

Spatial structure and regeneration of *Tetramerista glabra* in peat swamp rain forest in Indonesian Borneo

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Abstract

We examined the spatial structure and regeneration of *Tetramerista glabra*, a dominant canopy tree in peat swamp rain forest in Borneo (West Kalimantan, Indonesia). *T. glabra* has strong spatial structure that changes dramatically during the life cycle; seedlings were highly aggregated, saplings were random and trees were evenly distributed. Germination and seedling relative growth were highest within canopy gaps, but seedling densities were highest at gap edges. Concentration of seedlings in gap edges, rather than localized seed dispersal, was responsible for seedling patchiness. The slope of the relationship between relative growth rate and seedling height decreased from gap, to gap edge to understory habitats, suggesting that competition within the seedling layer is more important in gaps than in the understory. The processes that break down seedling aggregation, leading to over-dispersion of trees, must be density dependent, but remain unknown.

Introduction

The spatial structure of tropical tree populations has attracted special interest because of the potential relationship between spatial distributions and the coexistence of tree species in diverse forests. Janzen (1970) and Connell (1971) suggested that wide intraspecific spacing of adult trees could allow more species to coexist. The importance of spacing to coexistence was brought into question by the demonstration (Hubbell 1980) that spacing alone has limited potential to promote coexistence, and by the finding that very few tropical trees are over-dispersed at the adult stage (Lieberman & Lieberman 1994). Yet, as Janzen (1970), Connell (1971) and Hubbell (1980) recognized, spacing per se is not required for density dependent controls to limit species' abundances and to promote coexistence (see also Armstrong 1989). The existence of density dependence in a population does not necessarily imply that density dependent mechanisms are strong enough to regulate population size (e.g., Hubbell et al. 1990). However, marked changes in spatial distributions over

the life cycle of a species, from aggregated at the seedling stage to more even at the mature tree stage, are indicative of mortality trends consistent with the hypothesis that density dependence in population dynamics promotes coexistence of tree species.

Apart from community-level implications, the spatial structure of the juvenile stages of a tree population can also be very informative in terms of the regeneration requirements of the species. Conditions affecting the establishment of seedlings may largely determine the distribution and abundance of adults (Grubb 1977). In particular, it is well established that regeneration of many tree species is strongly influenced by light availability and canopy gap formation (e.g., Denslow 1987; Canham 1989).

In this paper, we examine the spatial structure and regeneration of a valuable timber tree, *Tetramerista glabra* Miq. (Tetrameristaceae), one of the dominant species in a Southeast Asian tropical peat swamp rain forest.

The objectives of this research were twofold. First, we set out to test whether changes in spatial distribu-

tions over the life cycle, for one of the most abundant species in a diverse tree community, support the hypothesis of density dependent controls. Our second objective was to identify the habitat conditions favoring seedling recruitment and seedling growth. The latter is important both in understanding the spatial distributions of seedlings and in providing an ecological basis for management of the population in logged rain forest. To date, there is little ecological information relevant to management for Southeast Asian tropical trees other than those in the predominant timber family, the Dipterocarpaceae.

To reach these objectives, we addressed the following specific research questions for *T. glabra*: (1) What is the spatial pattern of individuals in the population? (2) How does the spatial pattern change over the life cycle of the species? (3) How do germination rates and the size-specific growth rates of seedlings vary in relation to the structure of the forest canopy?

Methods

Species and study site

T. glabra is a canopy tree up to 150 cm dbh (diameter at 1.4 m), found on peat swamp soils throughout Sumatra, Borneo and peninsular Malaysia (Keng 1972); it is occasionally present on alluvial and hill sandstone soils adjacent to peat swamp. The ripe fruit is a round, 3 cm diameter, yellow to orange four seeded berry with a slightly coriaceous exocarp. Primates are the main consumers of fruit and disperse the seeds via defecation (D. Gavin, personal observation). The seeds are small (mass of dry seed = 0.086 ± 0.017 g, $n = 150$) with a thick seed coat.

T. glabra is a commercial timber species, valued for its dense, insect resistant, and easily sawn wood (Burgess 1966). It is also harvested for local use by villagers with access to swamp forest, where heavy machinery cannot be operated due to the high water table. *T. glabra* seedlings commonly establish vegetatively from other seedlings and saplings; most seedlings below 30 cm in height show clear evidence of vegetative propagation from stems that had previously fallen to the forest floor (D. G. Gavin, personal observation). The abundance, distribution and regeneration ecology of *T. glabra* have not been documented. Thus, its potential for management for long term sustainable production is unknown.

This study was conducted between September 1992 and August 1993 at the Cabang Panti Research Station in tropical peat swamp rain forest at the 90,000 ha Gunung Palung National Park, West Kalimantan, Indonesia (1° S, 109° E), at an elevation of 5–15 m above sea level. The mean daily temperature maximum and minimum are 32 °C and 21 °C respectively, and annual rainfall is 4000–4500 mm. The 22.5 ha study area occupied the central part of a 50 ha patch of peat swamp forest that was accessible from the Cabang Panti Research Station, and appeared typical of peat swamp forest in the region. Peat depth was ca. 1 m in the study area, which would be classified as a type 1 phasic community in the peat swamp classification of Anderson (1964). *T. glabra* was one of the most common canopy species at the site; other common canopy species included *Koompassia excelsa*, *Parkia speciosa*, *Palaquium* spp., *Dipterocarpus coriaceus*, and *Dyera costulata*.

The mean height of the peat forest canopy at the study site is 28 m (based on measures of 40 dominant trees), considerably less than that of the lowland dipterocarp forest that occurs on well drained soils in the region (Whitmore 1984). The lack of emergent trees results in a relatively uniform, continuous canopy, punctuated by very well defined, discrete canopy gaps. Recently formed canopy gaps occupy 8% of total area in this peat forest. Most of the gaps are small (81% <300 m² in area). More than 50% are <200 m² in area (Gavin et al. 1996).

Overall sampling design

Data on *T. glabra* were collected using two sampling schemes. First, in an extensive survey over the entire 22.5 ha study area, we recorded size-specific population densities of *T. glabra* and the association between seedling densities and canopy structure. Second, we sampled part (10%, or 2.25 ha) of the extensive survey area more intensively, establishing a marked sample of *T. glabra* individuals to quantify height growth over time.

Extensive survey

The extensive survey was based on forty five 250 m long parallel transects spaced 20 m apart. *T. glabra* trees > 30 cm dbh were inventoried within 10 m of the transect lines; thus large trees were censused over the entire 22.5 ha area. Individuals 5–30 cm dbh were inventoried within 3 m of transect lines (for a total

sample area of 6.75 ha), saplings 2–5 cm dbh within 1.5 m (sample area 3.375 ha). From preliminary sampling it was clear that seedlings <30 cm tall were far less abundant than those >30 cm, probably due to low germination rates and the high frequency of vegetative propagation (see below). We focus on seedlings >30 cm tall; seedlings (>30 cm tall and <2 cm dbh) were inventoried within 4 m of every fifth transect line (sample area 1.8 ha). For many analyses, individuals were classed as either seedlings (>30 cm tall and <2 cm dbh), saplings (2–10 cm dbh) or trees (>10 cm dbh). The sample sizes of trees and saplings were 55 and 63, respectively. Sample sizes of seedlings, in height classes of 0.5–1.29 m, 1.3–1.79 m, 1.8–2.29 m, 2.3–2.79 m, and 2.8 m to less than 2 cm dbh were 63, 71, 41, 28, and 7, respectively.

We used three classes of canopy structure (gaps, gap edges, and understory) to examine the association between canopy structure and the size class structure and abundance of seedlings. Gaps were defined as areas at least 5 m × 5 m in size lacking vegetation between 10 and 30 m above the ground (i.e. lacking canopy tree cover). ‘Gap edge’ was defined as the area in a 10 m wide perimeter zone around the edge of a canopy gap. ‘Understory’ was defined as all areas more than 10 m from a canopy gap. The distances from each *T. glabra* seedling to the nearest edge of a canopy gap were measured.

Intensive survey

The intensive 2.25 ha sampling area, measuring 150 m × 150 m, was chosen within the 22.5 ha area described above, to include several reproductively mature *T. glabra* trees and to contain a wide array of recent canopy disturbance. The purpose of these criteria were to increase the likelihood of including a large sample of *T. glabra* seedlings and to maximize the opportunity to detect influences of canopy structure on seedling growth. A contiguous area, rather than several smaller samples, was chosen to facilitate analysis of spatial patterns within the intensively sampled area. The 2.25 ha area was divided into 225 permanently marked 10 m × 10 m grid cells for seedling and sapling sampling. All *T. glabra* individuals (seedlings, saplings and trees) were measured within the 2.25 ha plot. Trees >10 cm dbh were also measured in a 30 m wide band around the periphery of the plot for a total sample area of 4.41 ha (210 m × 210 m).

For all *T. glabra* seedlings ($n = 426$), we recorded height to the apical meristem and location (with-

in 20 cm). Heights were measured at the beginning and end of an 11-month period. During this period, some branch and tree falls occurred, and some seedlings could not be relocated; 390 (92%) were found and measured. The sample was not used to estimate mortality because it could not be assumed that unrecovered plants had died. Extension growth was quantified as the relative height growth rate (RGR) calculated as $[\ln(H2) - \ln(H1)]/t$, where H1 and H2 are the initial and final heights to the tallest shoot, and t is the time interval in years (Hunt 1978).

We analyzed the spatial pattern of seedlings, saplings and trees using the Ripley K function (Cressie 1991). This function ($\hat{K}(h)$) quantifies the number of extra events (i.e., *T. glabra* locations) within a radius h of an arbitrary event, and scales the estimator so it approximates πh^2 under the assumption of complete spatial randomness (Cressie 1991). Values less than πh^2 indicate regularity (evenness or hyperdispersion) and values greater than πh^2 indicate clumping (patchiness or aggregation). The function also incorporates an edge correction based on distances of events from the edge of the plot. $\hat{L}(h)$ was calculated as

$$\sqrt{\hat{K}(h)/\pi} - h$$

thus linearizing the function, yielding expectation zero given randomness, and stabilizing the variance over h (Cressie 1991). 95% upper and lower simulation envelopes were constructed by calculating $\hat{L}(h)$ on simulated random dispersions generated with a homogenous Poisson process. Due to the low density of saplings and trees in the plot, a large number of simulations were needed to accurately determine the 95% upper and lower envelopes. We ran 2000 simulations for the tree and sapling data, and 200 simulations for the seedling data.

Germination

We tested the effects of fruit pulp removal and canopy structure on viability and germination rate. Primates remove the pulp and may thereby reduce the incidence of fungal attack, at least on some species (Janzen; 1977, Thomas 1995). We divided 774 seeds, collected from fallen ripe fruit, roughly equally among 2 seed preparation treatments and 3 site types (according to canopy structure). Seed preparation treatments were: none (i.e., seeds with pulp) and cleaned (pulp removed and seed coat scoured). Planting locations were in gap center, gap edge and forest understory, in and around a

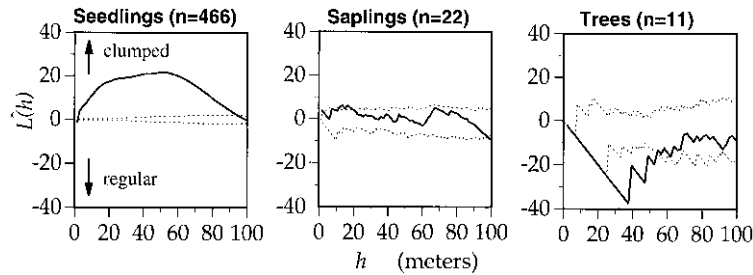


Figure 1. Ripley's K function of spatial dispersion for *Tetramerista glabra* seedlings (>30 cm to 2 cm dbh), saplings (2–10 cm dbh) in a 2.25 ha plot and trees (>10 cm dbh) in a 4.41 ha plot at Gunung Palung, Indonesia. $\hat{L}(h)$, the square root transform of Ripley's $K(\hat{K}(h))$, is presented. Dashed lines indicate the 95% upper and lower envelopes generated from simulated random dispersions based on Poisson expectation.

large, naturally occurring canopy gap (area ca. 900 m²). Seeds in all treatments were placed on trays filled with fine, well drained sand and enclosed by nylon net bags, and left in the field for five months. Seeds were not watered, but were exposed to natural precipitation.

Results

Spatial pattern and size structure

Seedlings were significantly aggregated at scales of 5 m to 90 m (Figure 1). Saplings (2–10 cm dbh) were randomly dispersed over all spatial scales. Trees (>10 cm dbh) were significantly evenly distributed on scales up to 50 m.

There was no evidence in the size class structure of the population for major pulses in recruitment, as would occur if establishment occurred during infrequent disturbance events. Overall, abundances declined with increasing size class, from more than 30 ha⁻¹ for seedlings <80 cm tall, to less than 1 ha⁻¹ for trees >64 cm dbh (Figure 2).

All size classes of seedlings occurred at higher frequencies in gap edges than would be expected if there were no association between seedling density and canopy structure. Observed frequencies of seedlings in gap and understory habitats were correspondingly lower than expected. Overall, the concentration of seedlings in gap edge habitats was highly significant (Table 1). Habitat-specific sapling distributions differed from that of seedlings in that saplings were more dense than would be expected by chance in both gap edges and gaps. Thus, it was not surprising that size structure of seedlings and saplings differed significantly among gaps, gap edges and understory ($\chi^2 = 20.7$, $df = 10$, $P = 0.02$; Figure 3).

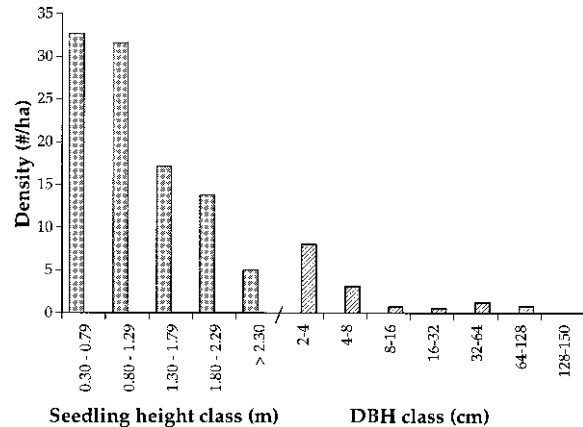


Figure 2. Seedling height class structure and sapling and tree DBH size class structure of *Tetramerista glabra* along forty-five 250 m transects in peat swamp forest in Gunung Palung, Indonesia. Total sample sizes were, for seedlings, 210, and for saplings and trees, 99. Side search distances were, for seedlings, 4 m on every fifth transect, yielding a total search area of 1.8 ha. For saplings and trees, side search distances were 1.5 m for size class 2–5 cm dbh, 3 m for size class 5–30 cm dbh and 10 m for size classes above 30 cm dbh yielding sample areas of 3.375, 6.75, and 22.5 ha respectively.

Seedlings were concentrated in areas near, but not in canopy gaps. With decreasing distance to gap edge (i.e., from 30 m to 0 m distance to gap edge) seedling densities increased dramatically (Figure 4a). This pattern was highly significant (compared to a random expectation of equal densities irrespective of distance from gap edge; $\chi^2 = 48.2$, $df = 6$, $P = 0.0001$). Seedlings were not concentrated around parent trees, but were actually highest far (25–30 m) from adults (Fig 4b). This inverse relationship between seedling density and proximity to adult was also highly significant ($\chi^2 = 24.9$, $df = 5$, $P = 0.0001$).

Table 1. Chi-square tests of seedling and sapling frequencies among habitat types at Gunung Palung, Indonesia. *P*-values represent the probability that seedlings are evenly distributed in canopy gap, gap edge and understory conditions (see Figure 3 for definition of canopy condition). Seedling and saplings were inventoried on forty-five 250 m transects, as summarized in Figure 3. The number in parentheses is the expected number of seedlings in each size class based on equal densities among canopy condition classifications.

Size Classes	No. individuals tagged (expected no.)			Total no. tagged	<i>Chi</i> ²	DF	P
	Canopy gaps	Gap edges	Understory				
Seedling height class (m)							
0.30–0.79	2 (4.6)	16 (11.5)	45 (46.9)	63	3.39	2	0.19
0.80–1.29	1 (5.3)	23 (12.9)	47 (52.8)	71	11.95	2	0.0025
1.30–1.79	1 (3.0)	13 (7.5)	27 (30.5)	41	5.88	2	0.053
1.80–2.29	3 (2.1)	8 (5.1)	17 (20.8)	28	2.78	2	0.25
2.30–2cm dbh	0 (0.5)	2 (1.3)	5 (5.2)	7	0.94	2	0.625
All seedlings	7 (15.5)	62 (38.2)	141 (156.3)	210	20.98	2	< 0.001
Saplings							
2–10 cm dbh	11 (4.6)	20 (11.3)	32 (47.1)	63	20.44	2	< 0.001

Growth

Growth rate of *T. glabra* seedlings increased dramatically with canopy openness. Mean absolute height growth ranged from 30 cm yr⁻¹ in gaps, to 10.4 cm yr⁻¹ in gap edges and 6.7 cm yr⁻¹ in the understory. Relative growth rate followed a similar trend; mean RGR differed significantly among canopy classes (ANOVA, $F = 8.96$, $P = 0.0001$). Pairwise differences in RGR were tested with ANOVA least square means comparisons. RGR in both gaps ($P = 0.004$) and in gap edges ($P = 0.0184$) was significantly higher than in the understory. RGR was also higher in gaps than in gap edges, although this comparison was only marginally significant ($P = 0.059$).

Changes in the slope of the relationship between RGR and plant size are indicative of a change in the degree of asymmetric competition (Weiner 1990). The relation between growth and plant size did change as a function of canopy structure. In the understory, RGR decreased significantly with increasing plant size ($F = 26.4$, $P = 0.0001$, $n = 285$). In gap edges, RGR decreased with increasing size, but the trend was only marginally significant ($F = 3.0$, $P = 0.086$, $n = 92$). In gaps, there was no significant trend in RGR with size ($F = 1.6$, $P = 0.23$, $n = 13$). When the data from all canopy classes were combined in a single analysis, the slope of the relationship between RGR and seedling height was significantly different among canopy classes ($F = 5.14$, $P < 0.01$); slopes declined over a gradient of canopy cover, from gaps to gap edges to understory conditions (Figure 5).

Germination

In the germination trials, only 17 out of 774 seeds germinated; 15 out of 285 in gap center (5.3% germination), one out of 237 in gap edge (0.4%) and one out of 252 in understory habitat (0.4%). The difference in germination frequency between gap edge, gap center and understory was significant ($\chi^2 = 19.32$, $P = 0.0001$). There was no difference in germination rates between cleaned seeds and those remaining in the fruit pulp ($\chi^2 = 1.0$, $P > 0.5$).

Discussion

Size and spatial structure

Although dynamic processes cannot be inferred directly from static patterns, the size structure of the *T. glabra* population was of the classic 'inverse J' form (Figure 2) expected for populations that recruit fairly regularly in time (e.g., Oliver and Larson 1990), as might be expected where recruitment is associated with individual canopy gaps and the edge habitats surrounding them (Figures 4 and 5).

The spatial structure of the *T. glabra* population was more unusual. First, *T. glabra* is unusual in the even spacing of adults. In a survey of studies of the spatial distributions of rain forest tree species, Lieberman and Lieberman (1994) cited 372 cases, of which only 8 showed evidence of even spatial distribution (159 were clumped and 205 were not distinguishable from

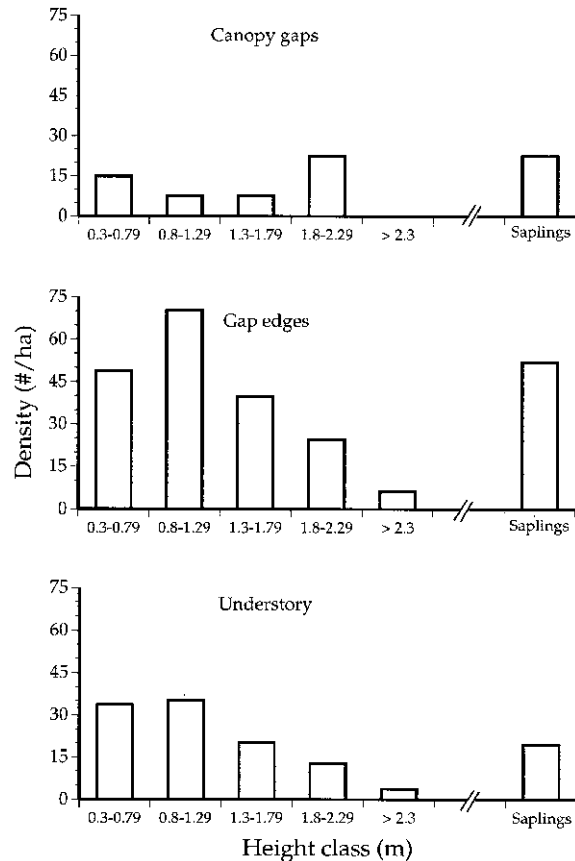


Figure 3. Seedling height class densities for *Tetramerista glabra* among three canopy types inventoried along nine 8 m × 250 m transects in peat swamp forest at Gunung Palung, Indonesia. Sapling densities are from inventories along forty-five 6 m × 250 m belts. Gap centers are defined as a break in the upper canopy at least 5 m × 5 m in area and extending to at least 10 m above the ground. Gap edges are the areas within a 10 m perimeter of canopy gaps, and understory areas are the remainder of the inventoried area. Sample sizes are shown in Table 1.

random). *T. glabra* was remarkable in the strength of its spatial patterns, the habitat association of seedlings, and the clear pattern of change from the seedling to the adult stages of the life cycle. The Janzen-Connell hypothesis (Janzen 1970; Connell 1971) proposed that seedlings aggregated around parent trees are subjected to distance or density dependent mortality that results in even spacing of trees. It is common for seedlings to be concentrated around adults, for species at our study site (Setiadi et al. 1996, Tanuwijaya et al. 1996) and elsewhere (e.g., Clark and Clark 1984). However, *T. glabra* seedling distribution differs greatly from this pattern, as seedlings were negatively associated with adults, but positively associated with a particular hab-

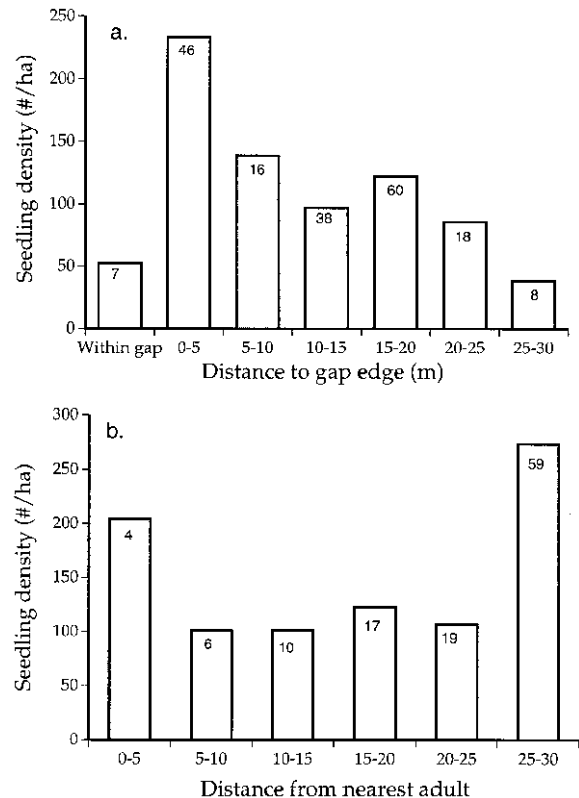


Figure 4. *Tetramerista glabra* seedling densities along nine 8 m × 250 m transects within and at different distances from canopy gaps in peat swamp forest at Gunung Palung, Indonesia. Seedlings were greater than 30 cm in height and less than 2 cm DBH. All canopy gaps were greater than 5 × 5 m in size. (b). *Tetramerista glabra* seedling densities at different distances from 3 parent trees in a 2.25 ha plot. Number of individuals is indicated within each bar in both figures.

itat, gap edges. Nevertheless, the same sequence of changes in the spatial distribution of individuals over the life cycle is seen for *T. glabra* as was proposed by Janzen and Connell, i.e., a progression from aggregated seedling distributions to evenly distributed adults.

The range of mechanisms that could produce the change in *T. glabra* distributions over time differs from those in the Janzen-Connell model. Mechanisms based on distance from adult cannot be responsible, nor can density dependent seed predation. In *T. glabra*, the change from aggregated seedlings to evenly distributed adults must involve density dependent mortality affecting the vegetative stages of the life cycle (seedlings and saplings). The mechanisms of such density-dependent effects remain unknown. Thus, it is not clear what causes the remarkably even spacing of adults, at scales up to 50 m (Figure 1).

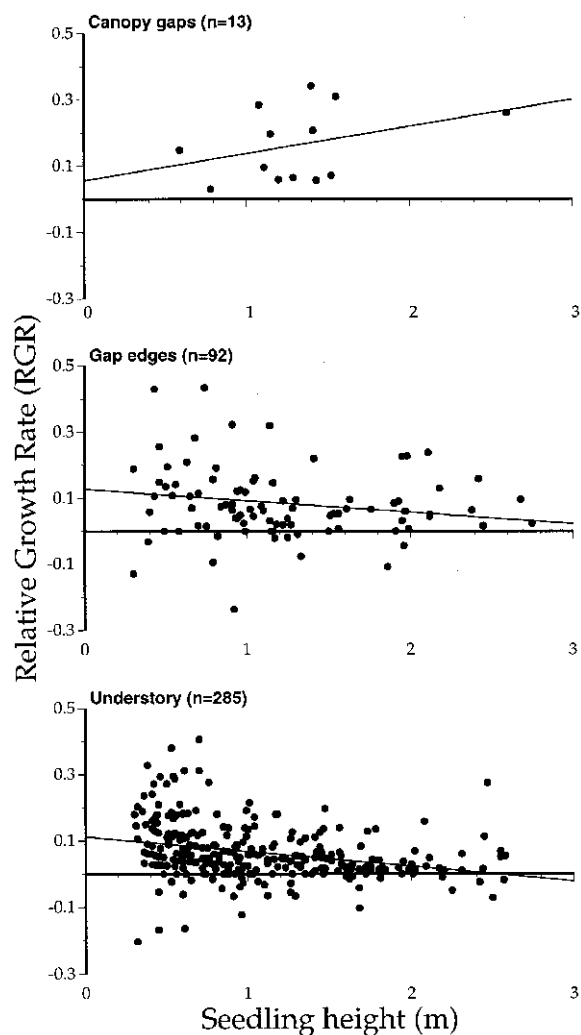


Figure 5. Relative height growth rates of *Tetramerista glabra* seedlings in a 2.25 ha plot in peat swamp forest at Gunung Palung, Indonesia. Canopy gaps, gap edges, and understory are defined in Figure 3. See text for details.

However, our specific results on germination and growth are relevant to understanding how seedlings become aggregated in gap edges. In following, we discuss those specific results and how they bear on seedling patchiness.

Dissemination and germination of seeds

Orang-utans consume much of the ripe fruit and travel widely through the forest at the study site (D. G. Gavin, personal observation). In combination with the evidence that the seed sources (adult trees) are evenly spaced, this suggests that *T. glabra* seeds are well

dispersed. However, orang-utans are almost totally arboreal and do not frequent gaps. Thus, gap centers probably receive few seeds, so that the relatively high germination rate in gaps (5.3%) has little influence on seedling densities there. The seedlings in gaps probably came from seed dispersed before gap formation.

Germination rates were even lower in gap edges (0.4%) and the understory (0.4%) than in canopy gaps. Ng (1980) found a somewhat higher (although still low) seed germination rate of 12% after 4.8 months with clean seed and 18% after 4.3 months with seed in pulp, using relatively small sample sizes ($n = 50$ for cleaned seed and $n = 11$ for seeds in pulp). However, Ng maintained conditions favorable for germination by daily watering and full sunlight, in contrast to the natural field conditions in our germination trials. We did not assess the viability of the remaining seed after five months; it is possible that *T. glabra* seeds could enter the seed bank and remain viable over a longer time.

Seedling growth

The stem-dominated, largely branchless architecture of *T. glabra* saplings is the ideal form for fast height growth in high light conditions (Kohyama 1991). *T. glabra* is clearly a species whose growth, like that of classic pioneer trees, can respond dramatically to high light conditions.

To understand the growth response of *T. glabra* seedlings to canopy structure, it is essential to analyze the effects of plant size. Growth is influenced by the balance between resource acquisition and metabolic demand. Resource demand is influenced by plant size in woody plants, because of the increasing ratio of non-photosynthetic to photosynthetic tissue as woody plants grow larger (Kozlowski et al. 1990). Thus, RGR is expected to decline with plant size, unless increasing size confers special advantages. Where plants are exposed to direct sunlight, access to resources differs greatly between large and small plants; interception of sunlight is not proportional to size, because large individuals can shade their smaller neighbors. This 'asymmetric competition' therefore contributes to higher RGR in larger plants (Thomas & Weiner 1989). In high light habitats, this effect could ameliorate the decrease in RGR with size, or even reverse the expected trend, for plants that respond strongly to high light conditions.

Height relative to neighbors is likely to be especially important in gaps, where plants may compete

for light and other resources in a densely packed and rapidly growing seedling layer. Thus, in gaps, the tallest *T. glabra* seedlings performed better than smaller seedlings, not only in absolute growth rate, but even when growth was expressed in proportion to height as RGR (Figure 5). In contrast, in the understory, RGR decreased with plant height (Figure 5). Here, taller seedlings do not have disproportionate access to direct sunlight. Light penetration to the understory is blocked by canopy trees, rather than by neighbors in the seedling layer. Further, because of the greater investment of taller seedlings in support tissue, maintenance costs divert a greater proportion of photosynthate from new growth than is the case for smaller seedlings.

Concentration of seedlings in gap edges

Despite regular seed input in understory and gap edge habitats, recruitment from seed, based on our germination experiments, is probably very low. The concentration of seedlings in edge areas around gaps cannot be explained by spatial patterns in dispersal or germination. Therefore, survival and/or rates of recruitment must be higher in gap edges than elsewhere. We do not have direct estimates of habitat-specific demographic parameters, but available evidence suggests that both survival and recruitment may contribute to the high densities of seedlings in gap edges.

From the limited data available, it appears that, for those species that have the capacity to grow rapidly in high light conditions, low growth rates of juvenile trees are associated with high mortality (Pacala et al. 1994). Relative growth rates of *T. glabra* seedlings were lower in the understory than in gap edges or gaps, suggesting that survival in the understory may be relatively low. In gaps, surviving seedlings grow quickly, but the slope analyses described above indicate that asymmetric competition within the seedling layer may be intense, leading to low growth and corresponding high mortality amongst the smaller seedlings, a phenomenon noted by Sasaki & Mori (1981) for dipterocarp seedlings in Southeast Asia. Thus, overall survivorship may be highest in the intermediate habitat of gap edges, due to chronic resource limitation in the understory and competitively induced stress in gaps.

Findings from related research on growth form and vegetative propagation of *T. glabra* (Gavin & Peart, submitted) suggest that vegetative recruitment of seedlings in gap edges also contributes to high seedling densities there. Ramification by stem sprouts was more common in the understory and gap edges than in gap

centers. In summary, seedling densities are most likely limited in the understory by low light conditions and in gaps by low seed input and competition for light in the rapidly growing vegetation of the seedling layer. In gap edges, relatively high growth rates and high rates of vegetative propagation contribute to the high seedling densities there.

Conclusions

Seed germination, seedling growth and seedling densities of *T. glabra* were strongly associated with canopy openings; germination and growth rates were highest in gap centers and densities were highest around gap edges. The concentration of seedlings in gap edges results from the combined effects of seed arrival, seed germination, vegetative propagation and survival. The striking progression in spatial distributions from aggregated seedlings to over-dispersed adults implies density dependent population dynamics beyond the seedling stage, but the mechanisms of such density dependence are not known. The high percentage of area in gaps at the study site results in a high proportion of area in the gap edge habitat that favors *T. glabra* seedlings; this may contribute to the abundance of *T. glabra* in this forest.

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