Journal of Tropical Ecology (2006) **22**:53–64. Copyright © 2006 Cambridge University Press
doi:10.1017/S0266467405002944 Printed in the United Kingdom

Competitive dominance in a secondary successional rain-forest community in Borneo

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(*Accepted 12 May 2005*)

Abstract: Competitive interactions among pioneer species may have a significant impact on the course of secondary succession in tropical rain forests. We predicted that the outcome of competitive interactions in early succession would vary with soil nutrient availability. To test this hypothesis we grew seven pioneer tree species alone and in dense competitive mixtures, with four nutrient treatments: no nutrient addition, and N, P, and N plus P addition. Performance of plants grown alone and in mixtures was strongly nutrient limited. However, contrary to expectation, the competitive hierarchy among the seven species was almost identical among the four nutrient treatments. The dominant species, *Melastoma malabathricum*, accounted for > 70% of total stand biomass in all nutrient treatments. Seedlings of this species had higher rates of gas exchange and initial growth, and lower root allocation than the other species. Profiles of light availability within the competitive stands indicated that light levels at ground level were well above levels at which pioneer species can successfully survive and grow, yet seedlings of species other than *Melastoma* remained stunted. Leaf N concentrations in all stands were 25–55% reduced by competitive interactions, and N addition increased relative competitive performance in only *Melastoma* suggesting that *Melastoma* was particularly effective at N acquisition, limiting nutrient uptake by the other species. Toward the end of the experiment individuals of *Melastoma* began to reproduce, suggesting that the competitive hierarchy would have changed in a longer-duration experiment.

Key Words: competition, *Dillenia suffruticosa*, *Duabanga moluccana*, *Ficus grossularioides*, *Melastoma malabathricum*, *Nauclea maingayi*, nutrient limitation, pioneer trees, succession, tree seedlings, *Trema cannabina*, tropical forest, *Vitex pubescens*

INTRODUCTION

The dynamics of secondary succession vary across tropical rain-forest landscapes. Rates of species and biomass accumulation, as well as the composition of successional communities vary. This variation results from a range of interacting factors including the availability of plant propagules, local climatic and edaphic conditions, and biotic interactions, all of which are affected by the nature of the disturbances that initiate successional dynamics (Brown & Lugo 1990, Guariguata & Ostertag 2001). Understanding factors constraining successional dynamics is an important objective of tropical forest ecology, and is of practical significance for managing the extensive areas of cleared tropical forests (Holl & Kappelle 1999).

The composition and dynamics of successional communities are strongly affected by edaphic conditions (Ewel *et al.* 1984, Mesquita *et al.* 2001, Sim *et al.* 1992, Uhl *et al.* 1988). Within Malaysian forests it has long been recognized that the floristic composition of secondary succession varies significantly across edaphic gradients (Holttum 1954). Wyatt-Smith (1963) recognized communities regenerating on land deforested and cultivated for less than 2 y to be dominated by species of *Trema*, *Mallotus* and *Macaranga* (Kochummen 1966), whereas communities regenerating on deforested and severely degraded land were initially dominated by species of *Melastoma*, *Chromolaena* and *Dicranopteris* (Kochummen & Ng 1977). This latter community, in extremely degraded conditions, develops into a vegetation type locally referred to as *Adinandra*-belukar which is

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dominated by a distinctive suite of pioneer species, including *Adinandra dumosa*, *Ploiarium alternifolium* and *Rhodamnia cinerea* (Holttum 1954, Sim *et al.* 1992).

A similar pattern of differentiation in successional dynamics across edaphic gradients is seen following natural disturbances within primary forest. For example, landslides create heterogeneous edaphic conditions within primary forest (Walker *et al.* 1996). Species composition and dynamics differ between the upper erosional zone and the lower nutrient-rich deposition areas at the base of landslides. In Sarawak, Malaysia, erosional zones of landslides are often colonized by *Dicranopteris linearis*, *Melastoma malabathricum* and species characteristic of degraded secondary successional sites, whereas depositional zones are usually crowded with species of *Macaranga* (Davies, *pers. obs.*).

Soil nutrient availability may be the key edaphic resource differentiating these types of successional communities. Logging followed by several cycles of intensive agriculture may deplete soil nutrient reserves and lower soil pH (Grubb *et al.* 1994, Nye & Greenland 1960, Nykvist 1998). Comparisons of lightly and heavily degraded forests usually show lower soil nutrient levels on more degraded sites. For example, in Malaysia soil nutrient levels in *Adinandra*-belukar are lower than in secondary forest dominated by *Macaranga* species (Grubb *et al.* 1994, Sim *et al.* 1992). In addition, soil nutrient levels are lower in the upper erosional areas on landslides, and experimental nutrient addition has shown that the growth of pioneer seedlings in these sites is nutrient limited (Dalling & Tanner 1995, Fetcher *et al.* 1996). Furthermore, Turner (1991) found that *Trema tomentosa*, a species of more fertile successional communities in Malaysia, was more responsive to the addition of fertilizer than *Melastoma malabathricum*, a species of succession on degraded sites.

Despite the evidence for the potential importance of edaphic effects on the course of early secondary succession, numerous recent studies have found that the availability of propagules is perhaps the most important constraint on secondary succession (Holl & Kappelle 1999). The most heavily degraded soils are often most distant from the seed sources of intact forest, and have a group of well-dispersed colonizing species. However, in the absence of limitations to seed dispersal, edaphic conditions and biotic interactions, including competition, may determine the composition of early successional communities. The occurrence of different successional communities on different soils in close proximity (e.g., on different zones within landslides), suggests that the outcome of competitive interactions among species may vary with edaphic conditions.

In this study, we investigate the effects of soil nutrient availability on the dynamics of early rain forest succession in Sarawak, Malaysia. Seven high-light-demanding pioneer species that are characteristic of early successional communities in Sarawak were grown in competitive mixtures and without neighbours across a soil fertility gradient. Soil nutrient availability was manipulated by the addition of nitrogen and/or phosphorus. The seven species chosen for the experiment span a broad range of successional communities in the region. *Melastoma malabathricum*, *Dillenia suffruticosa* and *Vitex pubescens* are common to successions on degraded sites, often occurring in *Adinandra*-belukar. *Trema cannabina* and *Duabanga moluccana* are commonly found in early successional communities on richer or less-degraded soils, and *Ficus grossularioides* and *Nauclea maingayi* have intermediate responses. We hypothesized that the outcome of competitive interactions among the seven species would vary with soil nutrient availability.

METHODS

Study species

The seven very high-light-demanding pioneer species selected for this experiment: *Dillenia suffruticosa* (Griff.) Martelli (Dilleniaceae), *Duabanga moluccana* Blume (Lythraceae), *Ficus grossularioides* Burm. f. (Moraceae), *Melastoma malabathricum* L. (Melastomataceae), *Nauclea maingayi* Hook. (Rubiaceae), *Trema cannabina* Lour. (Cannabaceae) and *Vitex pubescens* Vahl (Lamiaceae), hereafter referred to by their generic names, commonly regenerate in areas following logging and shifting cultivation, and in abandoned open areas. The species are often sympatric at the landscape scale in Sarawak (Mohizah & Davies, unpubl. data). However, our field observations suggest the species differ in their specific habitat preferences, for example, *Dillenia* is very common in swampy ground (Corner 1988), whereas *Duabanga* is often found on fertile clay-rich soils, and on river banks (Davies, *pers. obs.*). The species also differ in several other life-history characteristics, notably maximum tree size and age; the smallest species, *Melastoma* and *Trema*, are not typically more than 1–4 m tall at reproductive maturity, whereas the largest species, *Duabanga*, grows to *c.* 30 m tall in rich sites.

Experimental design and implementation

Plants of all seven pioneer species were grown as single plants and in mixed-species competitive stands. Four nutrient addition treatments were applied to single plants and to competitive stands: control with no nutrient addition (Control), nitrogen addition (N), phosphorus addition (P), and nitrogen and phosphorus addition (NP).

Competitive stands were planted in wooden tubs built with 12-mm-thick waterproof plywood. Each tub was 90.9 cm long × 52.5 cm wide × 30 cm deep (143.2 litres). Plants grown without neighbours were planted in wooden tubs divided into six smaller boxes of 29.7 × 25.6 × 30 cm (22.8 litres). Tubs were filled with sandy secondary forest topsoil over 5 cm of coarse gravel. The soil was collected from five areas of degraded mixed dipterocarp forest, sieved through 1-cm^2 wire screen and then mixed 3:1 with river sand to ensure good drainage and to enable root sampling at the end of the experiment. Tubs had holes drilled through the base and were elevated above the ground to facilitate drainage and to ensure the roots did not escape. All tubs were in full sunlight in the grounds of the Universiti Malaysia Sarawak campus in Kuching, Malaysia (1°28′N, 110°27′E). Mean annual rainfall in Kuching exceeds 4000 mm. Tubs were kept well-watered throughout the experiment.

Seeds of all species were collected from several mother trees in the Kuching area and then sown in nursery beds in February 1999. To ensure similar-sized seedlings at transplanting, planting in the seed beds was staggered by previously observed germination rate. Seed beds, with the same soil as in the experiment, were initially covered with shade cloth, but this was removed when the seedlings were *c.* 2 cm tall.

Once the seedlings were *c.* 3 cm tall, they were transplanted into the experimental tubs. Each competition stand included 98 seedlings consisting of 14 seedlings of each species. Within each competition stand seedlings were arranged in hexagonal arrays such that each seedling was surrounded by six equidistant neighbours, 7 cm apart, and all of which were of a different species. No individual had its own species as a nearest neighbour. In total there were 16 competition stands (4 nutrient treatments × 4 replicates per treatment) with 98 plants per tub, for a total of 1568 seedlings.

Of the 98 plants in each competitive stand, 38 plants (five for four species and six for three species) were on the edges of the stands and had fewer than six nearest neighbours. To reduce the number of times any one species had fewer than six edge plants, each replicate competitive stand had a slightly different seedling arrangement. Analyses were conducted to assess whether edge plants with 2–5 nearest neighbours had significantly different growth than plants with the full compliment of six nearest neighbours. Mean biomass of the edge plants was not significantly different than plants with six nearest neighbours, so all seedlings were included in the statistical analyses.

Five plants of each species were grown without competition in the four nutrient treatments: control, N, P and NP treatments. Single plants were planted in divided plant tubs, with six seedlings planted in each tub.

Nutrients were added every 4 wk after transplanting. Nutrient addition concentrations were based on Turner (1991). P was administered as tri-superphosphate (P_2O_5). N fertilizer was applied as NH_4NO_3. For the first fertilizer treatment 0.47 g m^{-2} of N and 1.14 g m^{-2} P were added. Subsequent additions were: 0.94 g m^{-2} of N and 2.34 g m^{-2} of P. Single plants and competitive stands received the same nutrient additions per unit soil surface area.

Soil nitrogen and phosphorus concentrations were assessed from 5–15 cm depth in all experimental tubs before and after the experiment. Soils were sieved and air-dried prior to analysis. Total P was determined following wet digestion on a Perkin Elmer inductively coupled plasma spectrophotometer. Available P was determined following extraction with ammonium fluoride and hydrochloric acid (Bray-2 method) followed by continuous flow analysis of the extracted solution with a ChemLab 4 autoanalyser (ChemLab, UK). Soil N was determined by Kjeldahl digestion.

Seedling assessment

Seedlings were transplanted to the experimental tubs in May 1999. The biomass of 10 randomly selected individuals per species was assessed prior to planting into the experimental tubs. Seedling survival, stem height, stem diameter (at 1 cm height), number of leaves and crown diameter (mean of longest and shortest axes) were measured every 4 wk for all seedlings. In November, above- and below-ground biomass for all seedlings in the experiment was measured. Leaf area was measured with a leaf area meter (T Delta Device, Burwell, Cambridge, England) connected to a video camera (Baxall model CD6252, UK). All plant tissue was dried to constant weight at 60 °C. Leaf nitrogen and phosphorus concentrations were measured on up to three leaves per species per treatment for single and competitive plants. Total leaf N was measured by Kjeldahl digestion, and P content was determined following digestion with sulphuric acid.

Maximum photosynthetic capacity was measured on plants grown without competition just before the end of the experiment. Measurements were conducted between 9h00 and 11h00 on clear sunny days on recently mature leaves using a portable closed gas exchange system (LI-COR Inc. Model 6200, Lincoln, Nebraska, USA). The CO_2 calibration was checked daily. Across all photosynthesis measurements, mean CO_2 concentration was 353 ± 2 ppm, mean PAR was 1757 ± 44 μmol m^{-2} s^{-1}, mean ambient temperature was 37 ± 0.3 °C, mean leaf temperature was 37.6 ± 0.3 °C, and relative humidity was 58.7 ± 0.8%.

Photosynthetically active radiation (PAR) was monitored monthly throughout the experiment using four LI-COR quantum sensors attached to a LI-COR 1000 data logger (LI-COR, Inc., USA). At the end of the experiment, PAR profiles within the canopy of the competitive stands

Table 1. Mean (± 1 SE) soil nutrient concentrations at the end of the experiment for plants grown alone (n = 5–6) and in mixtures (n = 3–4 samples per treatment). Plants were grown without nutrient addition (Control) or with added nitrogen (N), phosphorus (P) or nitrogen and phosphorus (NP). Significant differences among means for 'mixture' and 'single' plants are indicated with different superscripts.

	% N	Available P ($\mathrm{mg\,kg^{-1}}$)	Total P ($\mathrm{mg\,kg^{-1}}$)
Single plants			
Control	0.16 ± 0.00^{a}	13.2 ± 0.5^{b}	132.7 ± 1.9^{b}
N	0.17 ± 0.00^{a}	14.2 ± 0.7^{b}	132.8 ± 6.2^{b}
P	0.17 ± 0.01^{a}	39.8 ± 9.9^{a}	185.2 ± 17.1^{a}
NP	0.17 ± 0.01^{a}	24.3 ± 5.7^{ab}	152.5 ± 10.9^{ab}
Mixtures			
Control	0.17 ± 0.01^{a}	12.3 ± 0.9^{bc}	144.3 ± 1.8^{a}
N	0.17 ± 0.01^{a}	11.3 ± 1.0^{c}	138.5 ± 3.6^{a}
P	0.18 ± 0.01^{a}	21.0 ± 2.1^{a}	160.0 ± 8.3^{a}
NP	0.18 ± 0.01^{a}	18.8 ± 2.7^{ab}	146.0 ± 6.5^{a}

were measured with sensors at 5 and 20 cm above the soil, and in full sun above the canopy.

Analysis

Relative competitive performance (RCP) was calculated as: $\mathrm{RCP} = (B_{\mathrm{alone}} - B_{\mathrm{mixture}})/B_{\mathrm{alone}} \times 100$, where B is plant biomass for plants grown alone and in mixtures (Keddy *et al.* 2002, Weigelt & Jolliffe 2003). Differences in performance among nutrient treatments were tested with ANOVAs followed by Tukey HSD post-hoc comparisons. Comparisons of rank performance among nutrient treatments for species grown alone and in mixtures were made with Kendall's coefficient of concordance. Logistic regression was used to test for differences in mortality rates among species and treatments.

RESULTS

Soil nutrient treatments

Available soil P concentrations were 53–202% greater in P treatments for both competitive mixtures and single plants (Table 1). Total soil P concentrations were 15–40% greater in P treatments for single plants, but not significantly elevated in mixtures. Available P was significantly lower in competitive mixtures than for single plants, but total P was not. Soil N concentrations at the end of the experiment did not differ significantly among soil treatments or between single plants and competitive mixtures (Table 1).

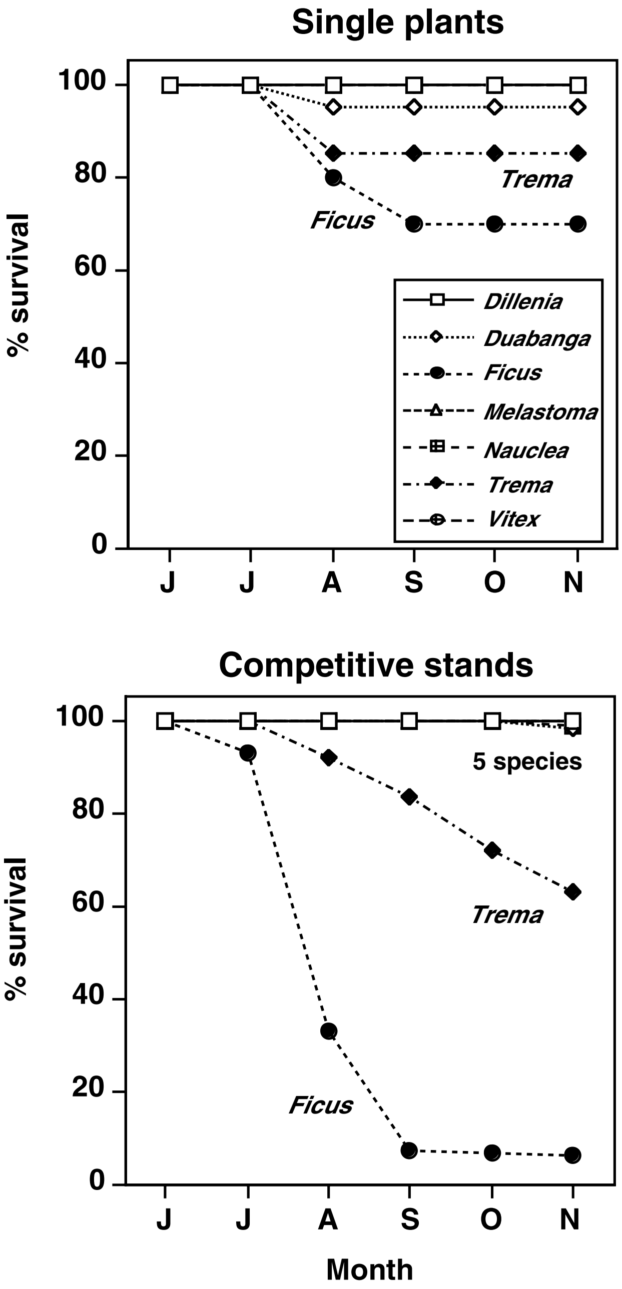

Figure 1. Seedling survival in competitive mixtures for seven pioneer species. Nutrient treatments were pooled for this figure since they had no significant effect on survival (logistic regression, $P > 0.5$).

Survival

Mortality of *Ficus* and *Trema* was significantly greater in competitive stands than in plants grown alone ($P < 0.05$, Figure 1). More than 90% of *Ficus* seedlings died in the competitive stands compared with only 30% in plants grown without competition. Competitive interactions did not significantly affect survival in the other five species. For plants grown alone, *Ficus* and *Trema* had significantly greater mortality than the other species ($P < 0.05$). Soil nutrient addition had no significant effect on mortality rates for any species with or without neighbours ($P > 0.5$, data not shown).

Table 2. Performance of seven species of pioneer trees in the competition experiment. Mean (± 1 SE) final biomass (g) of seedlings grown without neighbours (*Ficus* and *Trema* $n = 3–5$, other species $n = 5$) and in competitive mixtures (*Ficus* $n = 2–5$, *Trema* $n = 32–38$, all other species $n = 53–56$ per treatment). Relative competitive performance is the per cent reduction in total biomass due to competitive interactions. Plants were grown without nutrient addition (Control) or with added nitrogen (N), phosphorus (P) or nitrogen and phosphorus (NP). For final biomass, significant differences among species within each nutrient treatment indicated after each mean based on $\log_{10}$ transformed biomass. *Ficus* was excluded from the 'mixtures' analysis due to limited sample sizes. For relative competitive performance, significant differences among nutrient treatments indicated with different letters for *Melastoma*; there were no significant differences in the other species. Species arranged by competitive performance ranking.

Species	Control	N	P	NP
Final biomass: single plants				
Melastoma	96.4 ± 5.2^{a}	99.9 ± 19.3^{a}	112.0 ± 13.7^{a}	143.3 ± 18.3^{a}
Vitex	48.2 ± 4.7^{bc}	62.8 ± 3.6^{a}	60.2 ± 16.4^{bc}	75.9 ± 7.5^{ab}
Dillenia	51.2 ± 6.5^{bc}	80.8 ± 7.8^{a}	107.1 ± 15.5^{ab}	95.7 ± 8.5^{a}
Nauclea	32.2 ± 6.7^{c}	33.4 ± 4.9^{ab}	42.0 ± 6.2^{c}	52.8 ± 7.1^{b}
Duabanga	72.2 ± 8.2^{ab}	40.3 ± 2.6^{ab}	88.4 ± 12.9^{a}	155.0 ± 18.5^{ab}
Trema	15.2 ± 3.0^{d}	25.7 ± 9.5^{b}	19.8 ± 5.3^{d}	25.1 ± 1.9^{c}
Ficus	32.9 ± 2.1^{c}	63.2 ± 27.1^{ab}	40.1 ± 4.1^{bc}	63.2 ± 15.8^{bc}
Final biomass: competitive mixtures				
Melastoma	18.29 ± 1.73^{a}	28.17 ± 3.02^{a}	21.82 ± 2.01^{a}	38.36 ± 3.00^{a}
Vitex	2.98 ± 0.30^{b}	3.55 ± 0.45^{b}	2.96 ± 0.48^{bc}	5.17 ± 0.54^{b}
Dillenia	1.40 ± 0.13^{bc}	3.25 ± 0.31^{b}	2.47 ± 0.19^{b}	2.37 ± 0.34^{c}
Nauclea	1.15 ± 0.10^{c}	1.03 ± 0.14^{c}	0.96 ± 0.08^{d}	1.33 ± 0.11^{cd}
Duabanga	0.87 ± 0.12^{c}	0.75 ± 0.12^{c}	1.47 ± 0.19^{cd}	1.21 ± 0.17^{d}
Trema	0.17 ± 0.04^{d}	0.07 ± 0.03^{d}	0.14 ± 0.04^{e}	0.54 ± 0.23^{e}
Ficus	$0.15 \pm 0.11^{-}$	$0.09 \pm 0.00^{-}$	$0.06 \pm 0.02^{-}$	$0.43 \pm 0.20^{-}$
Relative competitive performance				
Melastoma	81.0 ± 2.70^{a}	71.8 ± 1.60^{b}	80.5 ± 1.73^{a}	73.2 ± 1.11^{ab}
Vitex	93.8 ± 0.97	94.4 ± 1.86	95.1 ± 0.74	93.2 ± 1.36
Dillenia	97.3 ± 0.87	96.0 ± 0.91	97.7 ± 0.24	97.5 ± 0.41
Nauclea	96.4 ± 0.63	96.9 ± 1.05	97.7 ± 0.35	97.5 ± 0.52
Duabanga	98.8 ± 0.24	98.1 ± 0.39	98.3 ± 0.21	99.2 ± 0.21
Trema	99.0 ± 0.67	99.7 ± 0.12	99.3 ± 0.26	97.7 ± 1.32
Ficus	99.3 ± 0.54	99.9 ± 0.01	99.9 ± 0.05	99.3 ± 0.32

Single plant growth: nutrient effects and rank performance

Nutrient addition had a significant positive effect on final plant biomass in only *Duabanga* and *Dillenia* (Figure 2). Mean biomass of *Dillenia* seedlings was greater in P and NP addition treatments than in control plants (Table 2). NP addition led to significantly greater final biomass in *Duabanga*. For the other species there appeared to be species-specific differences in response to nutrient addition, however significant effects may not have been detected due to limited sample sizes. *Melastoma*, *Nauclea* and *Vitex*, as with *Duabanga*, had highest mean biomass in NP addition treatments. *Dillenia* performed best with added P. *Ficus* and *Trema* performed best in N and NP addition treatments (Figure 2).

Mean final biomass differed significantly among species in all nutrient treatments (Table 2). *Melastoma* had the highest mean biomass in control, N and P treatments and *Duabanga* had the highest mean biomass in the NP treatment. *Nauclea* and *Trema* had the lowest mean biomass in all four treatments. Rank performance of the species did not differ significantly among nutrient treatments (Kendall's coefficient of concordance, $W = 0.857$, $P < 0.05$).

Dynamics of competitive mixtures

Melastoma dominated the competitive mixtures, accounting for 73–79% of total stand biomass in all nutrient treatments (Figure 3a). The next most important species were *Vitex* with 10–12% and *Dillenia* with 5–9% of stand biomass. *Nauclea* and *Duabanga* had 2–5% of stand biomass, and *Trema* and *Ficus* accounted for less than 1% of total stand biomass.

Nutrient addition significantly affected total stand biomass, with N-treated stands having 48% greater biomass than control and P-treated stands, and NP-treated stands having 33–97% greater biomass than other treatments (Figure 3b). Despite significant effects on stand biomass, nutrient addition did not affect stand composition. Rank performance was almost identical among nutrient treatments ($W = 0.987$; $P < 0.05$), with species in control, N and NP treatments having the same ranks, and just one rank difference in P-treated stands.

Individual performance in competitive mixtures

Compared with plants grown without neighbours, all species suffered > 70% reduction in mean individual

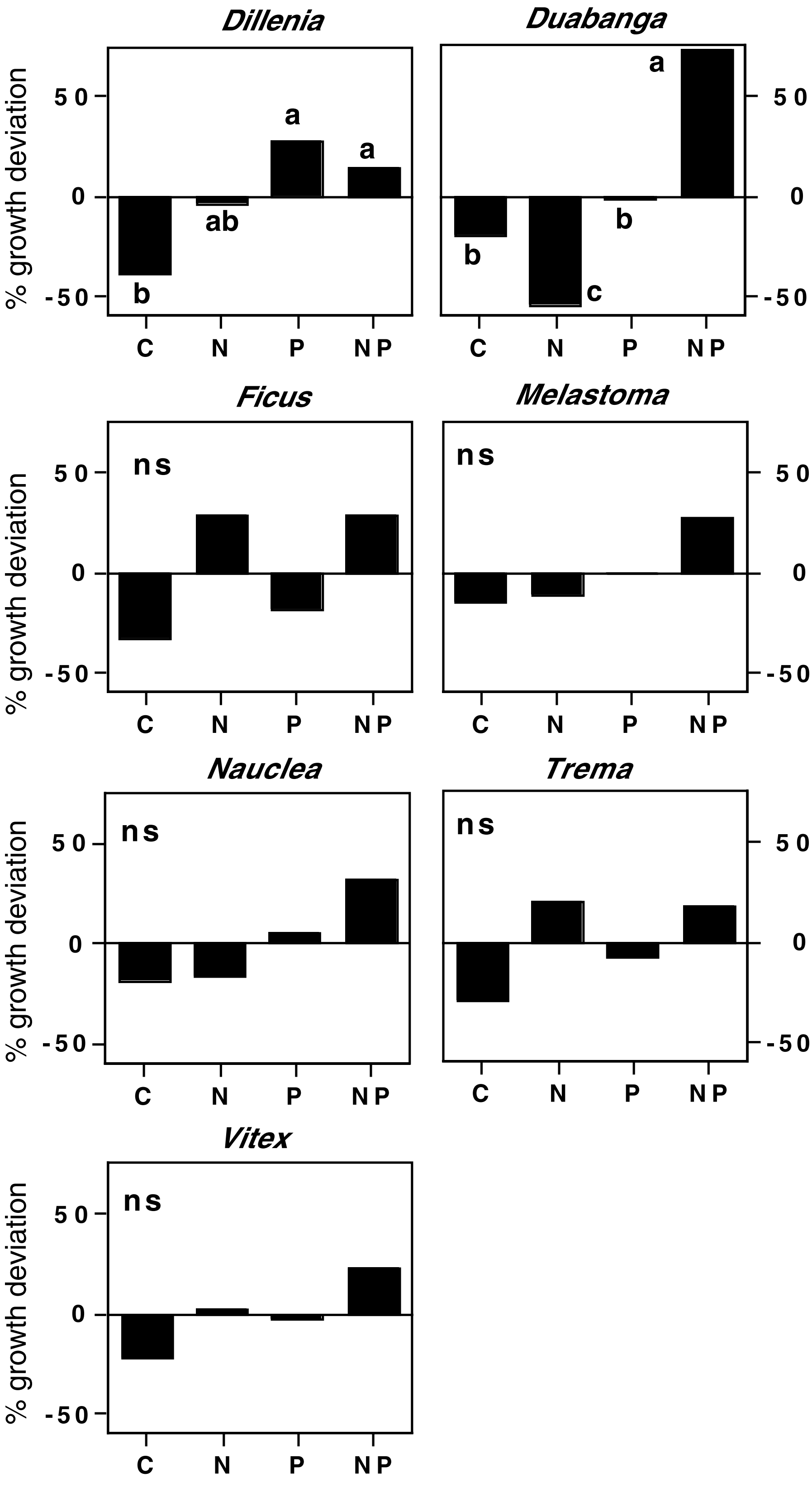

Figure 2. Mean growth rates as per cent deviation from the mean final biomass for each species. Deviations are for single plants grown in four nutrient treatments. Different letters indicate significant differences among means for *Dillenia* and *Duabanga*; ns indicates no significant differences among means.

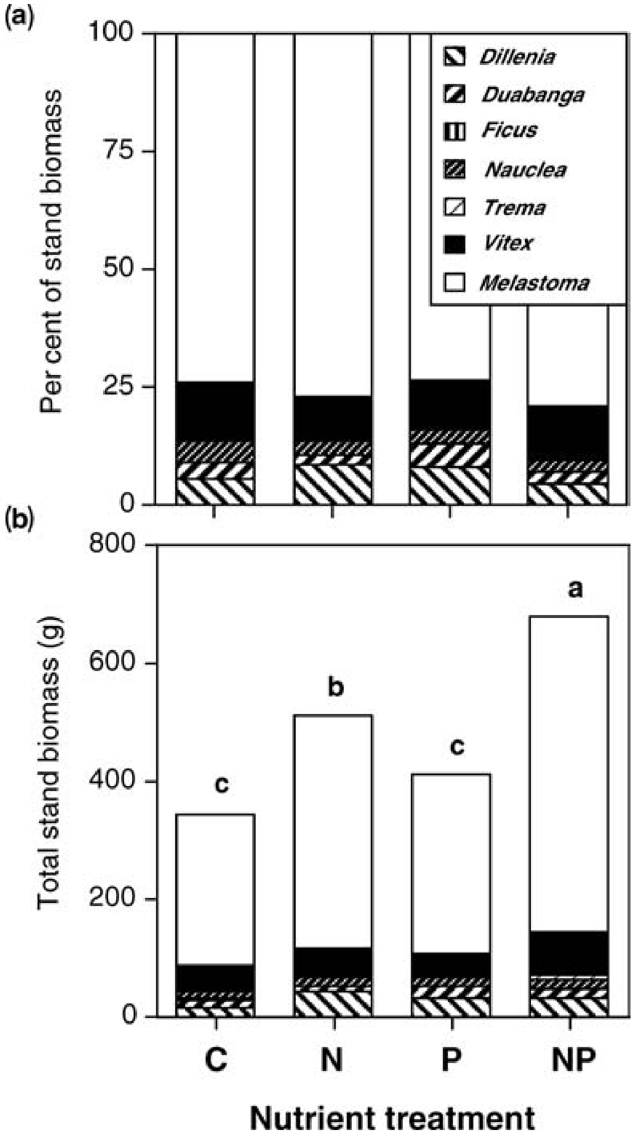

Figure 3. Relative biomass contribution (a) and mean stand biomass (b) for seven species of pioneer trees growing in competitive stands in four nutrient treatments: C, control; N, nitrogen addition; P, phosphorus addition; and NP, nitrogen and phosphorus addition. Different letters indicate significant differences in mean stand biomass (n = 4 per nutrient treatment). Relative contributions of species to stand biomass did not differ among nutrient treatments (G-test, $P > 0.5$).

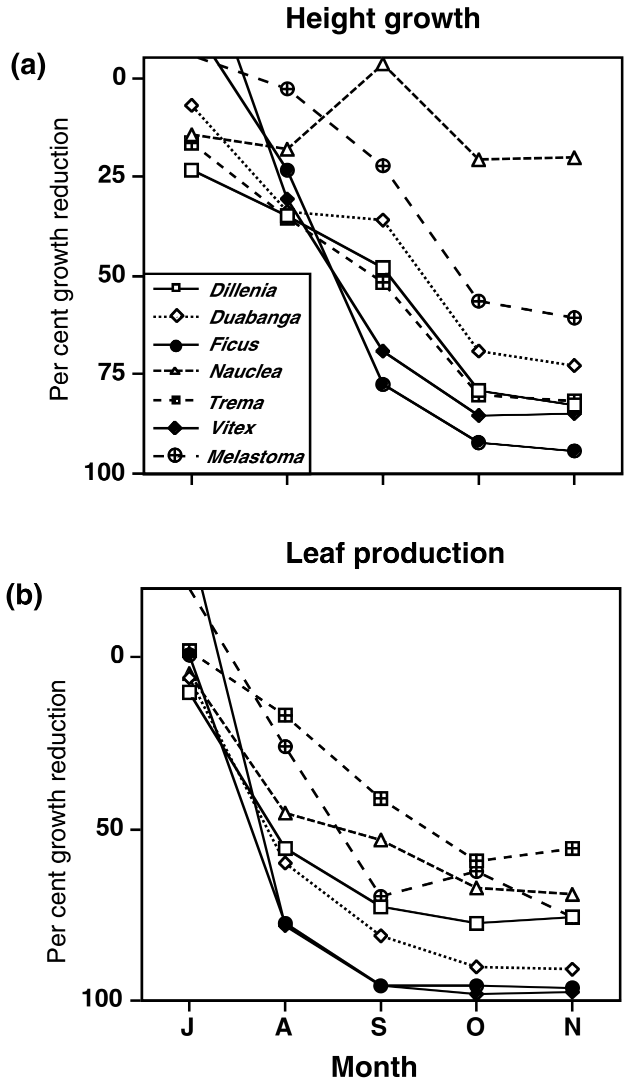

Figure 4. Time course of relative performance in (a) height growth and (b) leaf production for seven pioneer species grown in competitive stands. Relative performance is the relative difference in growth for plants in competitive mixtures versus plants grown alone. Prior to strong competitive interactions, some species growth was better in competitive stands than in single plants, although this effect is magnified for small plants.

biomass in the competitive mixtures (Table 2). *Melastoma* suffered least with 72–81% lower mean individual biomass in competitive stands relative to plants without neighbours. *Vitex* and *Dillenia* suffered 93–98% biomass reductions, and the other species suffered up to 99.9% reductions in growth relative to plants grown without neighbours. Nutrient addition significantly affected the relative competitive performance in only one of the seven species (Table 2). In *Melastoma*, N and NP addition resulted in significantly smaller reductions in mean individual biomass than control and P treatments.

Performance reductions due to competitive interactions were assessed monthly for height growth and leaf production (Figure 4). By August, the third month of the experiment, leaf production was reduced by more than 75% in *Trema* and *Ficus*, the two most heavily affected species. Height growth responded more slowly in all species.

Leaf nutrient concentrations

N addition did not affect leaf N in any species for single plants or competitive stands (data not shown).

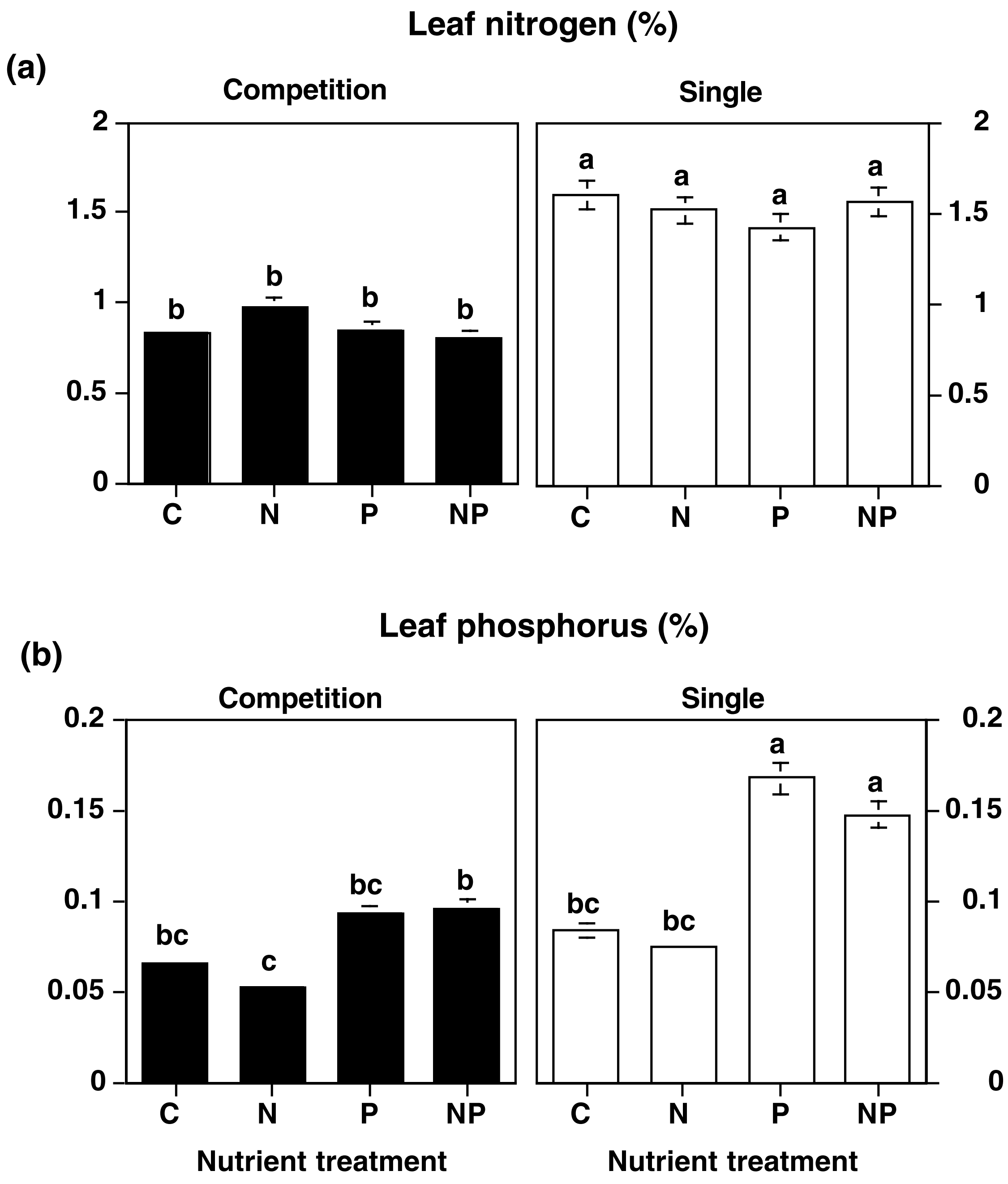

Figure 5. Mean (± 1 SE) leaf nitrogen (a) and phosphorus (b) concentrations for seedlings in four nutrient treatments based on n = 15–20 leaves with all species pooled. Significant differences among means are indicated by different letters.

However, leaf tissue N concentrations were significantly lower in competitive mixtures than in single plants for all treatments (Figure 5a) and for all species with sufficient leaf material for analysis. In addition, there were significant differences among species in leaf N content in plants with and without neighbours (Table 3). For single plants, *Ficus* and *Trema* had significantly greater mean leaf N than all other species except *Melastoma*, and *Dillenia*, *Duabanga* and *Nauclea* had significantly lower leaf N than the other species. In competitive mixtures, with *Ficus* and *Trema* having insufficient leaf material for analysis, *Melastoma* had the highest leaf N concentrations.

P addition resulted in higher leaf P concentrations in plants grown with and without neighbours in most species (data not shown). Leaf P concentrations were lower in competitive stands for most species for P and NP treatments (Figure 5b). As with leaf N, species also differed significantly in leaf P concentrations (Table 3). Single plants of *Trema* and *Ficus* had the greatest leaf P concentrations.

Table 3. Leaf nitrogen and phosphorus concentrations for seven pioneer species grown alone and in competitive mixtures at the end of the experiment. For leaf N means based on n = 12 for all species, except *Ficus* (single: n = 12, competition: n = 0) and *Trema* (single: n = 5, competition: n = 1). Nutrient addition treatments were pooled for this analysis as they did not significantly affect leaf N concentrations in any species. For leaf P, means based on n = 6 for leaves in control and N treatments pooled, except *Ficus* (competition: n = 0) and *Trema* (single: n = 2, competition: n = 0). Different letters indicate significant differences among species, with *Ficus* and *Trema* excluded from the competitive mixture comparison. Species arranged as in Table 2.

Species	Single plants	Competitive mixtures
Leaf nitrogen (%)		
Melastoma	1.75 ± 0.09^{bc}	1.07 ± 0.03^{a}
Vitex	1.59 ± 0.09^{c}	0.96 ± 0.06^{ab}
Dillenia	1.19 ± 0.04^{d}	0.89 ± 0.03^{bc}
Nauclea	1.07 ± 0.06^{d}	0.68 ± 0.03^{d}
Duabanga	1.10 ± 0.05^{d}	0.74 ± 0.03^{cd}
Trema	2.06 ± 0.25^{ab}	0.93
Ficus	2.21 ± 0.09^{a}	–
Leaf phosphorus (%)		
Melastoma	0.085 ± 0.00^{ab}	0.062 ± 0.01^{ab}
Vitex	0.100 ± 0.01^{a}	0.081 ± 0.00^{a}
Dillenia	0.058 ± 0.00^{bc}	0.051 ± 0.01^{b}
Nauclea	0.042 ± 0.00^{c}	0.046 ± 0.01^{b}
Duabanga	0.072 ± 0.01^{b}	0.061 ± 0.01^{ab}
Trema	0.112 ± 0.01^{a}	–
Ficus	0.111 ± 0.00^{a}	–

Light environment and photosynthetic capacity

PAR was measured above and within the canopy of competitive stands before the end of the experiment (Figure 6). Plants were grown in full sun which averaged 31.4 mol m^{-2} d^{-1} for 5 d of light measurements. At 20 cm above the soil within the stands, close to the mean height of *Vitex* and *Duabanga* seedlings, mean PAR was 15.4 mol m^{-2} d^{-1} (49% of full sun) and instantaneous PAR exceeded 1000 μmol m^{-2} s^{-1} for a significant period of the day. At 5 cm above the soil, close to the mean height of remaining *Ficus* and *Trema* seedlings, mean PAR was 5.1 mol m^{-2} d^{-1} (16.2%).

Rates of gas exchange measured on single plants on full-sun days differed significantly among the seven species (one-way ANOVA, $P < 0.001$). *Melastoma* had significantly higher rates of photosynthesis and stomatal conductance than most other species in the experiment. Mean rates of maximum photosynthesis (A_{max} in μmol m^{-2} s^{-1}) and stomatal conductance (g_s in mol m^{-2} s^{-1}) for the seven species were, from highest to lowest A_{max}: *Melastoma* ($A_{max} = 21.9$, $g_s = 1.25$), *Ficus* (17.5, 0.86), *Vitex* (15.3, 0.80), *Trema* (14.8, 0.83), *Nauclea* (14.5, 0.96), *Duabanga* (13.9, 0.70) and *Dillenia* (11.6, 0.70).

Competitive dominance

Plant size at the start of the experiment did not have a significant influence on the competitive outcome (Table 4). *Melastoma* seedlings grown without neighbours had significantly higher maximum rates of photosynthesis and stomatal conductance, and higher initial growth rates than the other species. These three traits were strongly positively correlated with performance in competitive stands (Table 6). Relative biomass allocation to roots in seedlings without neighbours was negatively correlated with performance in competitive mixtures

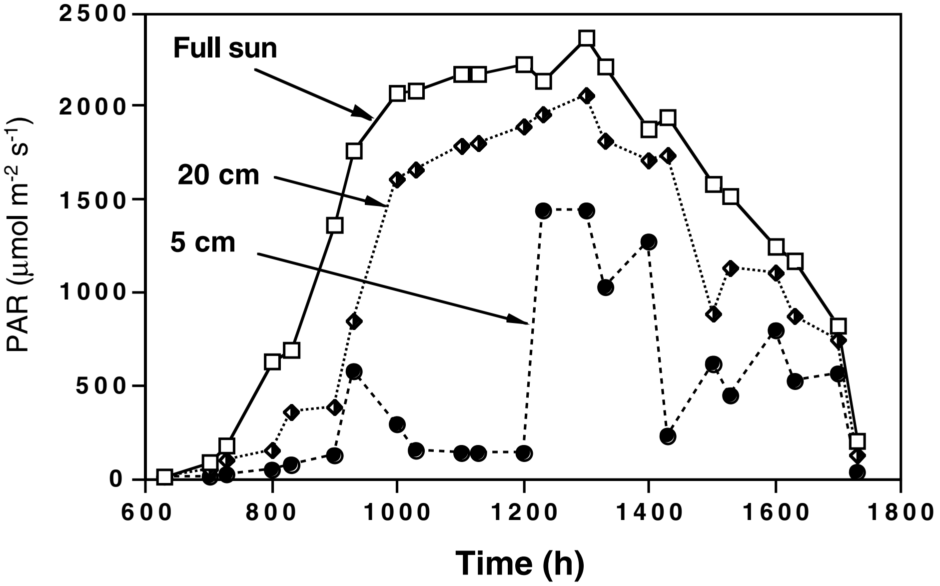

Figure 6. Time course of photosynthetically active radiation (PAR) above and within (5 and 20 cm above the ground) competitive stands just prior to the end of the experiment. Data are for one representative sunny day.

Table 4. Correlations (r) between mean final biomass in competitive mixtures ($\log_{10}$ transformed) and species' traits derived from plants grown without neighbours. A_{max}, leaf area-based maximum photosynthesis, g_s, stomatal conductance, leaf N and P concentrations, RWR, root weight ratio, LWR, leaf weight ratio, height growth in the first census interval ($t_2 - t_3$), and final and initial biomass. Correlations included values for each nutrient treatment separately, so $n = 28$ for each analysis.

Trait	r	P
A_{max}	0.39	0.040*
g_s	0.52	0.005**
Leaf N (%)	− 0.35	0.064
Leaf P (%)	0.22	0.262
RWR	− 0.45	0.015*
LWR	0.27	0.166
Height growth T_{2-3}	0.55	0.005**
Final biomass	0.68	< 0.001***
Initial biomass	0.07	0.727

(Table 4), as *Melastoma* had among the lowest root weight ratios and *Trema* and *Ficus* had high root allocation. Rapid early growth rates and high allocation to shoots enabled *Melastoma* to suppress the growth of the other six pioneer species in this experiment.

DISCUSSION

Melastoma malabathricum dominated competitive mixtures in all four nutrient treatments in this experiment, accounting for > 70% of stand biomass in all treatments. This result was contrary to expectation for two reasons. First, field surveys of secondary successional communities in South-East Asia (Ewel *et al.* 1984, Wyatt-Smith 1963), and elsewhere in the tropics (Mesquita *et al.* 2001, Uhl *et al.* 1988), have demonstrated differences in successional communities across edaphic gradients. Second, field and nursery experimental studies, particularly in the temperate zone, have revealed differences in the outcome of competitive interactions when levels of resource availability are altered (Gehring *et al.* 1999, Navas *et al.* 1999, Reekie & Bazzaz 1989, Tilman 1987).

Light profiles within the canopy of the competitive stands at the end of the experiment suggest that the competitive outcome was not determined primarily by competition for light. *Melastoma* has small leaves on relatively narrow upright shoots, and does not cast a deep shade. At the end of the experiment, light levels close to the soil surface were approximately 16% of full sun with instantaneous rates above 1000 μmol m^{-2} s^{-1} for part of the day. Most pioneer species that have been examined can grow rapidly in these light levels (Barker *et al.* 1997, Davies 1998, Kitajima 1994). Light levels in the forest understorey are typically around 1–3% of full sun, and are conditions in which pioneers rarely persist.

Seedling growth in competitive stands was nutrient limited. Mean plant biomass for five of the seven species in competitive stands was greater in at least one of the nutrient addition treatments than in control treatments. The two species without an effect, *Trema* and *Ficus*, had too few surviving seedlings for comparison. Despite strong nutrient limitation, N and/or P addition had no effect on the relative competitive performance of six of the seven species. If the competitive outcome in this experiment was determined by more effective competition for nutrients by *Melastoma*, then it might be expected that nutrient addition would reduce competitive suppression of the other species. However, this was not the case in the experiment. *Melastoma* effectively limited nutrient uptake by the other species in all nutrient treatments in this experiment. One possible explanation for the result is that the addition of N or P may not have raised soil nutrient concentrations to surplus levels for *Melastoma*, at which other species could effectively take up the added nutrients. Soils used for the experiment were relatively poor, but they were not unusually poor, having similar nitrogen and phosphorus concentrations to the lowland ultisols that are widespread in Borneo (see, for example, Palmiotto *et al.* 2004). At least for P, nutrient addition raised soil P concentrations to levels equivalent to the more fertile ultisols on clay soils (Palmiotto *et al.* 2004). Alternatively, competition may have been for another below-ground resource not measured in this study (e.g. Mg; Burslem *et al.* 1996),

Melastoma is known to accumulate Al in leaf tissues (Watanabe 1997, Watanabe & Osaki 2001). *Melastoma* may have dominated the competitive stands by modifying soil resource conditions through an allelopathic effect. It releases high concentrations of organic acids into the rhizosphere that help solubilize Al compounds, increasing Al concentrations in the rhizosphere (Watanabe & Osaki 2002). Al is toxic for many plant species and may have led to the stunted growth of the other surviving species in this study. Al concentrations were not measured in this study.

The only species for which nutrient addition changed relative competitive performance was *Melastoma*. Nitrogen addition (N and NP treatments) decreased the effect of stand competition on *Melastoma*. *Melastoma* also had higher mean plant biomass in N and NP treatments than in control and P treatments, and higher per cent contributions to total stand biomass in N and NP treatments. Since competitive interactions greatly reduced leaf N concentrations in all stands, *Melastoma* appears to have been particularly effective at N acquisition. This may have been a mechanism by which it dominated the competitive stands. Further experimental work with a broader range of N availabilities would provide a test of this hypothesis.

Competitive interactions significantly increased mortality in *Ficus* and *Trema*, and growth of these two species was the most severely reduced by competitive interactions. Although *Trema* grew more slowly than the other species without neighbours, single plants of *Ficus* had among the highest gas exchange and growth rates. *Ficus* and *Trema* had the highest leaf N and P concentrations when grown without neighbours. These two species are typically found in successional communities on higher-nutrient soils (Wyatt-Smith 1963), and appear to have relatively high nutrient requirements. In full sun with low leaf nitrogen concentrations, seedlings may suffer photodamage (Bungard *et al.* 2000). This effect may be more severe in species with high nitrogen requirements, and may exclude pioneers of typically high-nutrient soils from poorer sites. Single plants of both *Trema* and *Ficus* had relatively better performance in N and NP treatments. Further ecophysiological study of these species in high-light, low-nitrogen environments is required.

Melastoma is one of the characteristic species of *Adinandra*-belukar communities which grow in the very low-nutrient soils in South-East Asia. In natural successional communities in Borneo, *Melastoma* does not dominate early successional sites on more fertile soils. In fertile soils the chances of having individuals of other species outshading *Melastoma* individuals may be greater, and *Melastoma* is highly intolerant of shade (Turner 1991).

The experiment reported here lasted 6 mo. Most of the species in the experiment have life spans in excess of 10 y, and *Duabanga*, for example, can be a 30-m tree at maturity (Corner 1988). The outcome of the competitive interactions observed in this experiment is unlikely to have persisted over a much longer period. Although *Ficus* and *Trema* mostly died, almost all seedlings of *Vitex*, *Dillenia*, *Duabanga* and *Nauclea* survived. *Melastoma* usually reaches only 3–6 m in height at maturity (Corner 1988), and several individuals had started to flower as the experiment was ending. We predict that once *Melastoma* begins to change resource allocation with the onset of reproduction, and subsequently senesce, the other surviving pioneers in the experiment will increase growth rates and overtop the remaining *Melastoma*. In degraded old fields in Peninsular Malaysia, stands dominated in the early stages by *Melastoma* became dominated by other species after 4–8 y (Kochummen & Ng 1977). It was not known whether this change was due to shading by neighbouring successional species or to the natural senescence of the *Melastoma* individuals. The results presented in this study suggest that the competitive dominance of *Melastoma* was determined by below-ground competition. Once individuals of the other species shade *Melastoma* individuals, we expect there to be a rapid shift in the competitive hierarchy, perhaps driven by a shift from below-ground to above-ground (light) competition. Further experimental studies with a longer duration are required to investigate these possibilities.

ACKNOWLEDGEMENTS

The research was supported by IRPA grant #05-02-09-0508 to Unimas and SJD. We thank Professor Ghazally Ismail and the Unimas staff for facilitating the project. We thank the Forest Department of Sarawak for permission to work with the tree species. P.S. Ashton, D. King and S. Russo provided constructive comments on the manuscript.

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