GROWTH, MORPHOLOGY AND BIOMASS ALLOCATION IN RESPONSE TO LIGHT GRADIENT IN FIVE SUBTROPICAL EVERGREEN BROADLEAVED TREE SEEDLINGS

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CHENG X, YU M, WANG GG, WU T & ZHANG C. 2013. Growth, morphology and biomass allocation in response to light gradient in five subtropical evergreen broadleaved tree seedlings. We compared seedling growth, leaf morphology and biomass allocation of five widely distributed, evergreen species (Elaeocarpus sylvestris, Illicium henryi, Quercus phillyraeoides, Gardenia jasminoides and Ardisia crenata) under varying controlled light conditions using artificial shade houses. Regardless of species, higher height growth rate was observed at intermediate light levels (33–52% sunlight). Diameter growth rate, however, increased with increasing light level. Morphological variables (mean leaf area, total leaf area per plant, specific leaf area and leaf area ratio) were significantly affected by light, with greater variation occurring in deep shade treatment (6% sunlight). Total biomass increased with light levels for E. sylvestris, Q. phillyraeoides and G. jasminoides but larger biomass was found at intermediate light levels for I. henryi and A. crenata. Biomass allocation patterns displayed small variations in the five species. Although the five species differ in their growth strategy across a light gradient, their large plasticity allows them to grow well under a wide range of light environments. As a whole, E. sylvestris, Q. phillyraeoides and G. jasminoides showed their best growth above 52% sunlight. Optimal light condition for I. henryi and A. crenata were from 33 to 52% sunlight. Our findings support the underplanting of these five evergreen species in order to enrich the biodiversity of subtropical plantation ecosystems.

Keywords: Evergreen tree species, light environment, plasticity, shade tolerant, specific leaf area, leaf area ratio

INTRODUCTION

Light is an important factor influencing plant growth and survival. In forest ecosystems, understory light environment is largely determined by the degree of canopy cover (Masaka et al. 2011). Trees planted under a closed forest canopy must cope with low light environment and their survival depends on their phenotypic and/or functional plasticity (Kobe 1999, Jarčuška & Barna 2011). Therefore, changes in leaf size, specific leaf area and leaf

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537
area ratio often explain the variation in growth rate among different species growing under different light environments (Feng et al. 2007).

At the whole-plant level, shade-tolerant species generally have higher leaf area than shade intolerant species. By forming thinner leaves with low leaf dry mass per unit leaf area and/or having greater fraction of plant mass in leaves, shade tolerant species typically have greater leaf area per total plant mass (leaf area ratio). However, shade intolerant seedlings of temperate and tropical angiosperms often have lower leaf dry mass per unit leaf area and higher leaf area ratio and relative growth rate under both high and low light (Walters & Reich 1996, Reich et al. 2003). Despite having higher relative growth rate in shade and other traits that are predicted to increase shade tolerance, low-light mortality is still consistently higher in seedlings of shade-intolerant species when compared with shade-tolerant species (Walters & Reich 1996).

Plant phenotypic plasticity in response to light environment varies with species. Shade-tolerant species have lower physiological plasticity than intolerant species (Delagrange et al. 2004, Sánchez-Gómez et al. 2006). Negative correlations between the plasticity in traits that improve light capturing and enhance carbon gain have been postulated for species differing in shade tolerance (Henry & Aarssen 1997). However, until now, information on the correlations between structural plasticity and shade tolerance is limited and often contradicting. Some studies have shown that morphological plasticity is greater in shade-tolerant species, partly offsetting lower physiological plasticity (Delagrange et al. 2004, Niinemets & Valladares 2004) but other studies have observed lower morphological plasticity of shade-tolerant species (Bloor & Grubb 2004, Sánchez-Gómez et al. 2006).

The plantation area (5.33 × 10^7 ha) in China is the largest in the world and accounts for 29% of the total plantation area in the world (FAO 2007, SFA 2007). However, most of these plantations are monoculture, especially in the subtropical region where monoculture plantations have been established from a few selected species including Cunninghamia lanceolata, Pinus massoniana and several exotic pines (e.g. Pinus taeda and Pinus elliottii) (SFA 2007). Evergreen broadleaved species, which are believed to be major components of the zonal forest in this region, are seldom used in plantations (SFA 2007). There are evidences suggesting that monoculture plantations usually lead to the decline of ecosystem biodiversity and functions (Erskine et al. 2006, Richards et al. 2010). These problems have attracted increasing attentions in recent years. One possible solution is to select some species with high economic value but suitable for planting in the understorey of the monoculture timber plantations (Liu & Zheng 1999). For example, Schima superb, Michelia macclurei and Elaeocarpus sylvestris were planted in the understorey of C. lanceolata stand in south China (Xiong 2007). This practice not only improved stand structure and soil quality but also increased ecosystem production and, thus, economic return to the landowners. Although underplanting is now increasingly adopted by land managers, there are only a few studies of the survival and growth of the underplanted species in response to canopy shading or reduced light availability.

In order to select suitable species for underplanting in monoculture timber stands, we tested growth, morphology and biomass allocation in five widely-distributed subtropical evergreen broadleaved species (E. sylvestris, Illicium henryi, Quercus phillyraeoides, Gardenia jasminoides and Ardisia crenata) along an experimental light gradient. The main objectives of our study were to (1) identify how growth, morphology and biomass allocation change across a gradient of light availability and (2) determine the light requirements for optimal growth of each species.

MATERIALS AND METHODS

Study site

The experiment was conducted in Qianjiacun Tree Nursery (119° 86’ E, 30° 14’ N, mean altitude 265 m), Fuyang city, Zhejiang province, China. The area has subtropical monsoon climate. Average annual temperature is 16.4 °C (maximum 38.1 °C in July and minimum 6.8 °C in January). Average annual precipitation at the study site is 1814 mm, the frost-free period is 252 days and total annual sunshine hours are 1334.1 hours. The experimental site was farmland before 2005. Its soil type is red and yellow soil while soil pH is 6.5.

Plant material

Five subtropical evergreen broadleaved tree species were selected—E. sylvestris (Elacocarpaceae), I.
*Illicium henryi* (Illiciaceae), and *Q. phillyraeoides* (Fagaceae) are classified as trees, with maximum height of 20, 12 and 10 m respectively, and *G. jasminoides* (Rubiaceae) and *A. crenata* (Myrsinaceae) are shrubs with maximum height of about 2 m. *Illicium henryi*, *G. jasminoides* and *A. crenata* are of pharmaceutical values, while *E. sylvestris* and *Q. phillyraeoides* are of timber and ecological values. Seeds of these species were collected in near Hangzhou (120° 16' E, 30° 31' N) and Quzhou (118° 13' E, 29° 06' N). In April 2008, the seeds were sown in the field at the Qianjiacun Tree Nursery. Similar tending management was conducted for the five species after seed germination.

**Experimental design**

The study was conducted in a flat, open area. A total of 150 two-year-old seedlings for each species, relatively uniform in size, were randomly divided into five groups with 30 seedlings of each species per group. The five tree species of each group were randomly planted (the same species grown together) in a 15 m × 2 m plot on 14 March 2010.

One month after planting these seedlings, light treatment was randomly assigned to each plot. Seedlings planted in the same plot were thus subjected to the same controlled light condition. Five light treatments, i.e. 100, 52, 33, 15 and 6% full sunlight were created by building a shade house covered with an increasing number of layers of black nylon shade netting. The 17 m × 2.5 m shade house was 2.5 m high. Relative irradiance in each shade house was estimated using light meter during a clear day in the summer. A 20-cm slit was retained between soil surface and shade netting for ventilation in the shade house. In the experimental plot, weeds were periodically cleared and seedlings were watered whenever necessary.

**Growth, morphology and biomass measurement**

For every seedling, tree height and diameter at 5 cm above ground were measured on 15 April and 16 November 2010. Seedling mortality (ratio of dead seedling to total number of seedling in every light treatment) was recorded at the end of the experiment. The final harvest was carried out in mid-November 2010. Six seedlings of each species and light treatment were randomly selected and destructively sampled. Leaf, shoot and root dry mass of each sampled seedling were determined. Dry weight was obtained by oven drying fresh sample at 70 °C until a constant mass was reached. A subsample of 50 leaves of each species for every light treatment was randomly selected for leaf morphology measurements. Leaf area was measured by leaf area meter.

To characterise the functional traits of each studied seedlings, some indices were calculated, including growth parameters, i.e. net height growth (plant height at the end of experiment subtract initial height), net diameter growth (plant stem diameter at the end of experiment subtract initial diameter) and height/diameter (ratio of height to stem diameter at 5 cm above ground at the end of experiment). The morphological parameters calculated were mean leaf area (cm² per leaf), total leaf area (cm² per plant), specific leaf area (leaf area per unit leaf dry mass, cm² g⁻¹) and leaf area ratio (ratio of leaf area to plant dry mass). Architectural parameters included leaf mass ratio (ratio of leaf mass to plant dry mass), shoot mass ratio (ratio of shoot mass to plant dry mass) and root mass ratio (ratio of root mass to plant dry mass). Plasticity index was calculated as (maximum value – minimum value)/maximum value for each of these structural and morphological variables for the five species (Valladares et al. 2000).

One-way analysis of variance (ANOVA), followed by a Duncan’s post-hoc test, was used to test differences in growth (net height growth and net diameter growth), growth allocation (height / diameter), morphological traits (mean leaf area, total leaf area, specific leaf area and leaf area ratio) and biomass allocation (leaf mass ratio, shoot mass ratio and root mass ratio) between light treatments for each species. All data analyses were performed using SPSS 13.0. Statistical significance level was set at α = 0.05.

**RESULTS**

**Survival rate and growth**

Regardless of light treatments, all seedlings of *E. sylvestris*, *I. henryi* and *G. jasminoides* survived during the study. For *Q. phillyraeoides*, survival rate was 36.8% in the lowest light level (6%) and over 85.7% in the rest of the light treatments. Survival rate for *A. crenata* was 33.3% in full sunlight and over 87.5% in the rest of the light treatments (data not shown).
Net height growth increased with increasing light levels but declined at 100% sunlight for most of the species. Maximum height growth was observed at 52 or 33% sunlight (Figure 1). *Ardisia renata* had higher net height growth at much lower light levels (6–33% sunlight). Net diameter growth also increased with increasing light levels for the five species, except for *I. henryi* and *A. crenata* which had reduced growth at 100% sunlight (Figure 2). Height/diameter ratio decreased with increasing light for *E. sylvestris* and *G. jasminoides* (Figure 3). Height/diameter ratio was significantly lower at full sunlight compared with 6–33% sunlight for *I. henryi* (p < 0.05). The ratio was significantly lower at 52% sunlight compared with 6 and 33% sunlight for *A. crenata* (p < 0.05). No significant differences in height/diameter ratio were detected between the five light levels for *Q. phillyraeoides* (Figure 3).

**Morphology**

Mean leaf area decreased with increasing light level except for *Q. phillyraeoides* (Table 1). Total leaf area increased with increasing light intensity for most of species, but it reduced from 52 to 100% sunlight treatment for *E. sylvestris* and *A. crenata*. For *I. henryi*, total leaf area did not change much with light. Specific leaf area for *E. sylvestris*, *I. henryi*, *G. jasminoides* and *A. crenata* decreased with irradiance but increased from 6 to 15% sunlight for *Q. phillyraeoides* and then decreased with increasing light intensity. Leaf area ratio initially increased with decreasing...
Figure 3  Height/diameter of *Elaeocarpus sylvestris* (Es), *Illicium henryi* (Ih), *Quercus phillyraeoides* (Qp), *Gardenia jasminoides* (Gj) and *Ardisia crenata* (Ac) after one growing season at different light levels; different letters indicate significant difference (p < 0.05) between light levels based on Duncan’s post-hoc test.

Table 1  Mean leaf area, total leaf area, specific leaf area and leaf area ratio of *Elaeocarpus sylvestris* (Es), *Illicium henryi* (Ih), *Quercus phillyraeoides* (Qp), *Gardenia jasminoides* (Gj) and *Ardisia crenata* (Ac) at different light levels

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Parameter</th>
<th>6%</th>
<th>15%</th>
<th>33%</th>
<th>52%</th>
<th>100%</th>
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<tr>
<td>Es</td>
<td>Mean leaf area (cm²)</td>
<td>18.9 ± 2.3 a</td>
<td>15.4 ± 1.6 a</td>
<td>16.8 ± 1.3 a</td>
<td>13.4 ± 1.3 b</td>
<td>11.9 ± 1.5 b</td>
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<td>Total leaf area (cm²)</td>
<td>4070 ± 726 c</td>
<td>5734 ± 811 bc</td>
<td>9693 ± 534 a</td>
<td>11670 ± 750 a</td>
<td>6236 ± 728 b</td>
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<tr>
<td></td>
<td>Specific leaf area (cm² g⁻¹)</td>
<td>216.4 ± 13.5 a</td>
<td>204.0 ± 16.2 a</td>
<td>193.9 ± 10.9 a</td>
<td>156.5 ± 13.1 b</td>
<td>121.3 ± 10.6 c</td>
</tr>
<tr>
<td></td>
<td>Leaf area ratio (cm² g⁻¹)</td>
<td>58.8 ± 4.7 a</td>
<td>58.4 ± 3.5 a</td>
<td>63.7 ± 2.9 a</td>
<td>46.6 ± 2.5 b</td>
<td>26.6 ± 1.5 c</td>
</tr>
<tr>
<td>Ih</td>
<td>Mean leaf area (cm²)</td>
<td>21.8 ± 2.3 ab</td>
<td>24.9 ± 2.4 a</td>
<td>19.4 ± 1.3 b</td>
<td>19.3 ± 2.2 b</td>
<td>13.2 ± 0.9 c</td>
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<td></td>
<td>Total leaf area (cm²)</td>
<td>3111 ± 261 a</td>
<td>3273 ± 408 a</td>
<td>2808 ± 268 a</td>
<td>3143 ± 474 a</td>
<td>2623 ± 406 a</td>
</tr>
<tr>
<td></td>
<td>Specific leaf area (cm² g⁻¹)</td>
<td>95.8 ± 9.6 a</td>
<td>96.2 ± 7.8 a</td>
<td>79.4 ± 8.2 b</td>
<td>77.3 ± 4.9 b</td>
<td>65.9 ± 5.3 c</td>
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<td></td>
<td>Leaf area ratio (cm² g⁻¹)</td>
<td>25.4 ± 1.1 a</td>
<td>26.9 ± 2.4 a</td>
<td>21.3 ± 1.3 a</td>
<td>22.1 ± 2.8 a</td>
<td>23.0 ± 1.6 a</td>
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<td>Qp</td>
<td>Mean leaf area (cm²)</td>
<td>3.5 ± 0.2 b</td>
<td>5.3 ± 0.7 a</td>
<td>5.2 ± 0.6 a</td>
<td>4.8 ± 0.4 a</td>
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<td>Total leaf area (cm²)</td>
<td>230 ± 40 c</td>
<td>622 ± 185 b</td>
<td>636 ± 70 b</td>
<td>930 ± 242 a</td>
<td>941 ± 162 a</td>
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<tr>
<td></td>
<td>Specific leaf area (cm² g⁻¹)</td>
<td>72.7 ± 10.4 b</td>
<td>90.1 ± 6.9 a</td>
<td>82.2 ± 8.5 a</td>
<td>69.6 ± 9.3 b</td>
<td>64.1 ± 5.9 b</td>
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<td></td>
<td>Leaf area ratio (cm² g⁻¹)</td>
<td>17.0 ± 2.1 c</td>
<td>25.1 ± 2.8 b</td>
<td>34.4 ± 3.1 a</td>
<td>22.4 ± 3.0 b</td>
<td>15.0 ± 1.9 c</td>
</tr>
<tr>
<td>Gj</td>
<td>Mean leaf area (cm²)</td>
<td>11.8 ± 1.7 c</td>
<td>19.8 ± 2.3 a</td>
<td>15.7 ± 2.6 b</td>
<td>16.0 ± 2.4 b</td>
<td>12.4 ± 1.7 c</td>
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<td>Total leaf area (cm²)</td>
<td>461 ± 150 c</td>
<td>1371 ± 184 b</td>
<td>2030 ± 444 a</td>
<td>2363 ± 406 a</td>
<td>2375 ± 384 a</td>
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<td></td>
<td>Specific leaf area (cm² g⁻¹)</td>
<td>195.6 ± 12.8 a</td>
<td>175.1 ± 15.9 ab</td>
<td>153.3 ± 10.5 b</td>
<td>115.9 ± 9.6 c</td>
<td>107.9 ± 13.8 c</td>
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<td>Leaf area ratio (cm² g⁻¹)</td>
<td>32.0 ± 5.9 b</td>
<td>53.8 ± 4.6 a</td>
<td>39.5 ± 5.4 b</td>
<td>34.3 ± 2.8 b</td>
<td>28.2 ± 1.9 c</td>
</tr>
<tr>
<td>Ac</td>
<td>Mean leaf area (cm²)</td>
<td>17.3 ± 2.1 a</td>
<td>20.2 ± 2.5 a</td>
<td>12.6 ± 0.8 b</td>
<td>14.8 ± 2.1 b</td>
<td>5.8 ± 0.6 c</td>
</tr>
<tr>
<td></td>
<td>Total leaf area (cm²)</td>
<td>197 ± 27 b</td>
<td>575 ± 212 a</td>
<td>456 ± 112 a</td>
<td>553 ± 65 a</td>
<td>106 ± 37 c</td>
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<td></td>
<td>Specific leaf area (cm² g⁻¹)</td>
<td>138.7 ± 13.7 a</td>
<td>132.0 ± 9.1 a</td>
<td>112.3 ± 12.6 a</td>
<td>84.3 ± 5.7 b</td>
<td>67.2 ± 9.2 c</td>
</tr>
<tr>
<td></td>
<td>Leaf area ratio (cm² g⁻¹)</td>
<td>27.1 ± 1.8 b</td>
<td>49.5 ± 6.6 a</td>
<td>30.3 ± 3.6 b</td>
<td>26.1 ± 2.9 b</td>
<td>10.3 ± 2.1 c</td>
</tr>
</tbody>
</table>

Different letters in the same line are significantly different (p < 0.05) between light levels based on Duncan’s post-hoc test.

Irradiance, reached maximum at 15–33% sunlight, and then declined at deep shade treatment for *E. sylvestris*, *Q. phillyraeoides*, *G. jasminoides* and *A. crenata*. Leaf area ratio for *I. henryi* did not change with light.

**Biomass allocation**

Total dry biomass per plant of the five tree species in response to light levels is shown in Figure 4. For *E. sylvestris*, *Q. phillyraeoides* and *G. jasminoides*,
total dry biomass increased with increasing light level, with the greatest biomass observed at the high light levels (either at 100 or 52% sunlight). Total dry biomass values were greatest at 52% sunlight for *I. henryi* and *A. crenata*, with no significant difference between the rest of the light levels.

Light levels did not affect leaf mass ratio for *Q. phillyraeoides* and root mass ratio for *I. henryi*, *G. jasminoides* and *A. crenata* (Figure 5). Leaf mass ratio was higher in intermediate light levels (15–52%) for *E. sylvestris* and *A. crenata*, and lower in the deep shade (6% sunlight) for *I. henryi* and *G. jasminoides*. Shoot mass ratio for *E. sylvestris* and *G. jasminoides* did not change with light but *I. henryi* and *Q. phillyraeoides* allocated more biomass to shoot in the shade treatments compared with full sunlight. Shoot mass ratio was significantly lower at 15–33% sunlight than 100% for *A. crenata* (p < 0.05). Root mass ratio decreased in the shade treatments compared with full sunlight for *E. sylvestris* and *Q. phillyraeoides*.

**Phenotypic plasticity**

Plasticity indices of the five tree species are displayed in Table 2. Plasticity of growth parameters was relatively higher for *E. sylvestris*, *Q. phillyraeoides* and *G. jasminoides*. Among the leaf traits, plasticity of total leaf area and leaf area ratio were greatest for the studied species except for *I. henryi*. Biomass allocation was more plastic for *E. sylvestris* in terms of root mass ratio, for *G. jasminoides* in terms of leaf mass ratio, and for *A. crenata* in terms of leaf mass ratio and shoot mass ratio.

**DISCUSSION**

**Growth responses to light**

Growth response to light differs between species. For shade-tolerant species, previous studies found that growth rate of seedlings was highest in intermediate light levels (25–50%), above which it declined (Poorter 1999). In another study, highest relative growth rate of shade-tolerant species occurred at 16 or 27% sunlight while optimal light environment for early successional species were from 26 to 100% sunlight (Veenendaal et al. 1996). In addition, many researches showed that height growth of saplings increased with increasing light availability (Kunstler et al. 2005, Stancioiu & O’Hara 2006). In our study, height growth of *E. sylvestris, I. henryi, Q. phillyraeoides* and *G. jasminoides* increased with increasing light levels but declined at 100% sunlight. Highest height growth for these four species occurred in the intermediate light levels (33–52%) which was consistent with Poorter (1999). Height/diameter ratio decreased with increasing light for all species except for *A. crenata*. For *A. crenata*, height growth and height/diameter ratio did not change with shade treatments. It was likely that this species acclimated to different light environment through morphological (e.g. mean leaf area and leaf area ratio) change.
Our results partially confirmed the tendency that trees enhanced height growth for light capture when growing under a low light environment (Valladares & Niinemets 2008). However, height growth reduced significantly in low light condition (6–15% sunlight) for *E. sylvestris*, *Q. phillyraeoides* and *G. jasminoides* (Figure 1), suggesting that growth of these three species would be inhibited when planted under a closed overstorey canopy. Additionally, when underplanting *Q. phillyraeoides* in monoculture plantations, canopy disturbance (e.g. thinning) may be needed because of its low survival rate (36.8%) in 6% sunlight.

**Table 1.** Changes of leaf mass ratio (LMR), shoot mass ratio (SMR) and root mass ratio (RMR) of (a) *Elaeocarpus sylvestris*, (b) *Illicium henryi*, (c) *Quercus phillyraeoides*, (d) *Gardenia jasminoides* and (e) *Ardisia crenata* at different light levels.

**Table 2.** Plasticity indices of *Elaeocarpus sylvestris* (Es), *Illicium henryi* (Ih), *Quercus phillyraeoides* (Qp), *Gardenia jasminoides* (Gj) and *Ardisia crenata* (Ac).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Es</th>
<th>Ih</th>
<th>Qp</th>
<th>Gj</th>
<th>Ac</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net height growth</td>
<td>0.39</td>
<td>0.54</td>
<td>0.72</td>
<td>0.57</td>
<td>0.55</td>
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<tr>
<td>Net diameter growth</td>
<td>0.92</td>
<td>0.56</td>
<td>0.71</td>
<td>0.83</td>
<td>0.61</td>
</tr>
<tr>
<td>Height/diameter</td>
<td>0.56</td>
<td>0.10</td>
<td>0.18</td>
<td>0.46</td>
<td>0.17</td>
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<tr>
<td>Mean leaf area</td>
<td>0.37</td>
<td>0.47</td>
<td>0.39</td>
<td>0.40</td>
<td>0.71</td>
</tr>
<tr>
<td>Total leaf area</td>
<td>0.65</td>
<td>0.20</td>
<td>0.76</td>
<td>0.81</td>
<td>0.82</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>0.44</td>
<td>0.31</td>
<td>0.29</td>
<td>0.45</td>
<td>0.52</td>
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<tr>
<td>Leaf area ratio</td>
<td>0.58</td>
<td>0.15</td>
<td>0.57</td>
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<td>Total dry biomass</td>
<td>0.72</td>
<td>0.20</td>
<td>0.78</td>
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<td>0.66</td>
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<td>Leaf mass ratio</td>
<td>0.33</td>
<td>0.24</td>
<td>0.27</td>
<td>0.47</td>
<td>0.59</td>
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<tr>
<td>Shoot mass ratio</td>
<td>0.10</td>
<td>0.21</td>
<td>0.17</td>
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<td>0.49</td>
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<tr>
<td>Root mass ratio</td>
<td>0.41</td>
<td>0.21</td>
<td>0.28</td>
<td>0.29</td>
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</table>
Morphology responses to light

Variations in leaf traits are considered an efficient way for plants to acclimate to different light environment. Leaf area is an important leaf trait as it is the main attribute controlling light interception (Bartelink 1997). Our findings that mean leaf area reduces with increasing irradiance and that total leaf area per plant is higher in intermediate light levels are consistent with results of Poorter (1999) and Petritan et al. (2009). At 6% sunlight, mean leaf area of *Q. phillyraeoides* was significantly reduced and a leveling-off occurred at higher light levels (15–100% sunlight). For *I. henryi*, total leaf area changed little with irradiance. In general, at low light, plants enhance light interception by allocating more biomass to leaves and forming thin leaves with high specific leaf area, leading to high leaf area ratio (Poorter 1999). At high light penetration, plants reduce transpiration losses and increase carbon gain by making small, thick leaves with low specific leaf area (Poorter 1999). Small leaf has a thin boundary layer which allows for better convective heat loss to the environment. In this way less transpiration is needed for cooling down the leaf in a high-light environment (Givnish 1984). Greater specific leaf area and leaf area ratio confer plants higher efficiency in capturing light resources under low light environment (Wang et al. 2006, Saldaña-Acosta et al. 2009). In this study, specific leaf area and leaf area ratio for most species followed these general patterns, with seedlings grown in low light displaying greater specific leaf area than seedlings grown in increased light environments. However, *I. henryi* displayed limited variability in total leaf area and leaf area ratio along the light gradient. Similar results of increasing specific leaf area or leaf area ratio along decreasing light gradient have also been reported for other tropical tree species (Kelly et al. 2009).

Biomass allocation responses to light

In our study, total dry mass per plant increased from low light to high light and the patterns of biomass allocation varied between light levels. For *E. sylvestris* and *Q. phillyraeoides*, shade treatment (6–52% sunlight) resulted in more biomass being allocated to aboveground than belowground compared with 100% sunlight treatment. Our finding was consistent with the functional equilibrium theory which indicated that plants responded to a decrease in aboveground resources with increased allocation to shoots (leaves), whereas they responded to a decrease in belowground resources with increased allocation to roots (Poorter & Nagel 2000). Similar results were also found in other species studied (Montgomery 2004, Markesteijn & Poorter 2009). However, root mass ratio was less varied along light gradient for *I. henryi*, *G. jasminoides* and *A. crenata*. Some studies have reported that low-light plants minimise respiratory losses to survive (Walters & Reich 2000, Craine & Reich 2005) and maximise long-term storage in stems and roots rather than harvesting of resources via phenotypic plasticity of carbon to track environmental changes (Reich et al. 2003).

Evidence for the proposed biomass allocation trade-off is equivocal and the underlying mechanisms are not well understood (Poorter 2005). Root and leaf mass fraction affect belowground and aboveground foraging capacity only to a minor extent (Poorter & Nagel 2000). Moreover, some researches showed that low leaf mass ratio could be compensated for by gaining a large leaf area per unit leaf biomass invested, i.e. high specific leaf area (Poorter 2005) through the formation of thin or low density leaves (Witkowski & Lamont 1991). Similarly, low root mass ratio can be compensated for by producing small diameter roots (i.e. fine root) with large root length per unit biomass invested (i.e. a high specific root length). Our results partly supported the idea. In low light environment (6–15% sunlight), leaf mass ratio of *E. sylvestris*, *I. henryi*, *G. jasminoides* and *A. crenata* reduced or did not change compared with higher light levels, while specific leaf area enhanced for these species. Specific root length data were not measured in our study, but root mass ratio and specific root length were reported to be negatively correlated (Markesteijn & Poorter 2009).

Phenotypic plasticity responses to light

Phenotypic plasticity varied greatly between the five species along the light gradient. Growth plasticity was relatively higher for *E. sylvestris*, *Q. phillyraeoides* and *G. jasminoides*, and morphological plasticity was greater for *A. crenata*. Overall phenotypic plasticity was lowest for *I. henryi* compared with the rest of the species.
Total leaf area, specific leaf area and leaf area ratio had greater plasticity and these variables were more critical for leaf functioning in different light environments (Bongers & Popma 1988). Similar results were also found for tropical tree species (Rozendaal et al. 2006). In our study, leaf mass ratio, shoot mass ratio and root mass ratio had lower plasticity response to light. These results are consistent with biomass allocation in rainforest tree species (Kelly et al. 2009).

Our results indicated that the five species differed in their growth strategy across a light gradient. These species regulated their growth, morphology and biomass by acclimating to different light environment. *Elaeocarpus sylvestris*, *Q. phillyraeoides* and *G. jasminoides* displayed higher plasticity in growth and morphology and achieved their best growth above 52% sunlight. For *A. crenata*, more biomass allocated to leaf following the shade treatment and morphological (e.g. mean leaf area and total leaf area) plasticity played a key role for this species under variable light environments. The plasticity indices of morphological variables were lower for *I. henryi* and more biomass was allocated to the shoot in shade treatment. This suggested that this plant acclimated to different light environments and the process depended mainly on structural plasticity. Optimal growth light conditions for *I. henryi* and *A. crenata* were from 33 to 52% sunlight. Survival of *E. sylvestris*, *G. jasminoides* and *I. henryi* was not affected by light while *Q. phillyraeoides* had low survival (33.3%) in 6% sunlight and *A. crenata*, in 100% sunlight. These results suggested that partial shading did not compromise growth of the studied species. Indeed, partial shading would be needed for *I. henryi* and *A. crenata* to maintain their optimal growth, and for *A. crenata*, to achieve better survival. From this study, *A. crenata* could be ranked as very shade tolerant, *I. henryi*, *E. sylvestris* and *G. jasminoides* as shade tolerant, and *Q. phillyraeoides* as intermediate shade tolerant. Therefore, underplanting these species in monoculture plantation, especially when coupled with thinning, can be a viable option to enhance biodiversity without negatively affecting timber management objectives.

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