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ORIGINAL ARTICLE

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Growth and competition between seedlings of an invasive plantation tree, *Acacia mangium,* and those of a native Borneo heath-forest species, *Melastoma beccarianum*

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Abstract An introduced plantation tree species, *Acacia mangium* Willd., is becoming invasive in the Brunei region of Borneo. To examine its invasive potential, a greenhouse, additive series experiment (target–neighbour) involving seedlings of *A. mangium* and those of a common native heath-forest (kerangas), *Melastoma beccarianum* Cogn. was carried out under low and high light regimes in intra- and interspecific combinations over a 6-month period. Significant variations in growth parameters (other than biomass allocation patterns) existed amongst seedlings from different treatments. A major part of this variation in growth could be attributed to the main factors of target species, neighbour species, and competition (seedling density). For the growth variables examined, the target–species response was not consistent across light regimes. Under high light conditions, *Acacia* was the better competitor; the Lotka-Volterra competition coefficient effect of *Melastoma* on *Acacia* was lower ($\alpha = 0.30$) than the effect of *Acacia* on *Melastoma* ($\beta = 0.54$). However, the reverse occurred under low light conditions with *Melastoma* gaining the upper hand ($\alpha = 1.45$ and $\beta = 0.44$). These results show that light (and hence disturbance) can strongly influence the pattern and intensity of both intra- and interspecific competition between invasive and local flora species. Relatively intact forest is unlikely to be invaded by *Acacia* trees (as they are poor competitors under this scenario). On the other hand, the *Acacia* trees can easily invade disturbed forests, especially those prone to recurring drought and fire, and over time convert the habitats to nearly monospecific stands, as is presently being observed in Brunei.

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Introduction

Invasion of any natural ecosystem by alien organisms is a serious environmental problem. It threatens the sustainable use of resources derived from biological systems (Kaiser 1999; De Wit et al. 2001; Van Wilgen et al. 2001). Most studies on invasive organisms have examined the attributes of the invasive species and/or changes in the characteristics of the indigenous communities experiencing the invasion (e.g. Williamson and Fitter 1996; Mack 1996; Gorchov and Trisel 2003). The general consensus is that invasions often lead to major changes in the structure and composition of natural ecosystems, as well as disruptions of key ecosystem functions (Gordon 1998; Lodge and Shrader-Frechette 2002). Such effects result from a variety of mechanisms including competition, predation, disease and amensalism (Williamson and Fitter 1996).

For the past two decades or so, it has become increasingly clear that some exotic tree species used in the commercial and agro-forestry industries can cause major problems as invaders of natural and semi-natural/disturbed ecosystems as they become structurally dominant in terrestrial situations (Richardson 1998; De Wit et al. 2001). The problem is not likely to abate as afforestation and changes in land use intensify. Among commercial trees with invasive properties are species within the *Acacia* genus (Mimosaceae). *Acacia mangium* Willd., an evergreen tree up to 15–20 m tall is native to Australia (Coode et al. 1996; Turnbull et al. 1998). It was introduced as a plantation tree to Borneo Island, initially into the Malaysian states of Sabah and Sarawak in the early 1980s (Turnbull et al. 1998), and by the early 1990s into Brunei, northwest Borneo (4°44′N, 114°36′E). It was widely planted to contribute to the timber and furniture industry in Brunei.

By the mid-1990s, *A. mangium* trees, together with two other non-native conspecifics *(A. cincinnata, A. auriculiformis)*, were used for vegetation rehabilitation work following the construction of the 40-km Tutong–Muara highway—a coastal road that links the capital city, Bandar Seri Begawan, with the regional towns of Tutong and Kuala Belait. These species were chosen based on the need to mitigate, as fast as possible, the erosion of the highway embankments, which was becoming a huge environmental problem (O.O. Osunkoya, personal communication with Brunei Forestry Department). The *Acacia* species were prime candidates as they are fast growing, even in poor soils, and are known to fix nitrogen (Turnbull et al. 1998; Van Wilgen et al. 2001). While they have effectively contributed to reducing the erosion problem and closing up the side canopy on this highway, the *Acacia* species have since spread to other coastal land habitats and regions in Brunei. In particular they are colonizing disturbed heath (kerangas) vegetation—a major forest type in Borneo consisting of medium-height (≤ 20 m), slender, pole-size trees growing on nutrient-poor, sandy, often acidic soils (Davies and Becker 1996).

The *Acacia* trees are also spreading inland. They now inhabit degraded/disturbed forestlands where they appear to be displacing native, pioneer tree species such as those within the genera of *Alphitonia*, *Dillenia, Ploiarium*, *Melastoma, Gymnostoma*, *Commersonia*, and *Macaranga* and are turning such habitats into nearly monospecific tree stands. In Brunei, invasion by the *Acacia* species has been observed from managed *A. mangium* plantations set up in the early 1990s in Sungai Liang and Bukit Kukub (both in Tutong district) and in the Berakas recreational forest (Muara district) into the margins and interiors of disturbed heath forests (especially if prone to recurring disturbance, such as fire; O.O. Osunkoya, personal observation). The *Acacia* trees have also been observed spreading into adjacent native tree plantations of mixed dipterocarp species (*Dryobalanops, Dipterocarp*, *Shorea*, and *Vatica*) that were set up for commercial purposes. We know of fruit-tree farms of several hectares (including one of coffee) in Tutong district, Brunei, that were abandoned and declared economically unviable as the *Acacia* trees, initially planted on the farm periphery for hedge or shade purposes and as a nitrogen source, have now encroached on these farms.

We hypothesized that significant community-level interference by these invasive *Acacia* trees in disturbed Borneo forests is likely, but can this be explained by their superior competitive ability? Approach to the study of competition may involve either field or greenhouse experiments (see Keddy 1989; Gibson et al. 1999; Connolly et al. 2001). The greenhouse approach is taken in this paper to examine competitive ability of the invasive *A. mangium* in the presence of common native trees of Borneo heath vegetation. Many designs exist for examining competition in greenhouse studies—the famous ones being simple pair-wise design, replacement, response surface and additive series. The additive design (target–neighbour design) was used as it allows, elegantly, for the exploration of mechanistic questions about intra- and interspecific interactions (see Snaydon 1991; Gibson et al. 1999; Williams and McCarthy 2001; Weigelt and Jolliffe 2003) between the invader (*A. mangium*) and a locally abundant species, *Melastoma beccarianum* Sen. Lat. (Melastomataceae), a shrub or small tree (maximum height 6 m), common along edges and disturbed habitats of many forest types in Brunei. *M. beccarianum* produces copious amounts of very small seeds, some of which form persistent seed banks and help contribute to its local abundance. In some places where members of this genus have been introduced (e.g. Hawaiian Islands), they are regarded as invasive (Baruch et al. 2000). *M. beccarianum* was chosen as a test species because in disturbed forest sites it is one of the most dominant indigenous plants (Osunkoya et al. 2004) and thus might appear able to impede or slow down *Acacia* tree invasion. Also its seedlings are more abundant in the wild relative to other native species. The objective of the study was to examine:

1. The strengths of inter- and intraspecific competition in the native species versus the introduced species
2. The effect of light availability on patterns of competition

Methods

In September 2001, a greenhouse competition experiment with an additive design (target–neighbour type) was set up involving seedlings of *M. beccarianum* and *A. mangium* (henceforth referred to as *Melastoma* and *Acacia* respectively). The target–neighbour design involves growing an individual of a "target species" in the presence of varying densities or abundances of a "neighbour", which could either be a different species or the same. It is essentially an additive design in the sense that the density of the target species (e.g. *Melastoma*) is reduced to a single individual or a density low enough to preclude significant intraspecific interactions.

Seeding collection and transplanting

In September 2001, young seedlings of the two species (height range: 5–12 cm) were collected from seedling banks at several disturbed heath-forest sites in the Tutong/Muara districts of Brunei. They were raised in tray beds (35×30×8 cm) filled with commercial peat soil within the plant house of the Universiti Brunei Darussalam (UBD) Biology Department. Here, they received ~30% full sunlight for 4 weeks prior to the treatments.

The design

Seven densities (ranging from 2–14 seedlings/pot) were used for the competition experiments: for density 1 (no competition), two seedlings of the target species

(*Melastoma* or *Acacia*) were planted per pot and grown alone; for densities 2, 3, 4, 5, 6, and 7, two seedlings of the target species were grown in the same pot with 2, 4, 6, 8, 10 or 12 seedlings respectively of the neighbour (e.g. *Acacia* or *Melastoma*). Pot size was 20 cm in diameter and 18 cm in depth (i.e. 5 l). The pots were filled with soil from a nearby heath forest, which is generally sandy, slightly acidic and nutrient-deficient, especially in nitrogen and phosphorus (Davies and Becker 1996). For all densities, the seedlings were exposed to one of two light regimes: (1) full sunlight in an open field (but protected with wire mesh) next to the UBD Biology Department greenhouse (at midday, mean photosynthetically active radiation, PAR ± SE = 1,813 ± 32.18 μmol m^{-2} s^{-1}, $n = 20$), or (2) 30% of full sunlight within the UBD greenhouse (at midday, PAR ± SE = 450 ± 26.21 μmol m^{-2} s^{-1}, $n = 20$). These two light regimes shall henceforth be referred to as high light and low light conditions. The light readings were taken using a LICOR Steady State Porometer and are representative of mean readings taken over several days at the beginning, middle and at the end of the experiment (O.O. Osunkoya, unpublished data).

During transplanting, seedlings of the target species and hence with constant number of individuals (two seedlings per pot) were planted in the middle, and the seedlings of the neighbour species (with density varying per pot) were arranged concentrically around them. Each target plant was marked with a plastic ring tag around the stem. Seedlings were left to undergo acclimatization in their new soil environment for a further 2-week period in the low light (30% PAR) environment during which each pot was watered every other day, and given, on one occasion only, 500 ml of a liquid fertilizer (Yates Thrive). On 10 November 2001, half of the seedling pots were moved outside to full sunlight to establish the other light regime. In each light environment, pots were arranged in four blocks—with each block having pots of the seven plant densities with spacing of about 30 cm between pots to ensure equal reception of sunlight by each pot. At monthly intervals, pots were randomized within blocks to minimise location effects on seedling growth. Thus, the overall design involved two light treatments (low and high light), four target–neighbour combinations (*Acacia–Acacia*, *Acacia–Melastoma*, *Melastoma–Acacia*, and *Melastoma–Melastoma*) at seven neighbour densities (0, 2, 4, 6, 8, 10, and 12 neighbours per pot). There were two replicate pots for each treatment combination. Altogether a total of 896 seedlings were used.

Plant height (to apical meristem) and stem diameter were measured at monthly intervals. In May 2002, 6 months after the initiation of the experiment, surviving plants were carefully harvested. Separation of roots of individuals was made relatively easy by soaking the soil medium in running water. Thereafter, individual plants were separated into roots, shoots and leaves. Leaf area was determined with a Delta T area meter (LICOR, NE, USA), while dry-matter accumulation was obtained following drying to constant weight at 80°C.

Initial values for each seedling variable at 4 weeks (i.e. at the end of the acclimatisation period) were obtained from 10 set-aside seedlings of each species grown at 30% PAR. These values were entered during analyses as covariates to adjust for their possible effects on growth parameters. A number of growth parameters were calculated from the primary data collected at 1 and 6 months. These included changes in total biomass, plant height, leaf area, stem diameter, root-to-shoot ratio [RSR, root dry mass/(stem + leaf mass)] and relative growth rate [$\mathrm{RGR} = (\ln W_2 - \ln W_1)/(t_2 - t_1)$, where $\ln W$ is the natural logarithm of biomass, t is the time (in months), and the subscript refers to initial and final harvest].

Statistical analyses

Growth of the target seedlings was analysed with four-factor ANOVA, ANCOVA and regression models using SPSS statistical package (Version 11.5). The four factors examined were: (1) target species (T-SP) and (2) neighbour species (N-SP), each a fixed factor with two levels (*Acacia* and *Melastoma*); (3) competition (C), a fixed factor with seven levels of seedling densities used; and (4) light (L), a fixed factor with two levels (high and low light conditions). Prior to carrying out the above analyses, the dependent growth variables (i.e. RGR, leaf area, total biomass, plant height, stem diameter and RSR) of the two target seedlings in each pot were averaged when both seedlings survived to the 6-month harvest period. To obtain appropriate interactions and to reduce the heterogeneity in variances, total biomass and leaf area were ln-transformed (Underwood 1997). There was no need for transformation of other growth variables. If the relationship between a growth variable and level of competition is similar between *Acacia* and *Melastoma*, then the interaction term (T-SP×C) will not be significant; if on the other hand, intra- or interspecific competition are more important, then the interaction term will be large and significant. Thus the interaction term T-SP×C tests the strength of intra-and interspecific competition in the two-model species under investigation. Where there are significant main and interaction effects, all possible comparisons were made using Bonferroni post-hoc test, which adjusts the critical P value ($\alpha = 0.05$) by the number of pair-wise comparisons being made.

The competitive effect of a neighbour species on a target species was quantified as the slope of the regression of target-plant performance against number or biomass of immediate neighbours (see Goldeberg and Fleetwood 1987; Hartnett et al. 1993; Connolly et al. 2001). This approach measures competition on an individual or biomass basis and thus incorporates asymmetries of individual plant size between competing species. Zero slopes indicate no significant interaction or net effects, while slopes significantly greater or less than zero indicate facilitative and competitive effects respectively. The slopes were also compared using ANCOVA, with significant differences indicating that the identity of neighbour species altered competitive relationships.

In the regression analyses, using number of individuals of neighbour species or final mass of total neighbour in the pot as the independent variable yielded the same results, so only the result using number of neighbours is reported here. Also, the different measures of target-plant growth performance (biomass, total leaf area, plant height, stem size, and RGR) yielded identical results. Hence, only the total biomass, RGR and biomass ratio will be presented. We also used the slopes of the regression to calculate Lotka-Volterra (LV) competition coefficients (so-called equivalence ratio, sensu Freckleton and Watkinson 2001). For each species and light condition, this was obtained as the ratio of the slope under interspecific competition to the slope under intraspecific competition.

Results

General patterns

At the end of the experiment, 764 seedlings were harvested for growth measurements. An equal number of *Acacia* seedlings died in both high light and low light conditions [15.4% (69/448) and 13.2% (62/448) respectively], whereas for *Melastoma* a greater number of seedlings died under high light [20.5% (92/448)] than under low light [4.0% (18/448)]. Overall, mortality was marginally greater under high light conditions. We could not detect any significant relationship between seedling mortality and competition intensity (seedling density), though the trend was apparent under the high light but not under the low light conditions. The nonsignificance of the trend suggests that survival is not a good measure of differences in fitness within the time span of 6 months used.

In contrast, there were large and significant variations in growth parameters amongst seedlings from different treatments. The ANOVA (Table 1) showed that a major part of this variation could be attributed to the main factors of target species, neighbour species, and seedling density (competition). Light effect, as a main factor, was significant for some variables (e.g. RGR and plant height) and nonsignificant for others (leaf area, total biomass and stem diameter). Target species × light interaction effect was also highly significant for all the variables examined—an indication that target-species response was not consistent across light regimes (see Fig. 1). Other interaction effects were of minor magnitude, although some of them were significant, especially target species × density, and target species × neighbour species interactions. However, if Bonferroni correction is applied in view of correlations amongst growth variables measured (in which $\alpha = 0.008$), then the majority of these marginally significant interactions can be deemed nonsignificant.

Light effects

In most cases, growth performance was better under high light than low light conditions (Fig. 1). However, target species × light interaction effect was highly significant for all variables examined (Table 1), suggesting that response to a particular light condition was not the same for the *Acacia* and *Melastoma* seedlings (Fig. 1). This is partly responsible for the nonsignificant effect of light as a main factor in its own right for some of the variables examined (Table 1). For example, for the

Table 1 Summary ANOVA of tests of effects of intra- and interspecific competition for *A. mangium* and *M. beccarianum* under two light regimes

Factor	*df*	*F* ratio and probability					
		RGR	Leaf area[a]	Total biomass[a]	Plant height	Plant-stem diameter	RSR
Target species (T-SP)	1	44.67***	16.87***	10.92**	26.55***	0.4	217.15***
Light (L)	1	7.48**	0.23	3.92	45.42***	0.71	0.22
Density (D)	6	8.80***	4.20**	11.62***	5.71***	7.99***	0.69
Neighbour species (N-SP)	1	8.65**	6.01**	14.90***	8.31**	14.63***	0.05
T-SP×L	1	31.72***	20.66***	35.31***	94.45***	22.73***	14.81***
T-SP×D	5	4.45*	3.50*	6.67***	1.63	1.64	1.09
L×D	6	0.38	0.25	0.28	0.43	0.60	1.22
L×N-SP	1	1.56	4.94*	0.80	3.23	0.79	0.02
D×N-SP	5	0.43	0.27	0.63	0.58	1.62	0.76
T-SP×L×D	5	1.42	2.36	1.72	1.32	1.37	0.25
T-SP×N-SP	1	4.20*	0.48	6.62*	4.94*	3.56	0.34
T-SP×L×N-SP	1	2.93	0.87	2.99	0.03	0.17	1.76
T-SP×D×N-SP	5	2.31	1.62	2.23	1.14	1.61	0.59
L×D×N-SP	5	0.65	1.37	0.69	0.70	1.55	1.19
T-SP×L×D×N-SP	5	1.89	0.50	1.86	1.30	1.10	1.26
Residual	50						
Total	99						

[a] Total biomass and leaf area were ln-transformed prior to analyses

$*P \leq 0.05$; $**P \leq 0.02$; $***P \leq 0.001$

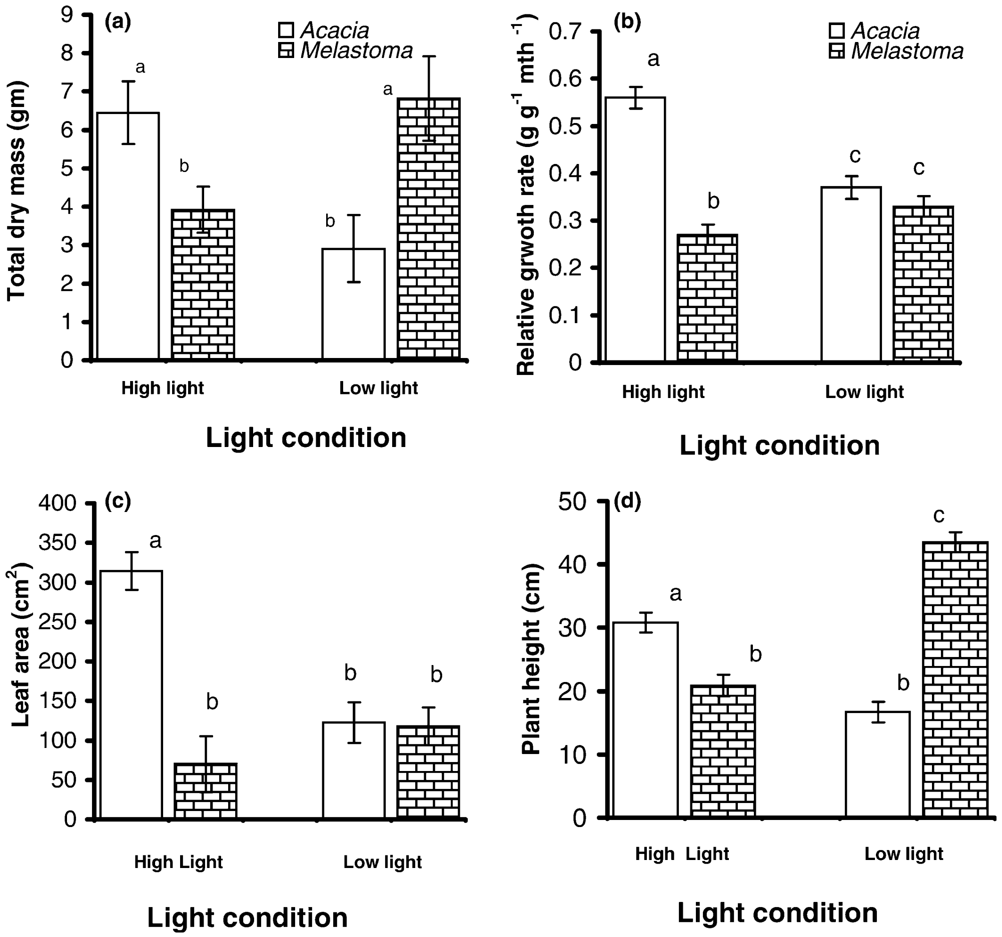

Fig. 1 Mean (±SE) response of the invasive *A. mangium* and the native *M. beccarianum* in high light and low light environments **a** Total biomass, **b** relative growth rate, **c** leaf area and **d** plant height. Biomass and leaf-area values are derived from their back-transformed natural log data. Values are based on the overall performance of the target species following correction for the influence of competition intensity (i.e. seedling density) and neighbour identity (using ANCOVA). *Bars* marked with different *letters* are statistically significant at $P \leq 0.01$ using Bonferroni post-hoc test

invasive *Acacia*, total plant biomass and height were higher in the high light environment than in the low light. For *Melastoma*, the opposite trend was observed with growth being higher under the low light conditions (Fig. 1a, d).

Species effects

Most growth variables examined differed significantly between the two species (Table 1). *Acacia* growth performances were significantly better than those of *Melastoma* (Fig. 1). After controlling for density effect using ANCOVA, growth of *Acacia* was significantly higher than that of *Melastoma* for RGR and leaf area ($P < 0.001$). For biomass and plant height, however, higher values were obtained for *Acacia* compared to *Melastoma*, but the differences were not statistically significant ($P > 0.05$). The interactions of target species × density (competition) and target species × neighbour species were significant for most growth variables (Table 1), indicating that (1) the effect of increasing neighbour density on target species was significant and (2) the target-species response differed depending on the identity of its neighbour, i.e. the strengths of inter- and intraspecific competition were different in both species. Finally, the interactions of light × density, and target species × light × density as well as neighbour species × light × density were all nonsignificant suggesting that competition intensity (seedling density) had similar effects on growth of target seedlings regardless of the light environment.

Competition (seedling-density) effects

The competition indices and trends obtained are summarised in Table 2 and Figs. 2 and 3. It was observed that for most growth variables, the proportion of variation explained (the R^2 value) was higher under the low light conditions than the high light conditions, indicating greater variability in the response of high light plants to their neighbours. Also overall, intraspecific competition was much stronger than interspecific competition (judging by the slope values and tests of the differences in these slope values using linear regression; see Table 2).

Response of target species to intraspecific competition

Under high light conditions, when *Acacia* seedlings were competing intraspecifically, RGR and total biomass decreased significantly with increasing number of

Table 2 Slope values (*b*), proportion of variance explained (R^2), and Lotka-Volterra (LV) competition coefficients for the invasive *A. mangium* and the native *M. beccarianum* growing in intra- and interspecific competition under two light regimes

Neighbour species	Target species									
	Acacia					*Melastoma*				
	Acacia		*Melastoma*			*Melastoma*		*Acacia*		
	b[a]	R^2	*b*	R^2	LV (α)[b]	*b*	R^2	*b*	R^2	LV (β)[b]
High light										
RGR	−0.034**a	0.83	−0.009a	0.08	0.265	−0.039***b	0.95	−0.019*c	0.53	0.514
Biomass (ln)	−0.137**a	0.83	−0.046a	0.12	0.336	−0.225***a	0.96	−0.122*a	0.51	0.567
RSR	0.008*a	0.56	−0.003b	0.40		0.009a	0.05	0.046**c	0.90	
Low light										
RGR	−0.021a	0.40	−0.030*a	0.57	1.429	−0.038***b	0.97	−0.016**a	0.81	0.421
Biomass (ln)	−0.083a	0.38	−0.122*a	0.58	1.470	−0.194***b	0.98	−0.089**a	0.79	0.443
RSR	0.002a	0.07	0.019**b	0.83		0.001a	0.06	0.016a	0.46	

[a] The slope values are based on linear regression of plant growth performance against number of neighbours

[b] LV is the ratio of slope under interspecific competition to slope under intraspecific competition. α Competitive effect of *Melastoma* on *Acacia*, β competitive effect of *Acacia* on *Melastoma*

Asterisks indicate slope values significantly different from zero: $*P \le 0.05$; $**P < 0.002$; $***P < 0.001$. Within a particular light treatment (i.e. a row), slopes that are not statistically different at $P \le 0.05$ are indicated by the same letter

conspecific neighbours (Fig. 2a; Table 2). In contrast, under low light conditions, the relationship, though also negatively related, was not significant, indicating minor intraspecific competitive effect at this light level (Fig. 2b; Table 2). *Melastoma* seedlings responded to intraspecific competition differently. Under high and low light conditions, *Melastoma* growth showed a significant density-dependent effect (Fig. 2; Table 2). In both light conditions, the slopes of the relationship between target *Melastoma* growth performance and number of conspecific neighbours were steeper, indicating more intense intraspecific competition than that observed for *Acacia* (Fig. 2; Table 2). ANCOVA and linear regression analyses showed that there was no significant difference in the slopes between high light and low light treatments for target seedlings of *Melastoma* growing intraspecifically (Table 2), indicating that light did not change the intensity of intraspecific competition significantly in *Melastoma*. Overall, growth in low light environment was significantly better than under high light conditions for *Melastoma*, whereas the opposite trend was observed for *Acacia* (Figs. 1, 2).

Melastoma seedlings allocated significantly more of their biomass to roots than did *Acacia* seedlings (Fig. 3). RSR for target *Melastoma* plants growing intraspecifically did not change significantly with increasing density of conspecific neighbours in both light conditions (Fig. 3; Table 2). RSR of *Acacia* was significantly affected under high light, but not under low light conditions. Under high light conditions, growth allocation to shoots by the target *Acacia* seedlings increased as the number of conspecific increased.

Response of target species to interspecific competition

Under high light conditions, *Acacia* target plants showed a trend of decreasing biomass and RGR with increasing number of *Melastoma* neighbours, but the slope of the relationships was shallow and not significant (Fig. 2a; Table 2). Under low light conditions, the same trend was observed but here the slopes were significant (Fig. 2b; Table 2), indicating that (1) low light conditions affect the response of *Acacia* in the presence of *Melastoma*, and (2) that *Melastoma* showed a strong and significant competitive influence on *Acacia* target plants.

In the treatments in which *Melastoma* individuals were grown as target plants with varying number of *Acacia* neighbours, very different patterns emerged from those observed above. Under high light conditions, growth of *Melastoma* was much more negatively and significantly affected by increasing density of *Acacia* neighbours (e.g. RGR, slope $b = -0.019$) than that observed when *Acacia* was the target and *Melastoma* the neighbour (RGR, slope $b = -0.009$; see Table 2; Fig. 2). Thus under high light conditions, *Melastoma* felt the interspecific effects more than *Acacia* plants. Under low light conditions, growth of *Melastoma* target plants was reduced by increasing density of its *Acacia* neighbours, but in most cases the slope of the relationship was only marginally significant. Overall, in low light conditions, the interspecific effect of *Acacia* neighbour on target *Melastoma* was much weaker (e.g. RGR, slope $b = -0.016$) than the interspecific effect of *Melastoma* neighbour on target *Acacia* plants (RGR, slope $b = -0.030$).

At high and low light conditions the root-to-shoot ratio of the target *Acacia* and target *Melastoma* changed with increasing density of heterospecific neighbours (Fig. 3). For *Melastoma*, root-to-shoot ratio increased significantly with increasing density of its *Acacia* neighbour in both light conditions, but the effect of interspecific competition was felt more in the high light environment. For *Acacia*, impact of interspecific competition on biomass allocation was minor and nonsig-

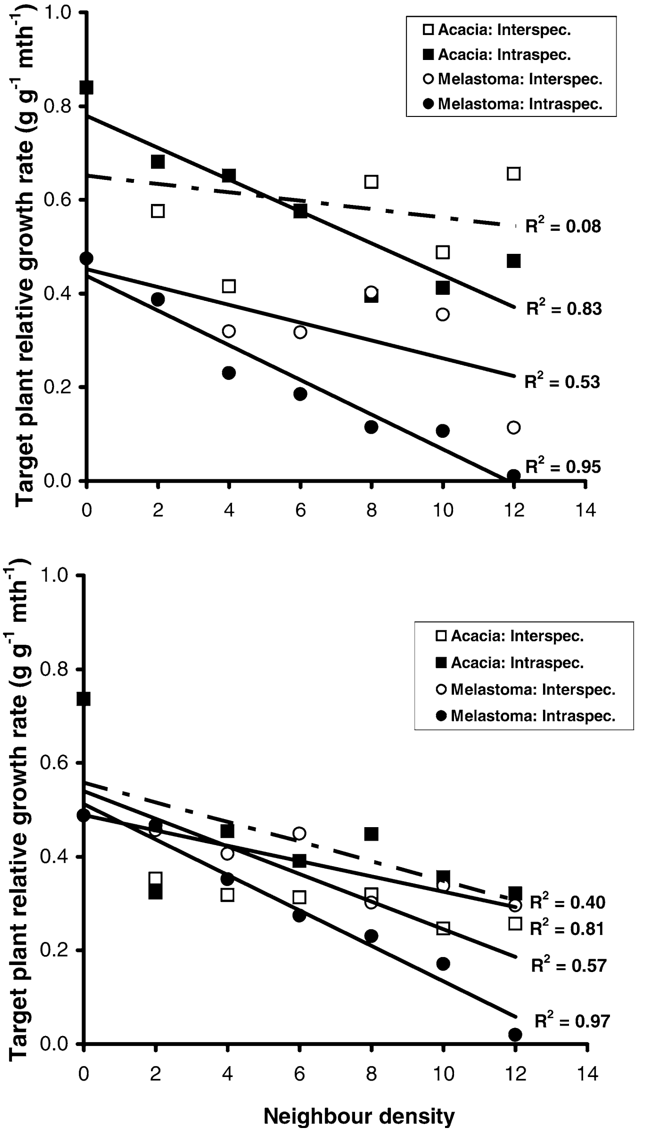

Fig. 2 Relationship between relative growth rate and numbers of neighbours for the invasive *A. mangium* and the native *M. beccarianum* competing intra- and interspecifically under high light (*above*) and low light (*below*) conditions. *Solid* and *dashed lines* respectively indicate significant and nonsignificant trend effects ($P \le 0.05$) of the neighbour species on growth performance of the target species. Slopes values for the relationship are given in Table 2. Similar trends were obtained for other growth variables, and hence these data are not presented

nificant under the high light conditions, but was significant in the low light environment where more biomass was put into the root with increasing density of *Melastoma* neighbours.

Overall competitive effect

The Lotka-Volterra competition coefficients are given alongside the slope values in Table 2. Under high light conditions, the mean *Melastoma* effect on *Acacia* was lower (with $\alpha = 0.30$) than the mean effect of *Acacia* on *Melastoma* ($\beta = 0.54$). Under low light conditions, the mean effect of *Melastoma* on *Acacia* was higher ($\alpha = 1.45$) than the effect of *Acacia* on *Melastoma* ($\beta = 0.43$). Thus the competitive effect of *Acacia* on *Melastoma* is higher in high light environments, but the reverse is the case under low light conditions.

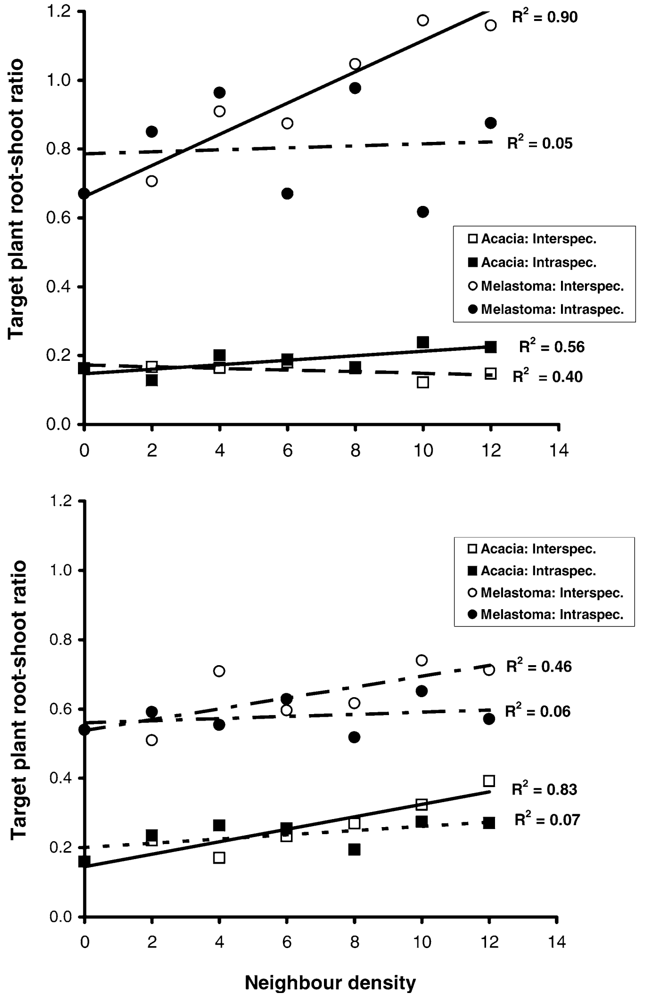

Fig. 3 Relationship between biomass ratio and number of neighbours for the invasive *A. mangium* and the native *M. beccarianum* competing intra- and interspecifically under high light (*above*) and low light (*below*) conditions. *Solid* and *dashed lines* respectively indicate significant and nonsignificant trend effects ($P \le 0.05$) of neighbour species on growth performance of the target species. Slopes values for the relationship are given in Table 2

Discussion

The target–neighbour regression approach used in this study indicates that in the high light environments that are typical of most disturbed forest habitats, *Acacia* plants are capable of outcompeting neighbouring local species, such as *Melastoma*. The superiority of *Acacia* is maintained via higher RGR, which appeared unaffected by increasing density of *Melastoma* (Figs. 1, 2; Table 2). Its ability to fix nitrogen (Turnbull et al. 1998) in a nutrient-poor (e.g. heath) environment could also be a contributing factor. In general, when seedlings of the two species were grown together under high light conditions, they both experienced adverse effects of intraspecific competition (irrespective of the growth variables examined; see Table 2), but *Melastoma* seedlings felt the negative effect more (i.e. its slopes were steeper). This fact is also corroborated by the LV competition coefficients obtained at this light condition ($\alpha = 0.265$–0.336 for *Melastoma* effect on *Acacia* and $\beta = 0.514$–0.567 for *Acacia* effect on *Melastoma*). This suggests that a high density of *Melastoma*, which is often recorded in disturbed forests (Kahar 2002), may not necessarily interfere with the invasive capability of *Acacia* trees. In a low light environment, however, *Acacia* may be the poorer competitor (Fig. 2; Table 2) as the *Acacia* seedling response to interspecific influence was significantly inferior to that of the *Melastoma*. Considering the fact that the performance of *Acacia* in low light was significantly reduced when grown both singly and in competition with con- and heterospecifics, it is safe to argue that the invasive *Acacia* will find it difficult to penetrate and establish in intact/moderately disturbed heath forest where light intensity is often less than 30% of that of the open condition (Kahar 2002). It also indicates that high densities of *Melastoma* may interfere with and slow down *Acacia* invasion into closed heath-forest habitats.

The above assertion might suggest that the debate on the adverse impact of the presence of *Acacia* trees in Brunei should abate as the exotic tree is less likely to invade relatively intact forests. But we know infrastructure development and hence forest disturbance is real. Thus this issue cannot be trivialized. Additionally, biological invasion is widely viewed as the product of a multi-step phenomenon: emigration, immigration, temporary residence as an adventitious species, persistence/naturalization, and invasion (proliferation and spread) (Groves 1986; Mack 2000), during which the exotic species will have to overcome numerous geographical, physiological and ecological barriers in order to become invasive. We contend that *A. mangium* (together with *A. auriculiformis*) has already overcome many of these stages in Brunei (and perhaps also in the Malaysia states of Sabah and Sarawak, where heath vegetation exists and similar problems have been documented; see Chey and Intachat 2000; Ajik 2002). *Acacia* invasiveness was indeed facilitated by the deliberate introduction and cultivation of the trees as a timber resource. Cultivation is known to foster the naturalization/persistence of any species by helping to buffer against environmental stochasticity (see Mack 2000). Another major ecological and contributing factor to the completion of these steps is the increasing prevalence of outbreaks of wildfire, which tend to occur every 2 years in response to drought—especially during the drier months of February–March (Davies and Becker 1996). The frequency and intensity of such fire outbreaks have increased in the last decade, coinciding with the introduction of *Acacia* into plantation forestry in Brunei (O.O. Osunkoya, personal observation and communication with the forest rangers and village elders in coastal areas of Tutong and Muara districts); making a direct link, however, will be difficult. However, as has already been documented in studies from other countries (e.g. South Africa and Australia: Milton 1981; Van Wilgen and Richardson 1985; Van Wilgen et al. 2001), we regularly observe huge litter layers (at times up to 40 cm deep) in *Acacia*-dominated landscapes both in plantations and invaded heath forests. This is a recipe for an increase in fire intensity and duration with significant negative effects on biodiversity, but data on this are scanty (see Van Wilgen et al. 2001). The fire outbreaks help to reinforce the spread of *Acacia* trees as germination of their buried seeds, which have a long viability period, is highly encouraged under this condition (Jeffrey et al. 1988; Holmes and Cowling 1997; O.O. Osunkoya, personal observation).

Biomass allocation

Patterns of biomass allocation differ between the species and under the two light conditions. In general the invasive *Acacia* allocates more towards the shoot (Fig. 3)—a refection of its ability to fix nitrogen and hence lack of a need for extensive root investment. In high light conditions, change in root-to-shoot ratio under intra- and interspecific competition for *Acacia* seedlings was minor. For *Melastoma*, as *Acacia* neighbour density increased, a significant increase in allocation to the root was observed. Such a major shift by *Melastoma* seedlings in biomass ratio in high light relative to low light may help balance demands for nutrients and light energy capture (Tilman 1988; Pattison et al. 1998), but there seems to be no need for such a strategy in *Acacia* due to the aforementioned ability. Under low light conditions, as interspecific competition intensifies, the shift in biomass allocation also tends to be more towards the root for both target *Melastoma* and target *Acacia* seedlings (Fig. 3b). Under low light conditions, irradiance is probably the more limiting resource, and the shift in allocation is expected to occur more towards the shoot (Osunkoya and Ash 1991; Gerry and Wilson 1995; Meekins and McCarthy 1999). We did not observe such a trend in the present study, perhaps because of demand for both light and nutrients. However it should be noted that reported effects of competition on biomass allocation to roots have not been consistent: increase, decrease, and no change have all been documented (see Goldberg and Fleetwood 1987; Osunkoya and Ash 1991; Pattison et al. 1998). The lack of consistency echoes the assertions by Goldberg and Fleetwood (1987) and Pattison et al. (1998) that the relative impact of below- and above-ground competition in response to density influence may vary in a much more species-specific manner than does the response of total biomass.

Conclusion

We have shown in this additive (target–neighbour) competition experiment that *A. mangium* trees may outcompete the native *Melastoma* in disturbed heath habitats, but only under high light conditions. Thus the effect of competition on growth is light dependent—the invasive *Acacia* being the superior competitor in high light environments and vice versa under low light conditions (or in a worse scenario, the two species can coexist). Thus the high abundance of *Acacia* trees we have seen in disturbed and degraded forests along the coast and in several inland sites in Brunei may be partly explained by the superior competitive ability of *Acacia* trees towards most indigenous species—though fuller analysis awaits us in terms of the mechanisms by which this is achieved and the guilds of local species which are more likely to be displaced. We have commenced greenhouse and field work in this area. In relatively intact forests and in disturbed but periodically wet habitats (e.g. low-lying, regularly inundated degraded forests), presence, and hence invasive ability, of *Acacia* trees has been observed to be limited or even nonexistent (O.O. Osunkoya, personal observation). This is much in line with *Acacia's* marginal competitive ability under low light conditions—just as shown in the greenhouse experiment reported herein. Nonetheless, it is becoming increasingly and visually clear that *A. mangium*, like many other exotic plantation trees that are invasive in their novel environment, accrues costs to the ecosystem that may far outweigh its benefits (see Gordon 1998; Van Wilgen et al. 2001; De Wit et al. 2001; Rouget et al. 2002 for a comprehensive synthesis of this treatise). Thus it is time to put in place regulatory mechanisms to contain further spread of the *Acacia* tree species in Brunei.

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