Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo

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Summary

1 We conducted a field experiment to test whether aggregated spatial distributions were related to soil variation in locally sympatric tree species in the rain forests of Sarawak, Malaysia. *Dryobalanops aromatica*, *Shorea laxa*, and *Swintonia schwenkii* are naturally aggregated on low-fertility humult ultisols, *Dryobalanops lanceolata* and *Hopea dryobalanoides* on moderate-fertility udult ultisols and *Shorea balanocarpoides* is found on both soil types.

2 Seedlings of all six species were grown in a nested-factorial experiment for 20 months in humult and udult soils in gaps and in the understorey to test for soil-specific differences in performance. Phosphorus addition was used to test for effects due to P-limitation.

3 Four species showed significantly higher growth on their natural soils, but one humult-soil species (*D. aromatica*) and the broadly distributed species were not significantly affected by soil type.

4 One udult-soil species, *D. lanceolata*, had both lower relative growth rate and lower mycorrhizal colonization on humult soil. However, humult soils also had lower levels of Ca, Mg, K, N and probably water availability.

5 The overall ranking of growth rates among species was similar on the two soils. Growth rates were strongly positively correlated with leaf area ratio and specific leaf area among species in both soils. With the exception of *D. aromatica*, species of the higher-nutrient soils had higher growth rates on both soils.

6 Although P addition led to elevated soil-P concentrations, elevated root- and leaf-tissue P concentrations on both soils, there was no significant growth enhancement and therefore no evidence that P availability limits the growth or constrains the distribution of any of the six species in the field. Differences in soil water availability between soils may be more important.

7 Our results suggest that habitat-mediated differences in seedling performance strongly influence the spatial distributions of tropical trees and are therefore likely to play a key role in structuring tropical rain forest communities.

Key-words: community assembly, edaphic specialization, soil nutrients, phosphorus limitation, mycorrhizae, niche partitioning, species coexistence, spatial aggregation of trees, tropical rain forest, tree seedlings.

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Introduction

Most tropical rain forest tree species have strongly aggregated spatial distribution patterns (Hubbell 1979; Condit *et al*. 2000). Neutral models of forest community assembly suggest that this aggregation is principally the result of limitations to seed dispersal (Bell 2000; Hubbell 2001). However, if communities are organized primarily by niche-assembly processes, aggregation is expected to be due to a high degree of species habitat specialization (Ashton 1998; Clark *et al*. 1999; Hubbell 2001). The extent to which these competing hypotheses explain aggregated species spatial distributions remains a central unanswered question in tropical forest ecology.

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Support for niche-assembly theory in tropical rain forests has mostly been sought through determination of differences in species distributions along gap–understorey gradients of light availability and their consequent physiological specializations (Denslow 1987; Brokaw & Busing 2000). However, an increasing number of studies demonstrate that species distributions are also strongly aggregated with respect to variation in topography, soil water and soil nutrient status (Clark *et al.* 1998; Duivenvoorden 1995; Swaine 1996; Svenning 2001). Because edaphic conditions tend to be spatially aggregated, using inventory or plot studies to distinguish between the effects of habitat association and dispersal limitation on tree species spatial aggregation is not straightforward. This problem has been addressed at the regional or landscape scale by testing whether the composition of different communities is more strongly correlated with habitat features (e.g. soil nutrients) than with the geographical distance among communities (Potts *et al.* 2002; Terborgh *et al.* 1996; Tuomisto *et al.* 2003). For local plot-based studies, randomization tests have been developed to test whether species distributions are significantly correlated with particular abiotic variables (e.g. topography), while accounting for the clumped distribution of individuals (Plotkin *et al.* 2000; Harms *et al.* 2001). However, these approaches are correlative and do not provide a mechanistic understanding of factors influencing the spatial distributions of tropical trees. A more rigorous test of habitat-related spatial aggregation in tropical tree communities should involve experimental evidence that species perform better in the habitat in which they are aggregated.

The most widespread lowland rain forest formation in Borneo is mixed dipterocarp forest (MDF). MDF occurs over a broad range of red–yellow ultisols and species composition and forest structure can vary quite dramatically with small scale edaphic and topographic gradients (Austin *et al.* 1972; Newbery & Proctor 1984; Baillie *et al.* 1987; Davies & Becker 1996). For example, there was almost no overlap in canopy species between two 4-ha plots that were < 700 m apart, but on soils of contrasting fertility within a 52-ha forest plot at Lambir Hills, Sarawak (Lee *et al.* 2002). Several such comparative floristic studies have suggested that soil nutrient availability, particularly phosphorus (P) and magnesium (Mg), directly influences species distributions and community composition in MDF (Baillie *et al.* 1987; Potts *et al.* 2002). Whether levels of either of these nutrients constrain the distribution or limit the growth of species in primary MDF soils in the field remains unknown. Nutrient-related community distributions would predict that the growth of species from more fertile MDF soils would be reduced when grown on the less fertile soils, but do not make specific predictions for factors constraining the distributions of species specializing on lower fertility MDF soils.

Phosphorus is widely reported to be the principal nutrient limiting tree growth and productivity in tropical forests (Vitousek & Sanford 1986; Sollins 1998; Tiessen 1998; Cleveland *et al.* 2002). For MDF, the only experi-

mental study that we are aware of that manipulated soil P for communities in the field, showed no significant effects of P addition on growth (Mirmanto *et al.* 1999), although the additional P was taken up by the plants and there was the suggestion that, given time, some of the faster growing species might have responded to P addition. For individual MDF species, there have been numerous experimental studies of seedling responses to soil nutrient manipulation, focusing particularly on important timber species of the Dipterocarpaceae. The majority of these studies have involved potted seedlings which may (Sundralingam *et al.* 1985; Lee & Alexander 1994) or may not (Alexander *et al.* 1992; Turner *et al.* 1993; Lee & Alexander 1994; Burslem *et al.* 1995) respond to P-addition. Nutrient addition experiments in the field for MDF species have usually involved enrichment planting in secondary forests where natural soil processes have been severely modified (Bungard *et al.* 2002; Nussbaum *et al.* 1995; Raja Barizan & Appanah 2000; Vincent & Davies 2003; but see Turner *et al.* 1993) and most have found strong nutrient limitation of growth. Although P does not therefore appear to be limiting in these predominantly mycorrhizal species when mycorrhizal associations are intact (Burslem *et al.* 1994), assuming mycorrhizal colonization is reduced following forest degradation (Alexander *et al.* 1992), its effect on undisturbed MDF in the field remains untested. Furthermore, the critical test of whether MDF species from soils of differing fertilities respond differently to the addition of nutrients when grown on a range of soils has yet to be undertaken.

We conducted a field experiment to investigate habitat-related spatial distributions of six MDF tree species in a tropical rain forest in Malaysian Borneo: three species are naturally aggregated on low-fertility soils, two species on moderate-fertility soils, and one occurs on both. Seedlings of all six species were grown in both low- and moderate-fertility soils in the field to test whether species have the soil-specific performance differences expected from their spatial distributions in the natural forest. We analyse patterns of growth, allocation and nutrient uptake of all species to investigate whether species aggregated on the different soils differ consistently in particular traits associated with the gradient in soil fertility, as has been reported for temperate and other forest communities (Chapin *et al.* 1986; Coomes & Grubb 2000). To investigate the hypothesis that P availability underlies the constrained distributions of these species, we added P to seedlings of all species in both low- and moderate-fertility soils. All treatments in the experiment were conducted in both the understorey and in forest gaps to investigate whether responses were light dependent.

Methods

SITE DESCRIPTION

The study was carried out in Lambir Hills National Park (4°20′ N, 113°50′ E; hereafter Lambir), on the north-west

coast of Borneo in Sarawak, Malaysia. Lambir includes 6800 ha of tropical, lowland, mixed dipterocarp and kerangas forest. The climate is aseasonal with average annual rainfall of *c*. 3000 mm and mean monthly rainfall > 100 mm for all months. Periodic short-term drought may have a significant impact on floristic patterns in this region (Becker & Wong 1992).

The topography of Lambir is dominated by an east–west escarpment which reaches a maximum elevation of 465 m (Watson 1985). This is the remnant of an uplifted and eroded coastal delta which formed during the early to mid-Miocene (Mulock Houwer 1967). The rocks are sedimentary, composed of alternating layers of sandstone and shale. Complex topography and frequent landslides have exposed and mixed these layers. The Lambir soils vary in depth, sand content and, consequently, water-holding capacity, as well as nutrient concentrations (Ashton & Hall 1992; Hirai *et al*. 1997; Palmiotto 1998). Sandstone ridges and dip slopes bear deep, yellow, nutrient-poor, leached, drought-prone humult ultisols with a thick (5–15 cm deep) surface horizon of densely rooted raw humus. In contrast, soils in gullies and lower areas over shale are deep yellow–red udult ultisols with higher nutrient concentrations, greater water-holding capacity and a surface organic layer of leaves with no root mat (< 1 cm deep).

In 1991, a long-term research project was initiated in Lambir to monitor all trees ≥ 1 cm diameter at breast height (d.b.h) in 52-ha of forest following similar studies at Barro Colorado Island, Panama (Hubbell &

Foster 1983) and Pasoh Forest Reserve, west Malaysia (Manokaran *et al*. 1990). The tree flora of Lambir is exceptionally diverse with 1173 tree species in the 52-ha plot. Both floristic composition and stand structure vary significantly between the humult and udult ultisols represented within the plot (Lee *et al*. 2002).

STUDY SPECIES

Six shade-tolerant canopy or emergent tree species were selected, five of which are abundant in the 52-ha plot. *Dryobalanops aromatica* Gaertn. f. (Dipterocarpaceae), *Shorea laxa* Sloot. (Dipterocarpaceae) and *Swintonia schwenkii* (Teijsm. & Binn.) Teijsm. & Binn. ex Hook. f. (Anacardiaceae) are largely restricted to nutrient-poor humult ultisols in the 52-ha plot, whereas *Dryobalanops lanceolata* Burck and *Hopea dryobalanoides* Miq. (both Dipterocarpaceae) are restricted to more nutrient-rich udult ultisols (S.J. Davies & M. Potts unpublished data; see also Ashton 1964; Itoh 1995a; Hirai *et al*. 1997; Lee *et al*. 2003; Fig. 1). For *D. aromatica*, *D. lanceolata* and *H. dryobalanoides*, these soil associations are known to occur throughout the species ranges in north-west Borneo (Potts *et al*. 2002). A sixth species, *Shorea balanocarpoides* Sym. (Dipterocarpaceae), al-though widely distributed, does not occur within the plot, but is thought to occur primarily on udult soils (Potts *et al*. 2002), it is regularly found on both soils and is therefore included as a relatively widely distributed species.
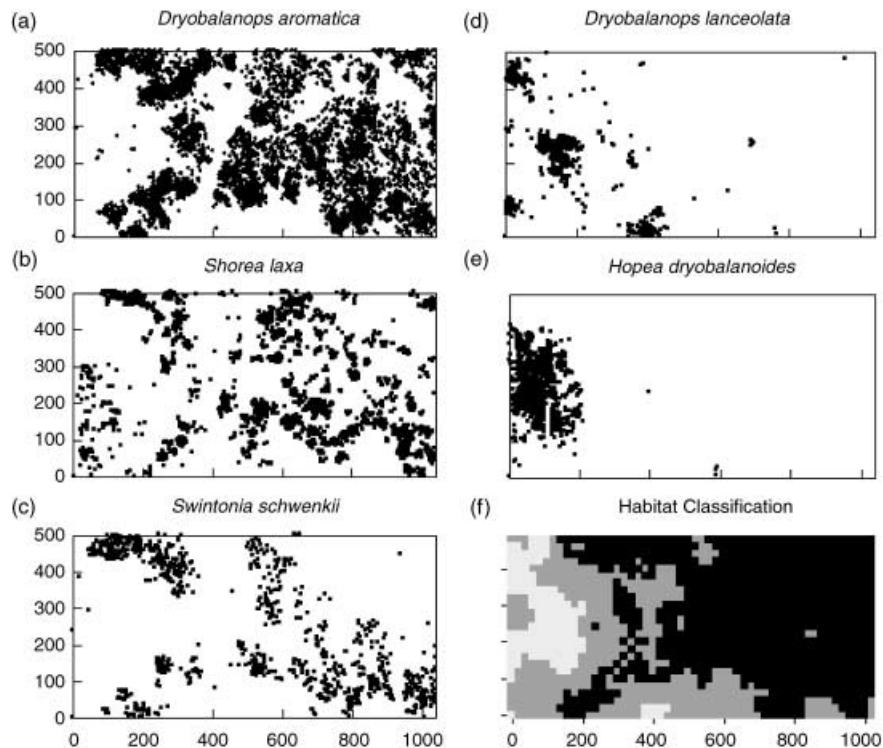

Fig. 1 Spatial distribution in the 52-hectare plot at Lambir Hills National Park, Sarawak, Malaysia, for five of the six species used in this study: (a–c) humult (d–e) udult soil species. (f) Habitat classification based on an analysis of soil and topographic variation in the plot (S.J. Davies, S. Tan & M. Potts, unpublished data): humult soils are in black and udult soils are in white, with intermediate soils in grey. *Shorea balanocarpoides* does not occur within the plot.

EXPERIMENTAL DESIGN AND IMPLEMENTATION

Six sites separated by at least 400 m were chosen within the primary forest at Lambir, three on humult ultisols and three on udult ultisols. Each of the six sites consisted of paired high-light and low-light plots located just below ridge tops and chosen to be similar in topographic features. High-light plots were established in canopy gaps and received 7.6 ± 3.5 mol m^{-2} day^{-1} ($17.1 \pm 7.4\%$ of full sunlight measured in the open), and low-light plots were in the adjacent forest understorey and received 0.6 ± 0.3 mol m^{-2} day^{-1} ($1.3 \pm 0.01\%$ of full sun). Photosynthetically active radiation was measured on several days in the centre of each plot at 1 m above the ground using quantum sensors (LI-190SA and 190SZ; LiCor, Lincoln, NE, USA). There were no significant differences in light levels between soil types in either high- or low-light plots.

Each of the 12 experimental plots (2 soils × 3 sites per soil type × 2 light treatments) was 5 × 9 m in size and was divided into six equal areas. Three soil treatments (P-addition, humus removal and control) were each applied to two areas (treated as blocks for analysis) in each plot, with a 0.5-m buffer zone between treatments. Phosphorus addition involved spreading 0.53 g m^{-2} of powdered super-phosphate evenly over the soil surface (Yates Gro-plus 0-10-0, Yates New Zealand Ltd, Auckland, NZ) monthly from July to December 1994. Humus layer removal involved the complete removal of the surface organic material (litter and root mat layers) down to the mineral soil, with new leaf-litter inputs removed every 2 weeks. Because the humus-removal treatment had no significant effects on soil properties or measured plant responses, the results of this treatment are not further considered in this paper. The remaining plots were untreated controls. Prior to transplanting, vegetation < 1 m in height was cleared from within all plots by cutting at ground level without physically disturbing the soil surface or roots.

Seedlings were collected from two or three parent tree populations per species from within Lambir in August and September 1993 and transplanted to the experimental plots in November 1993. Seedlings originated from the 1992 mast-fruiting event. To ensure that seedlings were from the same cohort and of a similar size, only seedlings with initial pairs of leaves were collected. Bare-root seedlings were temporarily planted into polythene pots (2250 cm^3) containing topsoil from either the udult or humult soil depending on the plot to which they were to be transplanted. The potting soil was collected from the top 20 cm of surface soil from the forest at Lambir, and was sieved using 2-cm wire mesh to remove large roots and woody debris. Seedlings were grown under 85% shade cloth for 6 to 8 weeks prior to transplanting to the field. Five or six seedlings of each of the six species were planted in each treatment combination. In total, 2379 seedlings were planted (6 species × 2 soil × 3 sites per soil type × 2 light × 3 soil treatments × 2 blocks × 5–6 seedlings). Seedling availability was limited in *Shorea balanocarpoides*, *S. laxa* and *Swintonia schwenkii*, so most treatment combinations had five seedlings. Two seedlings that died within the first month were replaced by conspecific seedlings from the nursery.

SOIL AND PLANT TISSUE ANALYSIS

Soil samples were collected from all 12 experimental plots prior to transplanting ($n = 3$ per plot) and at the end of the experiment ($n = 2$ per soil treatment per plot). Each sample was a composite of 10 randomly collected cores, 2 cm diameter × 15 cm deep, from the top of the mineral soil. The leaf litter and humus layer (where present) were removed before soil sampling. Soils were air dried prior to analysis. Soils were analysed for total P concentration using a modified wet digestion procedure with hydrogen peroxide, sulphuric acid and lithium sulphate (Parkinson & Allen 1975). Extractable soil P concentrations were determined by shaking 1 g of soil for 40 s in 10 mL of 0.03 M ammonium fluoride and 0.1 M hydrochloric acid (Bray-2 method), followed by continuous flow analysis of the extracted solution (Enviroflow 3500, Perstorp Analytical Environmental, Wilsonville, OR, USA). Exchangeable base cations were extracted from the soil using a neutral salt extractant of 1 M ammonium chloride in a mechanical vacuum extractor (Centurion International, Lincoln, NE, USA; Suarez 1996). Total and extractable nutrient concentrations were measured on a Perkin-Elmer Optima inductively coupled plasma spectrophotometer. Total C and N were analysed using a dry combustion technique on a Leco CHN-600 elemental analyser (Olsen & Sommers 1982).

Leaf and root tissue nutrient concentrations were determined on seedlings from a subsample of species and treatments at the end of the experiment. Leaf nutrient concentrations were determined on seedlings of four species from control treatments in gaps on both soils. In addition, for two species leaf and fine-root nutrient concentrations were determined for seedlings in control and P-added treatments in gaps on both soils. Tissue nutrient concentrations were determined using a modified wet oxidation procedure with sulphuric acid (Parkinson & Allen 1975). For fine roots, samples were a composite of 1–5 seedlings in each site for each treatment combination.

The degree of ectomycorrhizal colonization of fine roots was assessed in *D. lanceolata* and *D. aromatica*. Subsamples of roots were taken from four seedlings growing in gaps in control and P-addition treatments in each experimental site. Roots were stored in FAA in the field and ectomycorrhizal colonization was determined under a dissecting scope following Vogt *et al*. (1982).

DATA COLLECTION AND ANALYSIS

Initial seedling height and diameter were measured in November 1993 soon after transplanting. Height and

diameter growth, and survival were assessed after 20 months. Seedlings damaged by branch falls were excluded from height growth comparisons. After 20 months, approximately one third of the seedlings were harvested (144 seedlings per species: 2 soil × 3 sites per soil type × 2 light × 3 treatments × 2 blocks × 2 randomly selected seedlings). Harvested seedlings were separated into leaves, stems, and fine (< 2 mm diameter) and coarse (≥ 2 mm) roots, dried to constant weight at 70 °C, and weighed. Root systems were carefully excavated to minimize breakage and loss of fine-root biomass. The method was effective as severed roots ≥ 2 mm in diameter were found on only 4.6% of the individuals harvested. Specific leaf area (SLA) was also measured, but only on seedlings from control treatments in the two soils and two light environments.

Seedling growth was analysed with a nested-factorial analysis of variance (Montgomery 1991), using a linear model including the terms: species (six levels), light (two levels), soil (two levels), site (three levels, nested within soil), soil treatment (two levels, P addition and control) and all interactions, except site–soil interactions, which cannot be estimated. All factors were coded as fixed except site which was random. This model is one form of the widely used split-plot analysis of variance (Winer 1971; Underwood 1997). Species effects and interactions were significant in all analyses (see below) so species were analysed separately. Growth rates were $\log_{10}$-transformed prior to analysis. Comparisons of means were conducted for significant factors using Tukey HSD tests. Mortality was initially modelled using logistic regression with the same terms as in the linear model, although, due to limited sample sizes, sites had to be pooled. Data are presented with species analysed separately and with treatments pooled.

Biomass allocation ratios (e.g. leaf : root ratio) were analysed using the same model as for growth analyses. Species effects were again significant, so species were analysed separately. Site and treatment effects were pooled for data presentation. The few cases of significant P-addition effects are described in the text. Due to the potential for size-dependent shifts in allocation patterns, analyses of covariance (ANCOVAs) were used to test for differences in the slope and intercept of the relationship between leaf mass and root mass among soils and light levels for each species (Müller *et al.* 2000; Shipley & Meziane 2002). Single-factor ANCOVAs used reduced major axis (RMA) regression with (S)MATR (Falster *et al.* 2003). Two-factor (soils and light) ANCOVAs used least squares (LS) regression. Results of these LS regressions were consistent with single-factor RMA regressions, so only the two-factor LS analyses are presented.

Pre-experiment soils were compared with two-factor ANOVAs with terms for soil and light. Post-experiment soils were compared with three-factor ANOVAs with terms for soil, light and treatment. Due to limited sample sizes, sites were pooled for both analyses. All analyses were conducted using JMP version 4.0.4 (SAS Institute, Cary, North Carolina).

Results

SOILS

Prior to the experiment, extractable concentrations of Ca, K and Mg, and total P were significantly greater in udult than in humult soils (Table 1; Fig. 2). In addition, percentage C and consequently C : N ratios were lower in udult soils. Extractable P did not differ significantly between the soils prior to the experiment. There were no significant differences between gap and understorey nutrient concentrations for humult soils, but for udult soils, gap microsites generally had higher nutrient concentrations than understorey microsites, albeit significantly so only for Ca.

Adding P resulted in significantly greater levels of extractable P at the end of the experiment in both soils and light levels (Fig. 2). Concentrations of total P were not significantly greater in P-addition than in control treatments on either soil (Fig. 2). Adding P increased Ca concentrations in humult soils in gaps, but other measured soil nutrients were not significantly affected by P-addition (Table 1).

SURVIVAL

In gaps, *D. lanceolata*, *S. balanocarpoides* and *D. aromatica* had significantly higher survival rates in udult than in humult soils over the 20 months of the experiment (Table 2). For these three species, as well as *H. dryobalanoides*, survival rates were greater in gaps in either udult or both soil types (Table 2). P addition did not significantly affect survival in any of these four species.

Shorea laxa and *Swintonia schwenkii* had no significant differences in survival rates between soils or light levels. However, survival in both species was significantly affected by the addition of P; in *S. laxa* survival was 14% greater and in *S. schwenkii* survival was 13% less following P-addition (with soils and light levels pooled).

GROWTH

Seedling growth differed significantly among species, soils and light environments in this experiment (Table 3). Significant interactions in the full models indicate that soil and light effects on growth differed among the species (Table 3). The addition of phosphorus had relatively weak and overall non-significant effects on growth, although in some of the replicate sites growth was significantly affected by phosphorus addition (see below; Table 3).

All six species had significantly higher growth rates in gaps than in the understorey (Fig. 3). Low-light plants of all species had close to zero average growth over the 20-month period. Mean diameter growth in low light ranged from −0.1 to +0.3 mm year^{-1} and mean height growth ranged from 0.4 to 3.7 cm year^{-1} among species, soils and treatment combinations. In contrast, high-light growth averaged 0.4–2.5 mm diameter year^{-1} and

Table 1 Mean percentage C and N concentrations, C : N ratios, and extractable cation concentrations for soils in experimental sites in Lambir. Mean values (± 1 SE) were based on $n = 7–9$ samples for pre-experiment and $n = 4–6$ for post-experiment analyses, with values pooled among sites. Soil treatments were: Con, control; +P, phosphorus addition. Different letters following means indicate significant differences among means at a particular sampling time. Data were $\log_{10}$-transformed prior to analysis

Soil	Light	Treatment	C (%)	N (%)	C : N ratio	K (cmolc kg^{-1})	Mg (cmolc kg^{-1})	Ca (cmolc kg^{-1})
Pre-experiment								
Humult	Forest		1.95 (0.17) a	0.13 (0.005) a	14.6 (0.94) a	0.10 (0.02) b	0.17 (0.04) b	0.04 (0.01) c
Humult	Gap		1.93 (0.17) a	0.13 (0.012) a	16.4 (2.38) a	0.08 (0.01) b	0.18 (0.02) b	0.05 (0.01) c
Udult	Forest		1.42 (0.06) b	0.15 (0.005) ab	9.6 (0.35) b	0.13 (0.01) a	0.33 (0.05) a	0.14 (0.02) b
Udult	Gap		1.67 (0.13) b	0.18 (0.010) b	9.5 (0.51) b	0.14 (0.01) a	0.72 (0.14) a	0.40 (0.13) a
Post-experiment								
Humult	Forest	Con	2.21 (0.39) a	0.14 (0.015) bc	16.0 (1.10) abc	0.12 (0.03) abc	0.18 (0.04) b	0.04 (0.01) cd
Humult	Forest	+P	2.13 (0.34) a	0.13 (0.014) c	16.2 (1.24) abc	0.08 (0.01) bc	0.12 (0.04) b	0.13 (0.05) abcd
Humult	Gap	Con	2.43 (0.28) a	0.13 (0.019) c	20.9 (4.63) a	0.06 (0.01) c	0.15 (0.03) b	0.04 (0.02) d
Humult	Gap	+P	1.96 (0.16) a	0.12 (0.015) c	16.4 (0.93) ab	0.06 (0.00) c	0.12 (0.03) b	0.24 (0.12) abc
Udult	Forest	Con	1.69 (0.12) a	0.16 (0.006) abc	10.8 (0.71) cd	0.11 (0.01) abc	0.30 (0.05) ab	0.14 (0.03) bc
Udult	Forest	+P	2.24 (0.08) a	0.19 (0.009) ab	11.8 (0.36) bcd	0.18 (0.02) a	0.33 (0.07) ab	0.72 (0.14) ab
Udult	Gap	Con	1.99 (0.09) a	0.21 (0.009) a	9.8 (0.50) d	0.14 (0.01) ab	0.88 (0.20) a	0.38 (0.03) ab
Udult	Gap	+P	2.15 (0.09) a	0.21 (0.007) a	10.2 (0.49) d	0.14 (0.01) ab	0.57 (0.11) a	0.81 (0.14) a

Table 2 Percentage mortality after 20 months for seedlings of six species of trees in Lambir based on $n = 359–432$ seedlings per species. Different letters indicate significant differences in mortality within species from logistic regression analysis. Site and treatment effects were pooled for this analysis

		Mortality (%)	
Species	Soil	Forest	Gap
D. lanceolata	Humult	10.3 ab	4.7 b
	Udult	13.9 a	0.0 c
H. dryobalanoides	Humult	25.9 a	10.2 b
	Udult	38.0 a	12.0 b
S. balanocarpoides	Humult	27.5 a	22.8 a
	Udult	33.3 a	7.9 b
D. aromatica	Humult	25.0 a	11.3 b
	Udult	27.8 a	0.9 c
S. laxa	Humult	29.6 a	21.1 a
	Udult	28.0 a	19.3 a
S. schwenkii	Humult	16.1 a	11.7 a
	Udult	18.5 a	9.9 a

Table 3 Summary of *P*-values from full model analyses of relative diameter growth and final biomass. Analyses are based on $\log_{10}(x + 1)$ transformed values. Significant effects are indicated with asterisks (**$P < 0.01$; *$P < 0.05$)

Effect	Diameter growth	Final biomass
Species	< 0.001**	< 0.001**
Soil	0.942	0.784
Site(soil)	0.189	0.541
Light	< 0.001**	< 0.001**
Treatment	0.093	0.266
Species × soil	0.002**	0.077
Species × site(soil)	0.245	0.132
Species × light	< 0.001**	< 0.001**
Species × treatment	0.284	0.641
Soil × light	0.042*	0.049*
Soil × treatment	0.642	0.876
Site(soil) × light	0.465	0.600
Site(soil) × treatment	0.261	0.656
Light × treatment	0.129	0.176
Species × soil × light	0.005**	< 0.001**
Species × soil × treatment	0.099	0.287
Species × site(soil) × light	0.112	0.468
Species × site(soil) × treatment	0.777	0.393
Species × light × treatment	0.696	0.073
Soil × light × treatment	0.646	0.837
Site(soil) × light × treatment	0.159	0.005**
Species × soil × light × treatment	0.176	0.165
Species × site(soil) × light × treatment	0.064	0.045*

4.5–38.1 cm height year^{-1} among species, soils and treatments.

Four of the six species had significant differences in relative diameter growth rates (RGR$_d$) between humult and udult soils in at least one light environment (Fig. 3). *Shorea laxa* and *Swintonia schwenkii* had significantly higher RGR$_d$ in humult soils in both light environments (Fig. 3). In contrast, *D. lanceolata* and *H. dryobalanoides* had significantly higher RGR$_d$ in udult soils, but only
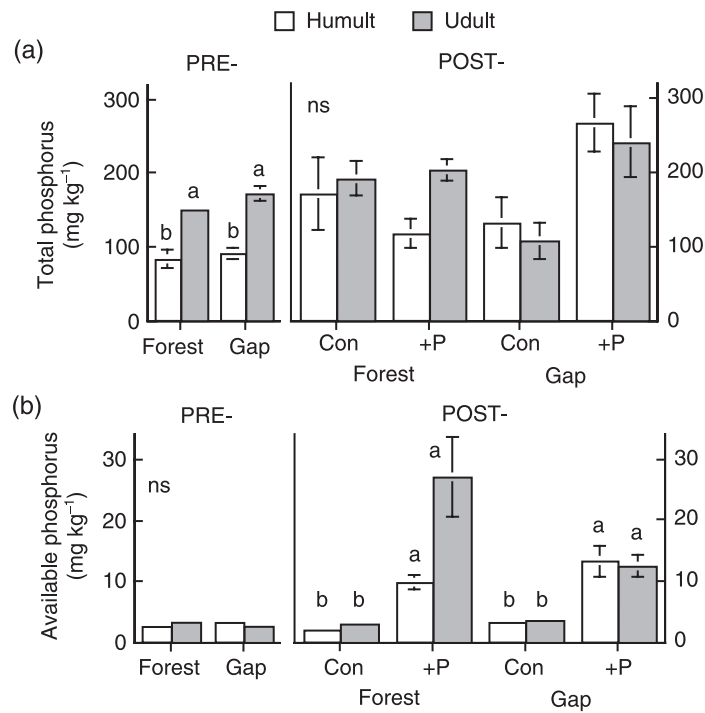
Fig. 2 Mean (± 1 SE) extractable and total soil phosphorus concentrations in the experimental plots prior to and at the end of the 20-month experiment. Pre-experiment samples are from gap and forest understorey microsites, based on 9 samples per soil. Post-experiment samples are from control (Con) and phosphorus addition (+P) treatments in gaps and the understorey, based on 6 samples per treatment combination. Different letters indicate significant differences among means within a sampling period, and 'ns' indicates no significant soil, light or treatment effects.

Table 4 Mean final biomass (g, ± 1 SE) of harvested seedlings of six tree species grown in two soil types (humult, udult) and two light environments (gap, forest understorey). Significant within-species differences in mean biomass among environments are indicated by different letters. Tests were conducted on $\log_{10}$-transformed biomass with $n = 33$–37 seedlings per environment. Sites and soil treatments were pooled for this analysis (see Methods section)

Soil	Light	*Dryobalanops lanceolata*	*Hopea dryobalanodes*	*Shorea balanocarpoides*	*Dryobalanops aromatica*	*Shorea laxa*	*Swintonia schwenkii*
Humult	Forest	3.18 (0.27) c	0.33 (0.03) c	2.36 (0.15) b	2.27 (0.18) b	3.05 (0.20) b	3.18 (0.19) c
Udult	Forest	2.51 (0.16) c	0.20 (0.02) c	2.18 (0.11) b	1.60 (0.11) b	2.91 (0.14) b	2.26 (0.18) d
Humult	Gap	14.82 (1.65) b	1.13 (0.18) b	6.28 (0.65) a	13.29 (1.38) a	9.56 (0.79) a	10.53 (1.19) a
Udult	Gap	33.93 (3.85) a	4.92 (0.79) a	5.32 (0.45) a	17.78 (2.72) a	8.22 (0.66) a	6.81 (0.66) b

for plants growing in gaps (Fig. 3). RGR_d of *S. balanocarpoides* and *D. aromatica* did not differ significantly between udult and humult soils (Fig. 3).

Differences in seedling biomass after 20 months were similar to those for RGR_d (Table 4). All species had significantly greater final biomass in gaps. In gaps, *D. lanceolata* and *H. dryobalanoides* had significantly greater biomass in udult than in humult soils, and *S. schwenkii* had significantly greater biomass on humult soils (Table 4).

In four of the six species, P addition had no significant effect on RGR_d or final biomass. In gaps, RGR_d and final biomass of *D. lanceolata* and *H. dryobalanoides* were negatively affected by P addition in some but not all of the replicate sites (Fig. 3).

BIOMASS ALLOCATION

The intercept and/or the slope of the allometric relationship between leaf mass and root mass differed

significantly among soil types or light environments in five of the six species (Table 5). In three species, *D. lanceolata*, *H. dryobalanoides* and *D. aromatica*, relative allocation to leaves was significantly greater in udult soils (Fig. 4; Table 5). For species other than *H. dryobalanoides*, this effect was only significant in gaps. In *S. laxa*, relative allocation to leaves was greater in gaps than in the understorey on both soil types (Table 5).

In two species, *D. aromatica* and *S. schwenkii*, P addition significantly affected leaf–root allometric relationships (data not shown). In both species, leaf allocation was reduced and root allocation increased in P-addition treatments on humult soils in gaps.

Biomass allocation to fine roots (fine-root weight ratio, FRWR) was greater in humult soils and in gaps (Fig. 4). In gaps, all species except *S. schwenkii* had significantly greater FRWR in humult soils. In the understorey, three species had significantly greater FRWR in humult than in udult soils.
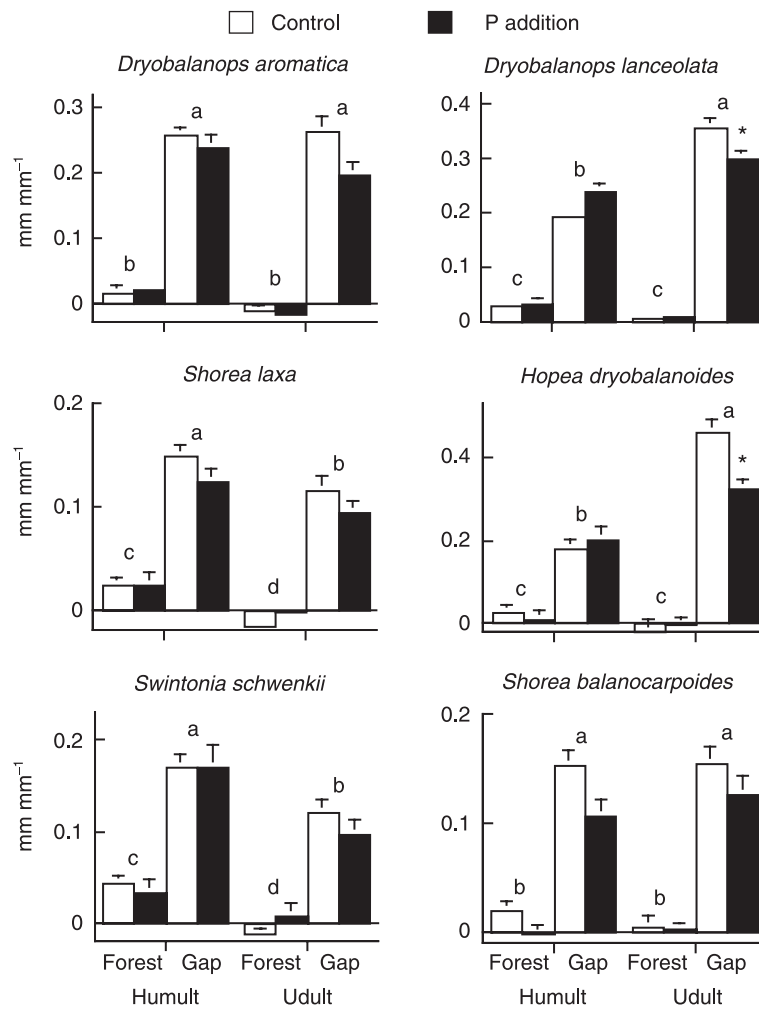
Fig. 3 Mean relative diameter growth rates (± 1 SE, *n* = 12–36) for seedlings of six species grown in two soils (humult, udult), two light environments (gap, forest understorey), and two soil treatments (control and P addition). Different letters indicate significant differences in relative growth rate among light and soil treatments. Asterisks in *D. aromatica* and *H. dryobalanoides* indicate that P addition had a significant negative effect on growth in some but not all sites.

Table 5 Summary of significant *P*-values resulting from least squares models relating leaf mass to root mass (RM) in seedlings of six tree species grown in two light environments (L) and two soils (S). Leaf mass was used as the dependent variable in these analyses. Values were log$_{10}$-transformed prior to analysis. Site and soil treatment effects were pooled for these analyses (see Methods section). Significant effects are indicated with asterisks (**$P < 0.01$; *$P \leq 0.05$). Results were consistent with single-factor reduced major axis regression results (see Methods section)

Effect	*Dryobalanops lanceolata*	*Hopea dryobalanoides*	*Shorea balanocarpoides*	*Dryobalanops aromatica*	*Shorea laxa*	*Swintonia schwenkii*
Log$_{10}$(RM)	< 0.001**	< 0.001**	< 0.001**	< 0.001**	< 0.001**	< 0.001**
Soil (S)	0.167	< 0.001**	0.509	0.108	0.247	0.020*
Light (L)	0.705	0.080	0.821	0.044*	0.016*	0.050*
S × L	0.009**	0.555	0.087	< 0.001**	0.491	0.215
Log$_{10}$(RM) × S	0.085	0.662	0.333	0.089	0.453	0.171
Log$_{10}$(RM) × L	0.498	0.884	0.285	0.014*	0.451	0.036*
Log$_{10}$(RM) × S × L	0.232	0.012*	0.099	0.322	0.183	0.033*

Specific leaf area (SLA) and leaf area ratio (LAR) were greater in the understorey for most species, although due to limited sample sizes these effects were significant in only four and three species, respectively (Table 6). Both SLA and LAR were significantly greater in udult soils than in humult soils for gap plants of *D. lanceolata* and *D. aromatica*.

NUTRIENT UPTAKE AND MYCORRHIZAL INFECTION

At the end of the experiment, leaf P concentrations were significantly greater for plants on udult soils than on humult soils for all four species tested (Table 7). Leaf concentrations of N, Al, Fe, Mn, Ca and Mg were
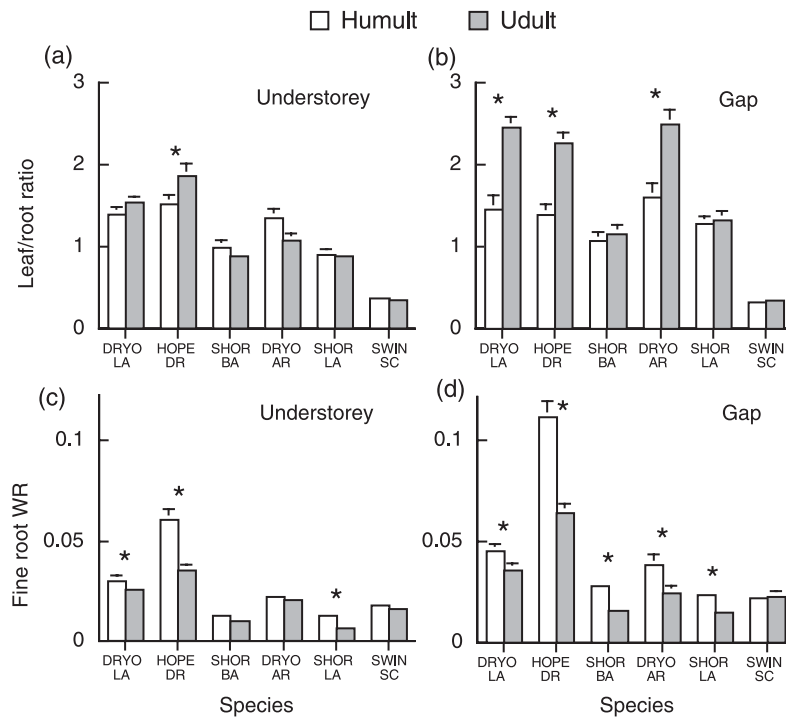
Fig. 4 Leaf:root weight ratio (a,b) and fine-root weight ratio (c,d) for seedlings of the six species grown in gaps and the forest understorey on humult and udult soils. Means ($\pm$ 1 SE) from values pooled for different soil treatments. Species are listed by 6-letter codes as in Table 6. Significant differences ($P < 0.05$) between soils for each light level are indicated with asterisks based on the allometric analysis in Table 5 for parts (a) and (b), and based on ANOVAs for parts (c) and (d).

Table 6 Leaf allocation patterns in seedlings of six species grown in two soils and two light environments. SLA and LAR were measured for untreated control plants only (see Methods section). Species are listed by the first four letters of the genus and the first two letters of the species. Different letters after the means indicate significant differences among species within the four growth conditions (two soils and two light levels). Different letters at the end of each row indicate significant within-species differences among environments. Means ($\pm$ 1 SE) based on n = 7–12 seedlings

	Forest understorey		Gap		Within-species comparisons
	Humult	Udult	Humult	Udult	
Specific leaf area (SLA, cm^2 g^{-1})					
DRYO LA	207.0 (4.9) b	205.7 (4.7) a	152.6 (4.6) a	172.0 (4.8) b	a/a/c/b
HOPE DR	246.5 (13.6) a	213.1 (7.5) a	189.4 (4.5) a	205.8 (4.6) a	a/b/b/b
SHOR BA	142.1 (6.0) d	144.8 (8.1) c	116.3 (3.0) a	117.5 (6.2) cd	a/a/b/b
DRYO AR	174.3 (5.3) c	183.1 (9.7) ab	137.2 (3.5) bc	153.1 (4.3) b	ab/a/c/ab
SHOR LA	111.3 (4.4) e	125.3 (11.8) c	90.9 (4.9) e	106.1 (4.5) d	ab/a/b/ab
SWIN SC	143.6 (3.7) d	154.0 (7.2) bc	129.7 (4.4) cd	131.9 (2.6) c	ab/a/b/b
Leaf area ratio (LAR, cm^2 g^{-1})					
DRYO LA	79.7 (7.3) b	87.9 (4.5) a	53.5 (5.2) b	78.2 (4.5) ab	a/a/b/a
HOPE DR	105.4 (10.0) a	88.1 (7.7) a	78.4 (6.9) a	96.2 (6.0) a	a/a/a/a
SHOR BA	51.2 (6.0) cd	53.3 (3.8) b	32.9 (3.6) c	37.4 (5.6) c	a/a/b/b
DRYO AR	70.4 (4.4) bc	62.9 (7.0) b	56.2 (2.3) b	74.5 (4.2) b	ab/ab/b/a
SHOR LA	34.5 (2.4) d	41.3 (5.8) b	34.8 (2.6) c	39.6 (3.9) c	a/a/a/a
SWIN SC	59.8 (3.5) bcd	64.2 (7.1) ab	48.8 (2.9) bc	50.6 (2.5) c	a/a/b/b

also greater on the more fertile udult soils for seedlings of one or more of the four species tested. In the two species that had their leaves and fine roots tested following P addition, P addition significantly increased leaf and fine-root P concentrations on both soil types (Fig. 5).

The roots of untreated seedlings of *D. lanceolata* had significantly greater mycorrhizal colonization on udult soils (5918 $\pm$ 1092 g^{-1} dry weight) than on humult soils (2519 $\pm$ 703 g^{-1}; $P < 0.05$; n = 11–13 seedlings). There was no significant difference in mycorrhizal colonization in *D. aromatica* between soil types (mean = 3321 g^{-1}). Phosphorus addition did not significantly affect mycorrhizal colonization in either species, although *D. lanceolata* seedlings had 33% lower colonization levels on udult soils following *P*-addition.

Table 7 Leaf nutrient concentrations in untreated (control) seedlings of four species at the end of the experiment. Species are listed as in Table 6. Leaves were only taken from seedlings in gaps in control treatments on the two soils (see Methods section). Nitrogen values are in percentage, and all other nutrients are in mg g^{-1}. Means (± 1 SE) based on 10–13 seedlings. Asterisks indicate significant differences ($P < 0.05$) in nutrient concentrations between the two soils for each species

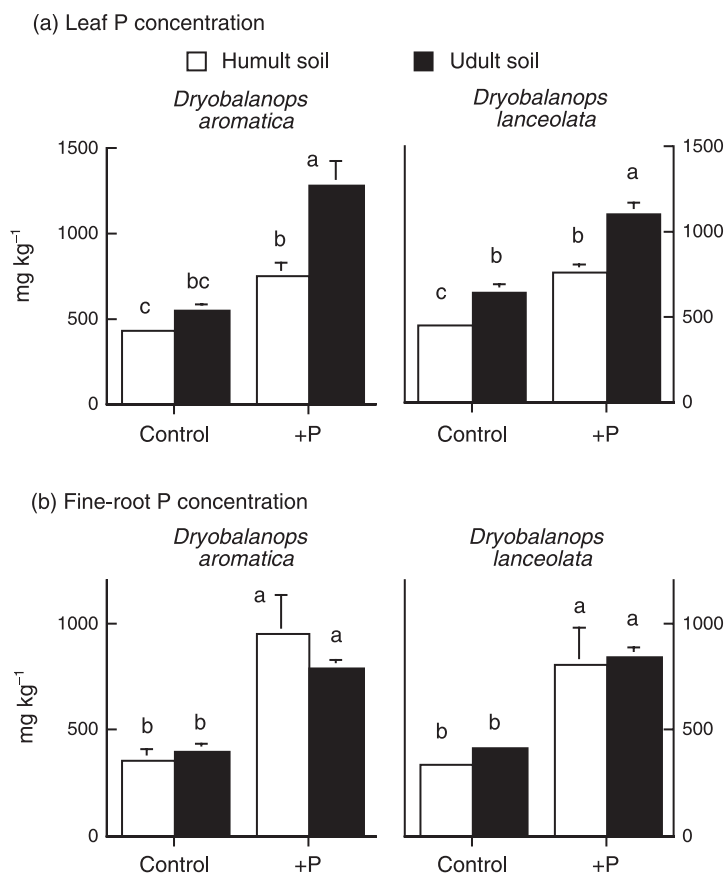| Species	Soil	P	N	Al	Fe	Mn	Ca	Mg
DRYOLA	Humult	0.45 (0.03)	1.17 (0.04)	0.06 (0.01)	0.05 (0.00)	0.03 (0.00)	1.64 (0.29)	1.59 (0.09)
DRYOLA	Udult	0.64 (0.04)**	1.41 (0.07)**	0.12 (0.03)**	0.10 (0.02)**	0.10 (0.03)**	3.06 (0.37)**	1.69 (0.12)
DRYOAR	Humult	0.44 (0.02)	1.41 (0.02)	0.07 (0.01)	0.06 (0.01)	0.13 (0.02)	1.84 (0.29)	0.99 (0.06)
DRYOAR	Udult	0.55 (0.03)**	1.48 (0.06)	0.07 (0.01)	0.07 (0.01)	0.34 (0.06)**	2.43 (0.11)**	0.98 (0.05)
SHORBA	Humult	0.42 (0.03)	1.18 (0.02)	0.07 (0.03)	0.09 (0.02)	0.05 (0.01)	2.57 (0.46)	1.01 (0.10)
SHORBA	Udult	0.56 (0.05)**	1.51 (0.18)	0.11 (0.01)**	0.09 (0.01)	0.09 (0.02)**	4.42 (0.37)**	1.13 (0.09)
SHORLA	Humult	0.43 (0.02)	1.14 (0.06)	0.08 (0.02)	0.08 (0.01)	0.11 (0.02)	1.61 (0.22)	2.17 (0.11)
SHORLA	Udult	0.55 (0.02)**	1.20 (0.06)	0.21 (0.03)**	0.16 (0.02)**	0.19 (0.02)**	2.72 (0.12)**	3.35 (0.19)**

Fig. 5 Leaf and fine-root P concentrations for two species for control and *P*-addition seedlings grown in two soils (humult and udult). Means (± 1 SE) based on 7–12 seedlings for leaves, and 3 samples for fine roots (see Methods section).

Discussion

Strong biases in the spatial distributions of tropical tree species in relation to edaphic variation have been widely reported (Swaine 1996; Clark *et al.* 1998; Svenning 2001; Lee *et al.* 2002). However, very few tests of soil-related differences in tree performance have been conducted in the field (e.g. Davies 2001; ter Steege 1994). Soil-related habitat specialization, as shown by significant differences in seedling performance between soil types, was found in four of the six species investigated in this study. *Dryobalanops lanceolata* and *Hopea dryobalanoides* had spatial distribution patterns in natural forest biased toward higher-nutrient udult soils, and had significantly greater relative growth rates in udult soils. *Shorea laxa* and *Swintonia schwenkii* had the opposite pattern with spatial distribution biases and higher growth rates on nutrient-poor humult soils. In contrast, the growth of *Dryobalanops aromatica*, a species of humult soils, and *Shorea balanocarpoides*, a more widely distributed species, were not significantly affected by soil type in this experiment.

PERFORMANCE AND ALLOCATION PATTERNS

Despite significant among-species differences in growth response to soils, the rank order of species performance

Table 8 Rank of relative diameter growth rates among the six species grown in two soils and two light environments, with treatments pooled. Ranks are indicated from highest, 1, to lowest, 6, growth rates. Different letters after the ranks for GAP treatments indicate significant differences in mean growth rates among species. There were no significant differences in growth rates among species for understorey plants. Species are arranged as in Table 2. Letters after the species codes indicate species habitat associations: h – humult, u – udult, w – widely distributed

Species		Understorey		Gap	
		Humult	Udult	Humult	Udult
DRYOLA	(u)	3	2	3 ab	2 b
HOPEDR	(u)	2	1	2 ab	1 a
SHORBA	(w)	6	3	5 c	4 d
DRYOAR	(h)	5	6	1 a	3 c
SHORLA	(h)	4	5	6 c	6 d
SWINSC	(h)	1	4	4 b	5 d

was similar between soil types (Table 8; Kendall's Coefficient of Concordance, $W = 0.5$, $P = 0.06$). In the forest understorey, growth rates did not differ significantly among species. In gaps on udult soil, udult-soil species significantly outperformed all other species, but, on humult soil, the humult-soil species did not significantly outperform the udult species (the udult species had similar mean growth rates to two of the humult species and had significantly higher growth rates than one of the humult species). Performance ranking on nutrient-poor humult soils was more strongly associated with allocation patterns than with soil preferences. *Dryobalanops lanceolata*, *H. dryobalanoides* and *D. aromatica* had the highest growth rates on both soils, and had significantly different allocation patterns to the other species. On udult soil in gaps, these three species had significantly greater relative leaf allocation (Fig. 4b), less root allocation, greater fine root allocation (Fig. 4d), and higher SLA and LAR than the other species (Table 6). On humult soils, these three species greatly increased allocation to roots, particularly to fine roots, and reduced leaf allocation. However, despite reduced allocation to leaves on humult soils, these species maintained greater LARs than the other three species, through the combined effects of greater leaf allocation and higher SLA (Table 6). On humult soils, RGR_d was strongly positively correlated with both LAR (Spearman $r_s = 0.886$, $P = 0.012$) and SLA ($r_s = 0.829$, $P = 0.042$) among species. Greater LARs probably resulted in higher growth rates on humult soils, because photosynthetic rates of seedlings differ only slightly among the six species (Palmiotto 1998). RGR is strongly positively correlated with LAR and SLA across a wide range of plant species (Reich *et al*. 1992; Cornelissen *et al*. 1996), and species with higher RGRs tend to perform better in both low and high soil nutrient environments (Grubb *et al*. 1996; Huante *et al*. 1995).

The species with the highest RGRs, LARs, SLAs and the greatest plasticities (*sensu* Strauss-Debenedetti

& Bazzaz 1991) in allocation patterns in this study were the species of the high-nutrient udult soils. This pattern has been reported from both temperate and tropical forests (Grime 1979; Chapin *et al*. 1986; Grubb *et al*. 1996). Species of low-nutrient, drought-prone soils typically have relatively thick, long-lived leaves, and low plasticities of SLA and root allocation (Coomes & Grubb 2000). Comparison of the species pairs that had significant soil-related growth responses in this experiment, *D. lanceolata* and *H. dryobalanoides* (udult species) vs. *S. schwenkii* and *S. laxa* (humult species), illustrates this pattern clearly. However, the humult-soil species, *D. aromatica*, did not fit the pattern. Although *D. aromatica* is a species associated with humult soils throughout its geographical range (Ashton 1964; Baillie *et al*. 1987; Potts *et al*. 2002), it had allocation patterns more similar to the udult species. Nevertheless, there were subtle differences between *D. aromatica* and the udult species that might explain their different distribution patterns. On udult soil in gaps, *D. aromatica* behaved similarly to the udult species, with greater survival, higher leaf allocation, higher SLA and consequently higher LAR than the other humult species, although it did not have significantly increased growth on udult soil. On humult soil it differed from the udult species in having somewhat lower SLA and LAR. This was especially the case for smaller seedlings on humult soils where the allometric relationship shows lower leaf and greater root allocation than in the two udult species (Fig. 6). This may provide *D. aromatica* with an advantage in the case of short-term drought on humult soil.

The udult-soil species live in close proximity to the humult soil (Fig. 1), and disperse at least some of their seeds onto the humult soil. At Lambir, seedling establishment for the udult-soil species, *D. lanceolata*, is significantly lower on humult soils (Itoh 1995b), but some seedlings do survive there. Seedlings of this species that survive on humult soil are expected to have higher growth rates than co-occurring humult-soil species. However, the higher growth rates of udult species on humult soils may be relatively unimportant if these species suffer a long-term performance disadvantage on humult soils. The contrasting characteristics of udult and humult species in this study suggest that there is a trade-off between high RGR, SLA, LAR and plasticity, and some aspect of performance on humult soils. Although north-west Borneo has an aseasonal climate (Walsh 1996), infrequent droughts occur in the region which may significantly affect tree survival (Becker *et al*. 1998; Nakagawa *et al*. 2000; Delissio & Primack 2003; Potts 2003). As mentioned above, humult soils in Lambir have significantly higher sand contents and significantly lower water-holding capacity than udult soils (Palmiotto 1998). High leaf allocation and SLA may be a significant liability in the event of unpredictable drought in soils of low water-holding capacity. Mortality was significantly elevated on humult soils in this experiment for one udult species (*D. lanceolata*). However, *D. aromatica* (humult) and *S. balanocarpoides*
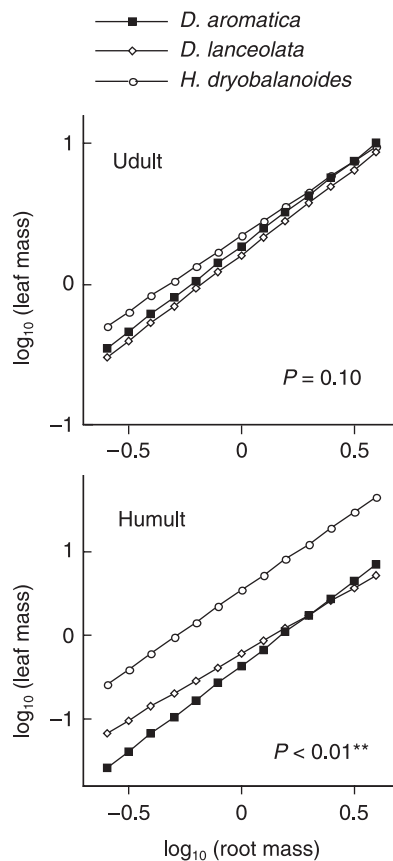
Fig. 6 Comparison of allometric relationships between leaf and root biomass allocation for the three species with the highest relative growth ratess. Relationships are for seedlings grown in gaps in udult and humult soils. *P*-values indicate the significance of differences in the intercept of the allometric model among species. Slopes did not differ significantly for either soil ($P > 0.3$). Reduced major regression results were: *D. aromatica* (udult: $r^2 = 0.73$, humult: $r^2 = 0.60$), *D. lanceolata* (udult: $r^2 = 0.70$, humult: $r^2 = 0.49$), and *H. dryobalanoides* (udult: $r^2 = 0.83$, humult: $r^2 = 0.60$).

(widespread) also had higher mortality rates on humult soils. During the almost 2 years of the experiment there was no significant dry period, and it seems unlikely that the seedlings experienced much drought stress. What caused these higher mortality rates on humult soils remains unknown.

PERFORMANCE AND SOIL RESOURCES

The two udult-soil species, *D. lanceolata* and *H. dryobalanoides*, performed significantly worse on humult soils than on udult soils. Greatly increased allocation to roots, particularly to fine roots, on humult soils by these species suggested the lack of a soil resource. Humult soils had significantly lower levels of total P than udult soils prior to the experiment, and seedlings on humult soils had significantly lower leaf-tissue P concentrations than seedlings on udult soils at the end of the experiment. The experimental addition of P increased available P in the soil, and increased leaf and fine-root P concentrations, however, there was no evidence that P availability

limited the growth of *D. lanceolata* or *H. dryobalanoides* in either soil or light environment. Furthermore, we found no evidence that variation in P availability constrains the distribution of any of the six species.

Responses to nutrient addition by both temperate and tropical tree species are known to depend on light availability (Latham 1992; Grubb *et al.* 1996; Bungard *et al.* 2000), with more positive responses usually occurring in moderate to higher light levels (Coomes & Grubb 2000). Seedlings in gaps in this experiment received around 17% of full sun (*c.* 7.6 mol m^{-2} day^{-1}). This would have resulted in significant periods at or above photosynthetic light saturation for these species (Barker *et al.* 1997; Bungard *et al.* 2000). Although these species can grow faster in even higher light levels (Zipperlen & Press 1996), it seems unlikely that the lack of a growth response to P addition by the species in this experiment was due to limited light availability.

All five dipterocarp species in this experiment are ectomycorrhizal and *S. schwenkii* is endomycorrhizal (P. A. Palmiotto, personal observation). Earlier work with potted seedlings has suggested that P is not limiting seedling growth in undisturbed forest for species that are mycorrhizal (Burslem *et al.* 1995). Our results support this finding. In one species, *D. lanceolata*, lower RGR$_d$ on non-native humult soils was correlated with lower mycorrhizal colonization. However, humult soils also had significantly lower levels of several other essential nutrients including Ca, Mg, K, and N, and *D. lanceolata* leaf-tissue on humult soils had significantly lower concentrations of several nutrients. Any one or a combination of these differences may explain the soil effects on growth. Lower growth rates of the udult forest species on humult soils may also be explained by the unfavourable water status on the more freely draining humult soil, although there was no significant drought during the experiment. Further work with interactions between mycorrhizas and soil nutrients, and with water relations is required for the species specializing on different soils at Lambir.

The three humult-soil species grew either more slowly (*S. laxa* and *S. schwenkii*) or no differently (*D. aromatica*) on the more nutrient-rich udult soils than on humult soils. For both humult-soil species that were tested, *S. laxa* and *D. aromatica*, leaf tissue concentrations of P and several other nutrients were significantly higher on udult soils. In addition, none of the humult species responded to P addition on either soil. These results suggest that the differential soil response in these species was not related to nutrient availability. Possible explanations for the reduced growth of these species on the clay-rich, udult soils may include greater water-holding capacity of udult soil resulting in occasional anoxic conditions in the rooting zone (Silver *et al.* 1999), an alien mycorrhizal flora on the udult soil, or the toxic effects of higher Al or Fe concentrations on udult soils (Sollins 1998). Trenching experiments coupled with careful monitoring of the mycorrhizal community might elucidate the causes of these performance differences.

In addition to differences in soil nutrient concentrations and water-holding capacity, humult and udult soils differ significantly in the depth of the organic humus layer (Palmiotto 1998). Experimental removal of the humus layer (see Methods section) was expected to influence either soil moisture or nutrient availability particularly on humult soils where the humus layer is up to 15 cm thick. However, humus removal had no significant effect on soil nutrient concentrations, and there were no significant effects of this treatment on growth (data not shown). The potential role of the humus layer in buffering soil moisture in the upper soil layers during episodic drought thus needs further study.

The evidence presented here strongly supports the hypothesis that edaphic variation directly contributes to the spatial aggregation of tree species in the Lambir forest. The six species used in this study coexist within the lowland dipterocarp forest in Lambir in north Borneo. Five of the six species are spatially aggregated on either nutrient-rich or nutrient-poor ultisols, and four of them perform better on their own soil. We found no evidence that this edaphic specialization is related to soil P. Further field experimental work on seedling water relations and a broader range of potentially limiting nutrients, coupled with studies of the role of mycorrhizas in these systems is required. It has been estimated that *c*. 60% of the tree species in the Lambir plot have spatial distributions biased across edaphic and topographic gradients in the 52-hectare plot. Edaphic specialization is therefore likely to be important for the coexistence of species in this diverse tropical forest.

Acknowledgements

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