


Fig. 3. Cumulative percentage (mass basis) of particle size of soils from (a) 10 to 15 cm in depth and (b) 30 to 35 cm depth. Particle size distributions were analyzed by a wet-sieving.

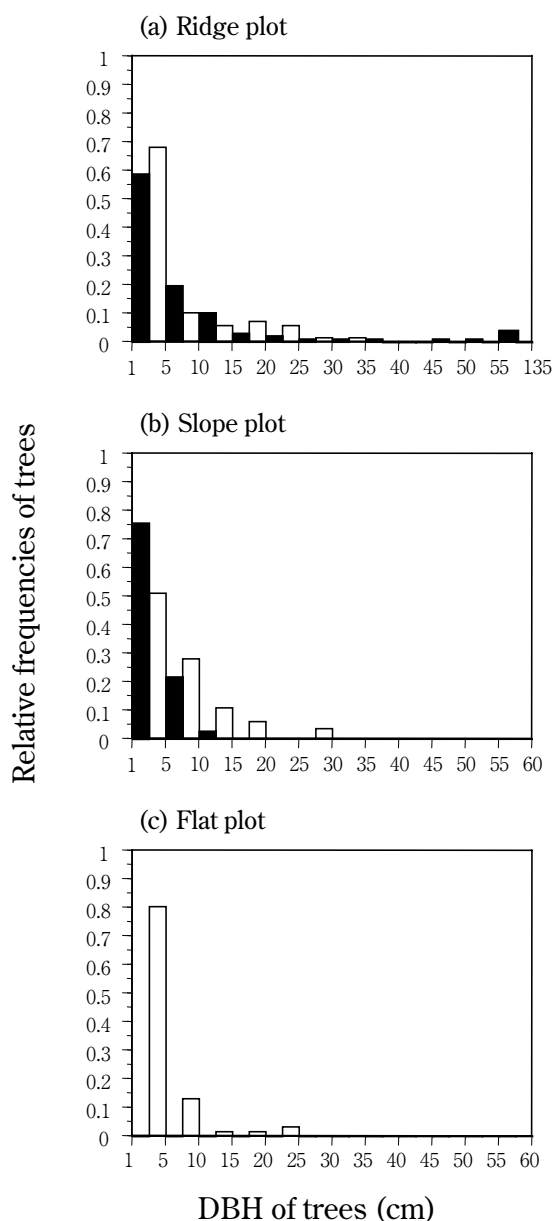


Fig. 4. Frequency distributions for the dbh of *P. diversifolium* (black bars) and *P. javanicum* (open bars) in the (a) ridge plot, (b) slope plot, and (c) flat plot.

DISCUSSION

The abundances and size distributions of *P. javanicum* indicate that this species has a wide habitat range, from flat plains to slopes and ridges, in the study area. We found no *P. diversifolium* in the flat plot. And we did not encounter this species in flat plains in the study site (T. Yamada, unpublished observation). The habitat of this species may be restricted to ridges and slopes. For this species, the abundance was larger in the ridge plot than in the slope plot. The size distribution was more right-

skewed in the ridge plot than in the slope plot (Fig. 4). These results suggest that *P. diversifolium* regenerates more successfully on ridges than on slopes.

The ridge plot had the brightest understory light conditions, and the abundance of *P. diversifolium* in this plot was greater than that of *P. javanicum*; we observed the opposite pattern in the other plots. This pattern is consistent with the hypothesis of Yamada *et al.* to explain the coexistence of these two species: *P. diversifolium* is favored over *P. javanicum* at high light levels, but the opposite is true at low light levels. The niche partitioning along light gradient between the two species would result in the observed interspecific difference in abundance.

The median value of light conditions above 67 understory *P. diversifolium* trees was 10.1% transmitted total radiation, with a range from 3.51% to 22.3% (Yamada *et al.* 2006). We found sites with light levels brighter than 10% of total transmitted light even in the flat plot, and these should be suitable for *P. diversifolium*. Furthermore according to the visual observation suggested that understory community structures were hardly different between the slope and flat plots. Thus, the absence of *P. diversifolium* in the flat plot cannot be explained by the light conditions alone. We propose two hypotheses that may explain why no *P. diversifolium* was found in the flat plot, even though suitable habitat exists in terms of understory light conditions.

The first relates to differences in soil water conditions. The soil textures differed little among the plots (Fig. 3), therefore the water-holding capacities of the soils do not appear to differ much among the plots. However, difference in topography and in the distance from the river would create variations in soil water content among the plots. The flat plot is located near a river; the flat, slope, and ridge plots were apart about 35, 115, and 270 m, respectively, from their nearest rivers (Fig. 1). And the flat plot is the lowest in elevation; the flat, slope, and ridge plots were higher by 3, 10, and 33 m in elevation, respectively, than the water level of their nearest rivers at a dry season. In floodplain forests, the sites near a river are frequently submerged during the rainy season. This creates anoxic soils that could be lethal to the roots of some species (Silver *et al.* 1999). We found visual symptoms of such flooding in the flat plot, for example the networks of gullies which might be formed by past flooding (data not shown), and these symptoms were absent from the other plots. Floods during the rainy season may thus limit the distribution of *P. diversifolium* in the flat plot. To verify this, we require more field observations and experiments to compare the

flood tolerance of the two species.

Second, dispersal limitations *sensu* Hubbell et al. (1999) may be responsible for the observed range of the two species. *Pterospermum* spp. produce small, winged seeds (0.22 g in dry mass; Yamada and Suzuki, 1999). Although we lack information on the dispersal distance of *P. diversifolium* seed, the density of winged seeds generally decreases with increasing distance from the maternal plant. If we assume that our study populations exhibit source–sink population dynamics *sensu* Pulliam (1988) and only ridge population of *P. diversifolium* is source population, the absence of *P. diversifolium* in the flat plot may be well explained by the limitation on seed migration from ridges to flat plain. However, some *P. diversifolium* trees were on the slope sites, and they are likely to be seed sources to the flat sites. This limits the adoption of the seed dispersal limitation hypothesis to this species. We must study seed dispersal of this species and the dynamics of local subpopulations, including seed migration among local subpopulations to verify the seed dispersal limitation hypothesis.

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