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

X Cheng[1], M Yu[1,] *, GG Wang[2], T Wu[1] & C Zhang[1]

[1]*Institute of Subtropical Forestry, Chinese Academy of Forestry, Fuyang, Zhejiang 311400, PR China*
[2]*School of Agricultural, Forest and Environmental Sciences, Clemson University, Clemson, South Carolina 29634-0310, USA*

Received August 2012

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

CHENG X, YU M, WANG GG, WU T & ZHANG C. 2013. Pertumbuhan, morfologi dan peruntukan biojisim sebagai gerak balas terhadap gradien cahaya dalam lima anak biji benih pokok berdaun lebar subtropika. Kami membandingkan pertumbuhan anak biji benih, morfologi daun serta peruntukan biojisim lima spesies (*Elaeocarpus sylvestris, Illicium henryi, Quercus phillyraeoides, Gardenia jasminoides* dan *Ardisia crenata*) malar hijau yang tersebar luas di bawah keadaan cahaya terkawal menggunakan rumah naungan tiruan. Kadar pertumbuhan ketinggian yang lebih besar dicerap dalam semua spesies yang didedahkan kepada tahap cahaya sederhana (33% hingga 52% cahaya). Bagaimanapun, kadar pertumbuhan diameter meningkat apabila aras cahaya meningkat. Pemboleh ubah morfologi (min luas daun, jumlah luas daun setiap pokok, luas daun spesifik dan nisbah luas daun) dipengaruhi dengan signifikan oleh cahaya. Perubahan yang lebih besar diperhatikan dalam ujian yang mempunyai nilai teduhan yang tinggi (6% cahaya). Jumlah biojisim *E. sylvestris, Q. phillyraeoides* dan *G. jasminoides* meningkat dengan peningkatan aras cahaya tetapi biojisim yang lebih tinggi direkodkan dalam aras cahaya sederhana bagi *I. henryi dan A. crenata*. Corak peruntukan biojisim mempamerkan variasi kecil dalam kelima-lima spesies. Walaupun semua spesies ini berbeza dalam strategi pertumbuhan merentas gradien cahaya, keplastikan yang besar membolehkan spesies-spesies ini tumbuh dengan baik dalam julat persekitaran cahaya yang besar. Secara keseluruhan, *E. sylvestris, Q. phillyraeoides* dan *G. jasminoides* menunjukkan pertumbuhan terbaik dalam cahaya melebihi 52%. Keadaan cahaya pertumbuhan yang optimum bagi *I. henryi* dan *A. crenata* pula adalah dari 33% hingga 52%. Keputusan kajian ini menyokong penanaman bawah kelima-lima spesies malar hijau ini untuk memperkaya biodiversiti ekosistem ladang subtropika.

INTRODUCTION

Light is an important factor influencing plant growth and survival. In forest ecosystems, understorey 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

**Present address: No. 73 Daqiao Road, Fuyang, Zhejiang Province 311400, PR China; ylsymk@gmail.com*

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 macclurel* 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.*

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 (cm^2 per leaf), total leaf area (cm^2 per plant), specific leaf area (leaf area per unit leaf dry mass, $cm^2\ g^{-1}$) 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 $\alpha = 0.05$.

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

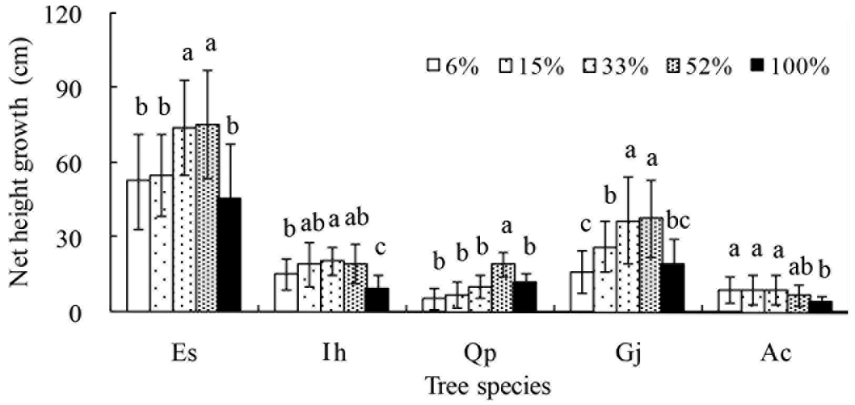

Figure 1 Net height growth of *Elaeocarpus sylvestris* (Es), *Illicium henryi* (Ih), *Quercus phillyraeoides* (Qp), *Gardenia jasminoides* (Gj) and *Ardisia crenata* (Ac) after one growing season at different light levels; different letters indicate significant difference ($p < 0.05$) between light levels based on Duncan's post-hoc test

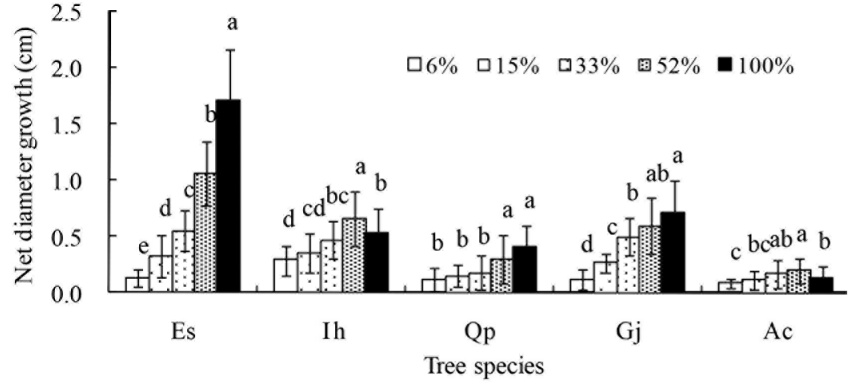

Figure 2 Net diameter growth of *Elaeocarpus sylvestris* (Es), *Illicium henryi* (Ih), *Quercus phillyraeoides* (Qp), *Gardenia jasminoides* (Gj) and *Ardisia crenata* (Ac) after one growing season at different light levels; different letters indicate significant difference ($p < 0.05$) between light levels based on Duncan's post-hoc test

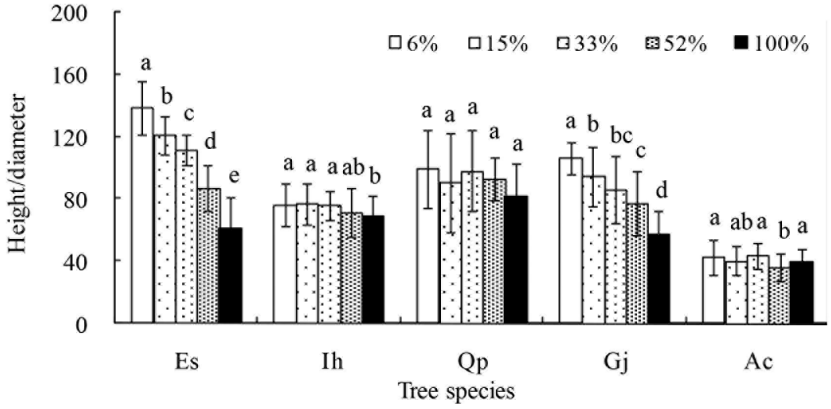

Figure 3 Height/diameter of *Elaeocarpus sylvestris* (Es), *Illicium henryi* (Ih), *Quercus phillyraeoides* (Qp), *Gardenia jasminoides* (Gj) and *Ardisia crenata* (Ac) after one growing season at different light levels; different letters indicate significant difference ($p < 0.05$) between light levels 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

Tree species	Parameter	Light level				
		6%	15%	33%	52%	100%
Es	Mean leaf area (cm^2)	18.9 ± 2.3 a	15.4 ± 1.6 a	16.8 ± 1.3 a	13.4 ± 1.3 b	11.9 ± 1.5 b
	Total leaf area (cm^2)	4070 ± 726 c	5734 ± 811 bc	9693 ± 534 a	11670 ± 750 a	6236 ± 728 b
	Specific leaf area ($cm^2\ g^{-1}$)	216.4 ± 13.5 a	204.0 ± 16.2 a	193.9 ± 10.9 a	156.5 ± 13.1 b	121.3 ± 10.6 c
	Leaf area ratio ($cm^2\ g^{-1}$)	58.8 ± 4.7 a	58.4 ± 3.3 a	63.7 ± 2.9 a	46.6 ± 2.5 b	26.6 ± 1.5 c
Ih	Mean leaf area (cm^2)	21.8 ± 2.3 ab	24.9 ± 2.4 a	19.4 ± 1.3 b	19.3 ± 2.2 b	13.2 ± 0.9 c
	Total leaf area (cm^2)	3111 ± 261 a	3273 ± 408 a	2808 ± 268 a	3143 ± 474 a	2623 ± 406 a
	Specific leaf area ($cm^2\ g^{-1}$)	95.8 ± 9.6 a	96.2 ± 7.8 a	79.4 ± 8.2 b	77.3 ± 4.9 b	65.9 ± 5.3 c
	Leaf area ratio ($cm^2\ g^{-1}$)	25.4 ± 1.1 a	26.9 ± 2.4 a	21.5 ± 1.3 a	22.1 ± 2.8 a	23.0 ± 1.6 a
Qp	Mean leaf area (cm^2)	3.5 ± 0.2 b	5.3 ± 0.7 a	5.2 ± 0.6 a	4.8 ± 0.4 a	5.8 ± 0.6 a
	Total leaf area (cm^2)	230 ± 40 c	622 ± 185 b	636 ± 70 b	930 ± 242 a	941 ± 162 a
	Specific leaf area ($cm^2\ g^{-1}$)	72.7 ± 10.4 b	90.1 ± 6.9 a	82.2 ± 8.5 ab	69.6 ± 9.3 b	64.1 ± 5.9 b
	Leaf area ratio ($cm^2\ g^{-1}$)	17.0 ± 2.1 c	25.1 ± 2.8 b	34.4 ± 3.1 a	22.4 ± 3.0 b	15.0 ± 1.9 c
Gj	Mean leaf area (cm^2)	11.8 ± 1.7 c	19.8 ± 2.3 a	15.7 ± 2.6 b	16.0 ± 2.4 b	12.4 ± 1.7 c
	Total leaf area (cm^2)	461 ± 150 c	1371 ± 184 b	2030 ± 444 a	2363 ± 406 a	2375 ± 384 a
	Specific leaf area ($cm^2\ g^{-1}$)	195.6 ± 12.8 a	175.1 ± 15.9 ab	153.3 ± 10.5 b	115.9 ± 9.6 c	107.9 ± 13.8 c
	Leaf area ratio ($cm^2\ g^{-1}$)	32.0 ± 5.9 b	53.8 ± 4.6 a	39.5 ± 5.4 b	34.3 ± 2.8 b	28.2 ± 1.9 c
Ac	Mean leaf area (cm^2)	17.3 ± 2.1 a	20.2 ± 2.5 a	12.6 ± 0.8 b	14.8 ± 2.1 b	5.8 ± 0.6 c
	Total leaf area (cm^2)	197 ± 27 b	575 ± 212 a	456 ± 112 a	553 ± 65 a	106 ± 37 c
	Specific leaf area ($cm^2\ g^{-1}$)	138.7 ± 13.7 a	132.0 ± 9.1 a	112.3 ± 12.6 a	84.3 ± 5.7 b	67.2 ± 9.2 c
	Leaf area ratio ($cm^2\ g^{-1}$)	27.1 ± 1.8 b	49.5 ± 6.6 a	30.3 ± 3.6 b	26.1 ± 2.9 b	10.3 ± 2.1 c

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*,

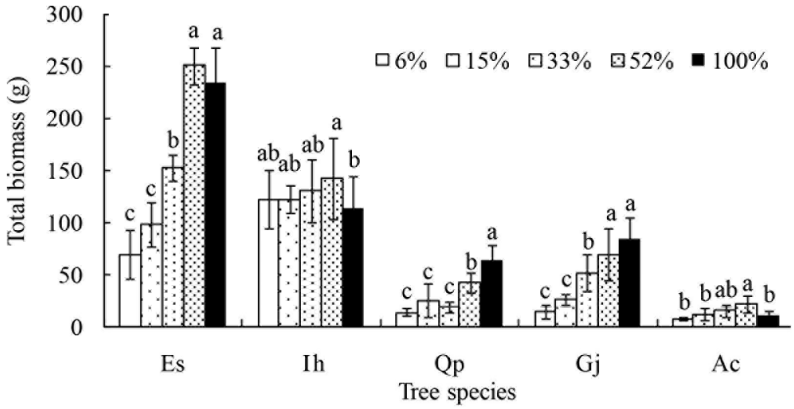

Figure 4 Total biomass per plant of *Elaeocarpus sylvestris* (Es), *Illicium henryi* (Ih), *Quercus phillyraeoides* (Qp), *Gardenia jasminoides* (Gj) and *Ardisia crenata* (Ac) after one growing season at different light levels; different letters indicate significant difference ($p < 0.05$) between light levels based on Duncan's post-hoc test

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

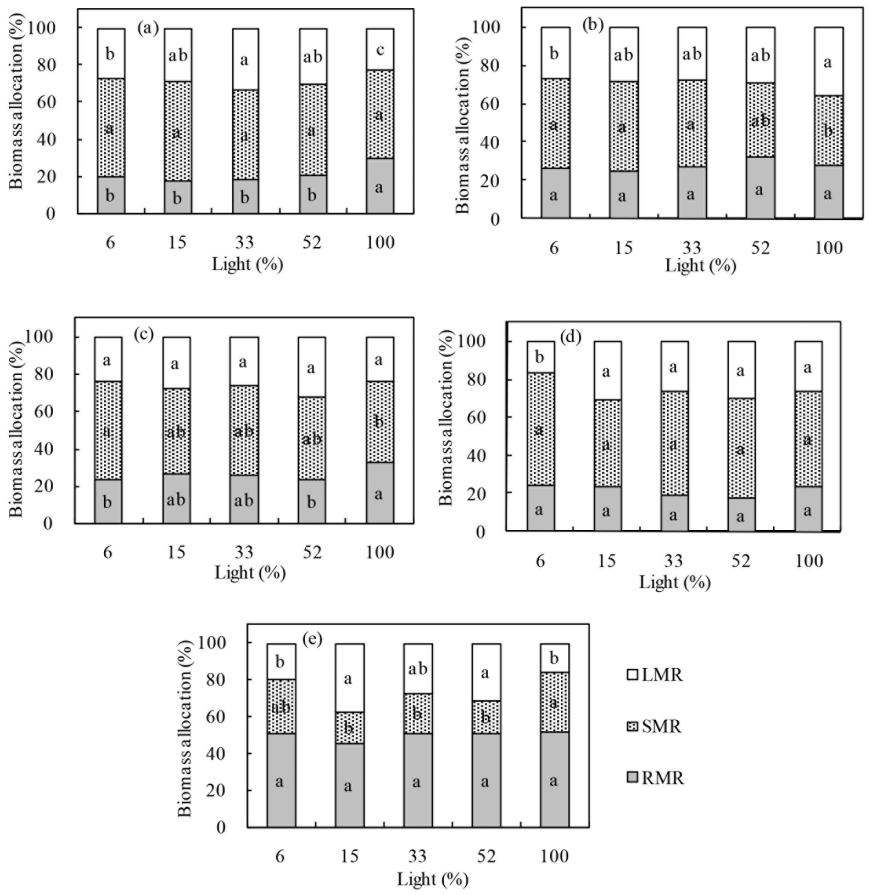

Figure 5 Changes of leaf mass ratio (LMR), shoot mass ratio (SMR) and root mass ratio (RMR) of (a) *Elaeocarpus sylvestris*, (b) *Illicium henryi* , (c) *Quercus phillyraeoides*, (d) *Gardenia jasminoides* and (e) *Ardisia crenata* at different light levels

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

Parameter	Es	Ih	Qp	Gj	Ac
Net height growth	0.39	0.54	0.72	0.57	0.55
Net diameter growth	0.92	0.56	0.71	0.83	0.61
Height/diameter	0.56	0.10	0.18	0.46	0.17
Mean leaf area	0.37	0.47	0.39	0.40	0.71
Total leaf area	0.65	0.20	0.76	0.81	0.82
Specific leaf area	0.44	0.31	0.29	0.45	0.52
Leaf area ratio	0.58	0.15	0.57	0.48	0.65
Total dry biomass	0.72	0.20	0.78	0.83	0.66
Leaf mass ratio	0.33	0.24	0.27	0.47	0.59
Shoot mass ratio	0.10	0.21	0.17	0.23	0.49
Root mass ratio	0.41	0.21	0.28	0.29	0.12

(Table 1). 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.

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.

ACKNOWLEDGEMENTS

This study was funded by the National Agriculture Science and Technology Achievement Transformation Foundation (No. 2011GB24320013), and supported by the Fundamental Research Funds for the Public-Interest Scientific Institution (No. RISF61257, RISF6930) and the National Introduction of International Advanced Forestry Science and Technology Projects (No. 2008-4-50).

REFERENCES

Bartelink HH. 1997. Allometric relationships for biomass and leaf area of beech (*Fagus sylvatica* L). *Annals of Forest Science* 54: 39–50.

Bloor JMG & Grubb PJ. 2004. Morphological plasticity of shade-tolerant tropical rainforest tree seedlings exposed to light changes. *Functional Ecology* 18: 337–348.

Bongers F & Popma J. 1988. Is exposure-related variation in leaf characteristics of tropical rain forest species adaptive? Pp 191–200 in Werger MJA et al. (eds) *Plant Form and Vegetation Structure*. SPB Academic Publishing, The Hague.

Craine JM & Reich PB. 2005. Leaf-level light compensation points in shade-tolerant woody seedlings. *New Phytologist* 166: 710–713.

Delagrange S, Messier C, Lechowicz MJ & Dizengremel P. 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiology* 24: 775–784.

Erskine PD, Lamb D & Bristow M. 2006. Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? *Forest Ecology and Management* 233: 205–210.

FAO (Food and Agriculture Organization). 2007. *State of The World's Forests 2007*. FAO, Rome.

Feng YL, Wang JF & Sang WG. 2007. Biomass allocation, morphology and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels. *Acta Oecology* 31: 40–47.

Givnish TJ. 1984. Leaf and canopy adaptions in tropical forests. Pp 51–84 in Medina E et al. (eds) *Physiological Ecology of Plant of the Wet Tropics*. Kluwer Academic Publishers Group, The Hague.

Henry HAL & Aarssen LW. 1997. On the relationship between shade tolerance and shade avoidance strategies in woodland plants. *Oikos* 80: 575–582.

Jarčuška B & Barna M. 2011. Plasticity in above-ground biomass allocation in *Fagus sylvatica* L. saplings in response to light availability. *Annals of Forest Research* 54: 151–160.

Kelly J, Jose S, Nichols JD & Bristow M. 2009. Growth and physiological response of six Australian rainforest tree species to a light gradient. *Forest Ecology and Management* 257: 287–293.

Kobe RK. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80: 187–201.

Kunstler G, Curt T, Bouchaud M & Lepart J. 2005. Growth, mortality, and morphological response of European beech and downy oak along a light gradient in sub-Mediterranean forest. *Canadian Journal of Forest Research* 35: 1657–1668 .

Liu DL & Zheng XX. 1999. Studies on artificial multiple storied stands. *World Forest Research* 12: 24-27. (In Chinese)

Markesteijn L & Poorter L. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* 97: 311–325.

Masaka K, Sato H, Kon H & Fukuchi M. 2011. Demographic and height growth response of native broad-leaved deciduous tree saplings to overhead canopy release in a coastal *Pinus thunbergii* forest in Hokkaido, northern Japan. *Journal of Forest Research* 16: 1–11.

Montgomery R. 2004. Relative importance of photosynthetic physiology and biomass allocation for tree seedling growth across a broad light gradient. *Tree Physiology* 24: 155–167.

Niinemets Ü & Valladares F. 2004. Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. *Plant Biology* 6: 254–268.

Petritan AM, Von Lüpke B & Petritan IC. 2009. Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings. *European Journal of Forest Research* 128: 61–74.

Poorter L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* 13: 396–410.

Poorter L. 2005. Resource capture and use by tropical forest tree seedlings and their consequences for competition. Pp 35–64 in Burslem DFRP et al. (eds) *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species*. Cambridge University Press, Cambridge.

Poorter H & Nagel O. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology* 27: 595–607.

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M & Walters MB. 2003. The evolution of plant functional variation: traits, spectra and strategies. *International Journal of Plant Sciences* 164: 143–164.

Richards AE, Forrester DI, Bauhus J & Scherer-Lorenzen M. 2010. The influence of mixed tree plantations on the nutrition of individual species: a review. *Tree Physiology* 30: 1192–1208.

Rozendaal DMA, Hurtado VH & Poorter L. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology* 20: 207–216.

Saldaña-Acosta A, Meave JA, Sánchez-Velásquez LR. 2009. Seedling biomass allocation and vital rates of cloud forest tree species: responses to light in shade house conditions. *Forest Ecology and Management* 258: 1650–1659.

Sánchez-Gómez D, Valladares F & Zavala MA. 2006. Functional traits and plasticity in response to light in seedlings of four Iberian forest tree species. *Tree Physiology* 26: 1425–1433

SFA (State Forestry Administration). 2007. *China's Forestry 1999–2005*. China Forestry Publishing House, Beijing.

Stancioiu PT & O'Hara KL. 2006. Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. *Journal of Forest Research* 125: 151–162

Valladares F & Niinemets Ü. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology Evolution and Systematics* 39: 237–257.

Valladares F, Wright SJ, Lasso E, Kitajima K & Pearcy RW. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* 81: 1925–1936.

Veenendaal EM, Swaine MD, Lecha RT, Falsch MF, Abebrese IK & Owusu-Afriyie K. 1996. Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology* 10: 501–511.

Walters MB & Reich PB. 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* 77: 841–53.

Walters MB & Reich PB. 2000. Seed size, nitrogen supply and growth rate affect tree seedling survival in deep shade. *Ecology* 81: 1887–1901.

Wang GG, Bauerle WL & Mudder BT. 2006. Effects of light acclimation on the photosynthesis, growth, and biomass allocation in American chestnut (*Castaneadentata*) seedlings. *Forest Ecology and Management* 26: 173–180.

Witkowski ETF & Lamont BB. 1991. Leaf specific mass confounds leaf density and thickness. *Oecologia* 88: 486–493.

Xiong HB. 2007. Study on variation of the properties of soil in multi-storied Chinese fir plantation. *Subtropical Agriculture Research* 4: 283–286. (In Chinese)