

INTERACTIONS BETWEEN NATIVE TREE SPECIES AND A DOMINANT SHRUB *RHODOMYRTUS TOMENTOSA*

N Liu¹, H Ren¹*, L Yang², SF Yuan¹, J Wang¹ & ZY Sun¹

¹Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

²Guangzhou Institute of Geography, Guangzhou 510070, China

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LIU N, REN H, YANG L, YUAN SF, WANG J & SUN ZY. 2012. Interactions between native tree species and a dominant shrub *Rhodomyrtus tomentosa*. A study was carried out on degraded hilly land in South China to reveal the interspecific relationships between the shrub *Rhodomyrtus tomentosa* and four target tree species over time. The 3-year experiment showed that the shrub selectively improved or inhibited seedling growth. The photosynthetic performances of target tree species were altered by the nursing effect of the shrub in terms of photosynthesis–light response curves and showed maximum photosynthetic rates and stomatal conductance. Shrub interactions with all the target tree species were commensal (+0, for target and shrub) in year 1 but maintained or changed to amensal (-0) or antagonism (+-) along with the ontogenesis of different target tree species. The poor growth of *Pinus elliottii* and *Michelia macclurei* seedlings in the presence of the shrub indicated that they had lower potential to become forest restoration target tree species. In contrast, *Schima superba* was facilitated by the shrub in years 1–3 and inhibited the shrub in year 3, indicating that it had substantial potential to replace shrubs and trigger reforestation. Selection and silvicultural techniques of target tree species were both important in forest restoration.

Keywords: Nurse plant, subtropical degraded shrubland, woody plant, restoration, reforestation

LIU N, REN H, YANG L, YUAN SF, WANG J & SUN ZY. 2012. Interaksi antara spesies pokok asli dengan pokok renek dominan *Rhodomyrtus tomentosa*. Kajian dijalankan terhadap tanah berbukit yang usang di China Selatan untuk memperlihatkan hubungan interspesies antara pokok renek *Rhodomyrtus tomentosa* dengan empat spesies pokok sasaran dengan masa. Uji kaji tiga tahun menunjukkan yang pokok renek memperbaiki atau merencat pertumbuhan anak benih secara memilih. Prestasi fotosintesis spesies pokok sasaran diubah oleh kesan mengasuh pokok renek dari segi lengkok fotosintesis–gerak balas cahaya dan menunjukkan kadar fotosintesis dan konduktans stomata yang maksimum. Interaksi pokok renek dengan kesemua spesies pokok sasaran adalah komensal (+0, untuk pokok sasaran dan renek) pada tahun 1 tetapi kekal atau berubah menjadi amensal (-0) atau antagonisme (+-) berserta dengan ontogenesis spesies pokok sasaran yang berlainan. Pertumbuhan anak benih *Pinus elliottii* dan *Michelia macclurei* yang kurang baik dalam kehadiran pokok renek menunjukkan yang spesies ini kurang berpotensi sebagai spesies pokok sasaran dalam pemulihan hutan. Sebaliknya, pertumbuhan *Schima superba* bertambah baik apabila ditanam bersama-sama dengan pokok renek pada tahun 1–3 tetapi ia merencat pertumbuhan pokok renek pada tahun 3. Ini menunjukkan yang *S. superba* berpotensi menggantikan pokok renek dan mencetuskan penghutanan semula. Pemilihan spesies dan teknik silvikultur pokok sasaran adalah penting dalam pemulihan hutan.

INTRODUCTION

Plant interactions, in particular facilitation and competition, are key drivers in community structures, dynamics and ecosystem functions (Armas & Pugnaire 2005, Callaway 2007, Brooker et al. 2008). Balances between facilitation and competition are strongly influenced by spatial and temporal changes of resource availability and environmental stresses (Callaway 2007, Armas & Pugnaire 2009, Soliveres et al. 2010). A meta-analysis demonstrated that the magnitude of the plant interaction changes with

environmental conditions across a large set of species and sites (Gómez-Aparicio et al. 2004). The spatio-temporal variations of facilitative and competitive plant interactions along abiotic stress gradients have been largely analysed (Maestre & Cortina 2004, Brooker et al. 2008, Soliveres et al. 2010).

Studies in spatial plant interactions have revealed that facilitations are more likely to dominate competitive interactions at harsh environments where one species or cohort acts

*renhai@scib.ac.cn

as nurse plant for another in semi-arid, arid and alpine environments, whereas negative interactions prevail under more favourable conditions (Maestre et al. 2005, Lortie & Callaway 2006, Forrester et al. 2011). In addition to effects of spatial variation on facilitation and competition, temporal variation also changes the balance, causing interactions to shift throughout the ontogeny of a plant (Gasque & García-Fayos 2004, Miriti 2006, Forrester et al. 2011). For instance, previous study examined the facilitation process of long-lived plants and provided evidence that facilitation gradually shifted to competition as plants matured (Miriti 2006). However, another research showed contrary results, i.e. reduction of competition was found as the plant aged due to differences in ecological traits of species involved (Soliveres et al. 2010). Moreover, research findings in plant interactions in arid and semi-arid environments may not coincide with those in temperate environments, such as subtropical degraded shrubland in China, where there is a surplus of rainfall and competitive resources are mainly light or nutrients (Valladares 2003, Gasque & García-Fayos 2004, Yang et al. 2009). Thus, empirical studies did not provide sufficient information in helping us understand temporal changes of plant–plant interactions between a dominant shrub (nurse plant) and its facilitated tree species (target plants) as they developed in subtropical degraded shrubland.

Due to deforestation, large areas of regional evergreen broadleaved forest have degraded into grass–shrub-possessed complex mainly covered by native grass and shrubs species such as *Rhodomyrtus tomentosa*, *Miscanto sinensis* and *Dicranopteris dichotoma* in South China. With relatively large canopy size and tolerance to rigid environment, the dominant shrub *R. tomentosa* was considered to be an optimal nurse plant to increase the recruitment of native tree species on degraded shrubland which might accelerate reforestation process (Ren et al. 2008). The shrub *R. tomentosa* was found to reduce light penetration, increase soil porosity and elevate soil moisture under its cushion-shaped canopy (Yang et al. 2010). Based on this paper, it is concluded that the nurse effect of the shrub is positive for all the target tree species, i.e. the ameliorated microenvironment provided by the shrub increases the establishment of seedlings of native woody plants (*Schima superba*, *Michelia macclurei* and *Castanopsis fissa*). As the

experiment progresses, interactions between shrub *R. tomentosa* and target tree species seedlings/saplings must have changed and it is necessary to understand the effects of planted seedlings/saplings on nurse plant, which may have important consequences on the dynamics of community. Short-term studies concentrating on facilitation/competition research are not sufficient to fully explain the magnitude of ontogenetic changes in plant interactions (Callaway 2007). Thus, some ecologists extended their studies to 4–6 years in order to further understand nurse effects of plants in longer time ranges (Castro et al. 2004, 2006). However, long-term studies are often restricted by logistic constraints (Soliveres et al. 2010). Hence, studies by sampling temporal windows of the plant life cycle are preferred (Armas & Pugnaire 2005, Miriti 2006, Valiente-Banuet & Verdú 2008).

The current study reported data from years 2 and 3 of the field experiment that was initiated by Yang et al. (2010) and concerned the interactions between the shrub nurse plant and target tree species. In addition to collecting data on plant growth, plant physiological characteristics were also measured because repeated measurements were crucial to reveal interactive mechanisms and the consequences on community dynamics (Forseth et al. 2001, Armas & Pugnaire 2005, 2009). Specifically, we want to answer the following questions in the current study: (1) as the target tree species seedlings develop from year 1 to years 2 and 3, how do interspecific relationships between shrub and each target tree species change? and (2) what are the implications of the interspecific relationship alterations on community dynamics and reforestation of degraded shrubland?

MATERIALS AND METHODS

Study site

The experiment was conducted in a typical subtropical shrubland system located in the Heshan National Field Research Station of Forest Ecosystems (112° 50' E, 22° 34' N, Heshan City, Guangdong Province, China). The station is one of the national forest restoration research stations of the Chinese Ecological Research Network (CERN) and the Chinese Academy of Sciences (CAS). Due to deforestation, the climax subtropical monsoon evergreen broadleaved

forest has disappeared from this region. Instead, shrub and grass species including *R. tomentosa*, *Ilex asprella*, *Melastoma candidum*, *Clerodendron fortuneatum* and *D. dichotoma* occupy most of the hilly land and compose a degraded shrubland community. The laterite soil in this region is severely eroded because of lack of forest coverage. The region has subtropical monsoon climate and is characterised by hot and humid summers and cold and dry winters. The mean annual precipitation is 1460–1820 mm, which mainly occurs as rain between March and August. The mean annual temperature is 21.7 °C and the mean solar radiation measured at the station is 435.47 KJ cm⁻² year⁻¹.

Tested plant species

Rhodymyrtus tomentosa was selected as the nurse plant. The shrub species is a dominant shrub in subtropical shrublands, where it grows naturally. Adult individuals of this shrub have cushion-shaped canopy and can grow as tall as 2 m (Ren et al. 2010). Three target tree species are *S. superba*, *M. macclurei* and *C. fissa* which grow naturally in subtropical forests in South China. A fourth target tree species *Pinus elliotii* is an introduced species. It was included in the current study but was not part of the study in Yang et al. (2010).

In addition to assessing the effects of the shrub *R. tomentosa* on the four target tree species, the present study also assessed the effect of one of the target tree species *S. superba* on the shrub. In the latter case, we focused on *S. superba* because our observations indicated that *S. superba* was a promising target tree species that was not only facilitated by *R. tomentosa* but also affected *R. tomentosa* negatively.

Experimental design

A 2-ha experimental field was divided into three blocks. Each block had four 5 m × 5 m plots, one plot for each of the four target tree species (in total, three plots for each target tree species). For target tree species and nurse plant, the plant that grew individually was designated as open site (OS) and that which grew adjacent to another species was named as canopy site (CS). Specifically for measurement of target tree species, half of each plot was fully occupied by one *R. tomentosa* plant (mostly 1.5 m high with a 1.5 m canopy radius) and was referred to as CS. The other half of each plot was without vegetation and was referred to as

OS. As indicated earlier, measurements of nurse plants were limited to plots with *S. superba*. Five or six *R. tomentosa* plants that were adjacent to each *S. superba* plot were used as controls and measured. To determine effects of *S. superba* on *R. tomentosa*, the term CS was used to describe sites in which the two species were growing together and the term OS was used to describe sites in which *R. tomentosa* was growing separate from *S. superba* and other plants.

Seeds of target tree species were collected in a village forest near the field site in the autumn of 2006, germinated and grown in a greenhouse for 6 months to prevent frost damage. In April 2007, 6-month-old seedlings (similar in size and vigour; 5–10 cm in height) of the target tree species (50 replications; 15–20 cm between each other) were transplanted individually under the shrub canopy (CS) and outside the shrub canopy (OS). Before seedlings were transplanted to the experimental plots (in CS and OS), their bare roots were dipped into mud from soil in the field site. The plots were not watered or fertilised. The number of survived seedlings in both CS and OS decreased with time; the greatest decline was found at the beginning of the experiment (Yang et al. 2010). The target tree seedling survival rates were quite stable (< 75%) in both CS and OS since 2008 (year 1, Yang et al. 2010) and from our observations, no seedling naturally died in 2009 (year 2) and 2010 (year 3). Two-thirds of the target tree species seedlings were harvested for biological analysis at the end of 2008 with 10–15 seedlings of each species left in CS and OS of each plot.

Plant growth parameters

The growth of target tree species and the nurse plant were measured and calculated at the end of 2009 (year 2) and 2010 (year 3). Basal diameter and shoot height were determined for all target tree species in each plot and for nurse plants in some plots (with and without *S. superba*), as indicated before. According to Callaway et al. (2002), the redefined relative neighbour effect index (RNE) was calculated on the basis of basal diameter or shoot height to determine whether the effect of the nurse plant on the target species (or the effect of *S. superba* on *R. tomentosa*) was positive (RNE > 0) or negative (RNE < 0). The formula is as follows:

$$\text{RNE} = (S_c - S_o) / x$$

where S is basal diameter or shoot height in OS (S_o) or CS (S_c) treatments and $x = S_c$ when $S_c > S_o$ or $x = S_o$ when $S_o > S_c$.

Photosynthesis–light response curves

Photosynthesis–light response (A–PPFD) curves were determined on three to five leaves from three to five plants for each target tree species in each site and for nurse plants (growing with or without *S. superba*) using a portable gas exchange analyser. The plants were measured in the early to mid-morning of sunny days. Photosynthetic parameters were obtained automatically under 14 photosynthetic photon flux densities (PPFD) in the order of 1800, 1500, 1200, 1000, 800, 600, 400, 200, 100, 80, 60, 40, 20, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. With four to seven leaf replications on three to five plants per species, the net CO_2 assimilation rate (A) for target tree species and nurse plant were averaged and plotted against instant PPFD. Curves were obtained by fitting the data to a non-rectangular hyperbola model according to Lambers et al. (2008):

$$A = \frac{\Phi I + A_{\max} - \sqrt{(\Phi I + A_{\max})^2 - 4\Phi I A_{\max}}}{2\Phi} - R_d$$

where I is PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$), Φ is the apparent quantum yield (AQY) ($\text{mol CO}_2 \text{ mol}^{-1} \text{ photos}$), $A_{\max}$ is the maximum light saturated net photosynthesis and R_d is dark respiration (units for A, $A_{\max}$ and R_d are $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$). Parameters were calculated using the non-linear estimation module in SPSS 11.5. While data for the A–PPFD curves were obtained, maximum stomatal conductance (G_s) was measured simultaneously.

Anti-oxidant capacity (DPPH-scavenging capacity)

DPPH- (1,1-diphenyl-2-picrylhydrazyl) scavenging capacity can be used to indicate the capacity of plant tissue in removing free radicals (reactive oxygen species) caused by various environmental stresses (Peng et al. 2000). Leaf samples (1.413 cm^2 per site for broadleaved plants and 5 cm per site for conifers) from three to five leaves of three to five plants in each site obtained from four target tree species and nurse plant (both in OS and CS) were ground with 50% ethanol and centrifuged for 15 min at 5000 g. The DPPH solution has a unique absorption (OD) at 525 nm.

The decline in OD_{525} can be used as an index of the organic free radical-scavenging capacity (ORSC) of a plant extract. The total reaction volume was 2 mL and DPPH was dissolved using 0.5 mL methanol followed by the addition of 50% ethanol to obtain final concentration of 120 μM DPPH. Then, 0.2 mL of plant extract (dissolved in 50% ethanol) was added to 1.8 mL of DPPH and OD_{525} was measured after 20 min. The remaining DPPH (R%) and scavenging ratios (ORSC) were determined using the following formulae:

$$R (\%) = [(\text{OD}_A - \text{OD}_B) / \text{OD}_o] \times 100$$

$$\text{ORSC} (\%) = (1 - R) \times 100$$

where OD_o is DPPH absorption in the absence of leaf extract (0.2 mL of 50% ethanol + 1.8 mL DPPH), OD_A is DPPH absorption after reaction with the sample and OD_B is the absorption of the blank (0.2 mL sample + 1.8 mL of 50% ethanol). The DPPH-scavenging capacity was calculated as $\text{ORSC} (\%) \times \text{DPPH in the reaction (mg) / sample area (cm}^2 \text{) or sample length (cm)}$, as described by Peng et al. (2000).

Statistical analysis

Results are presented as means $\pm$ SD. One-way ANOVA was applied to compare seedling growth (seedling height, basal diameter and RNE), photosynthetic performance and anti-oxidant capacity of nurse plant and each target plant grown in both OS and CS in each year. SPSS 13.0 was used for all statistical analyses.

RESULTS

Changes of plant interactions

In terms of seedling height, mean RNE values were negative for *P. elliotii* and *C. fissa* but positive for *S. superba* and *M. macclurei* in both years 2 and 3 (Figure 1a). In terms of basal diameter, RNE values were all negative for almost all target species except for *S. superba* in both years (Figure 1b). Interestingly, *R. tomentosa* increased the height of *M. macclurei* but decreased its basal diameter. For the nurse plant *R. tomentosa*, the RNE value based on seedling height was positive in year 2 but negative in year 3, while the RNE based on basal diameter was negative in both years. In other words, *S. superba* inhibited both the height and diameter of *R. tomentosa* in year 3.

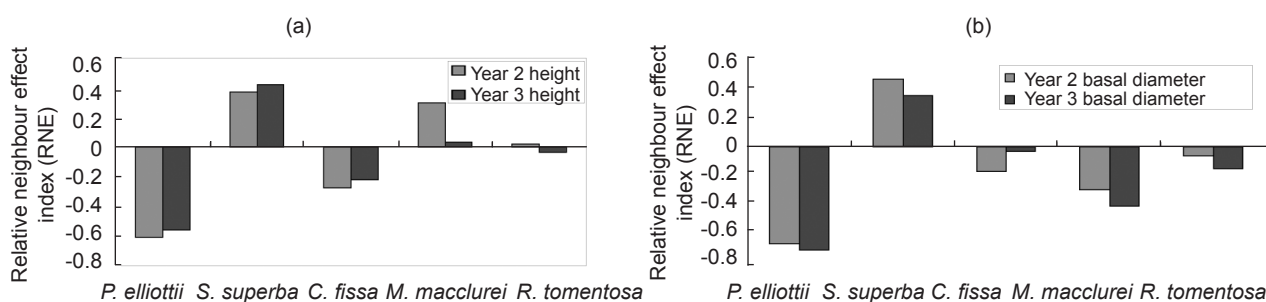


Figure 1 Relative neighbour effects (RNE index) based on (a) shoot height and (b) basal diameter of target species (*Pinus elliotii*, *Schima superba*, *Castanopsis fissa* and *Michelia macclurei*) and the shrub (*Rhodomyrtus tomentosa*); for the target species, positive and negative RNE values indicate positive or negative effects of the shrub; for *R. tomentosa*, positive and negative RNE values indicate positive or negative effects of *S. superba*

Although leaf fall was not quantified, we observed in year 3 that leaf fall for *R. tomentosa* was substantial in the CS treatment but insignificant in the OS treatment, i.e. the shrub appeared to be senescing in the CS treatment.

Changes of nurse plant and target tree seedling growth

The treatment effects on plant growth occurred with *P. elliotii* and *S. superba*. In years 2 and 3, seedling height and basal diameter of *P. elliotii* were significantly higher ($p < 0.05$) in OS than in CS but the opposite was true for *S. superba* ($p < 0.05$) (Figures 2a and b). For seedlings of *M. macclurei*, the height was higher and not obviously changed by nurse plant in each year, but the basal diameter was obviously lowered by the nurse effect of the shrub in both years. The seedling height and basal diameter of the mature nurse plant shrub *R. tomentosa* were not significantly altered by *S. superba* in years 2 and 3 when *S. superba* was present (CS) or when *S. superba* was absent (OS).

Changes of leaf photosynthesis

Photosynthetic rates of the four target tree species and nurse plant in CS and OS were usually saturated between 1500 and 1800 $\mu\text{mol m}^{-2}\text{s}^{-1}$ as indicated by the A–PPFD curves (Figure 3). The CS and OS curves were close together at low PPFD values but separated when PPFD exceeded 200 $\mu\text{mol m}^{-2}\text{s}^{-1}$. For *P. elliotii* and *M. macclurei*, A–PPFD curves and A_{max} were higher in OS than in CS in years 2 and 3. For *S. superba*, *C. fissa* and *R. tomentosa*, the relative positions of the OS and CS curves differed between years. Interestingly, the relative positions of A–PPFD

curves for *R. tomentosa* switched in years 2 and 3, i.e. its photosynthetic performance was improved in year 2 but inhibited in year 3 when grown with *S. superba*.

In years 2 and 3, stomatal conductance (G_s) of *P. elliotii* was significantly lower ($p < 0.05$) in CS than in OS (Figure 2c). For *S. superba*, G_s was greater in CS than in OS in year 2 ($p < 0.05$) but not in year 3. G_s value of *R. tomentosa* was unaffected by *S. superba* in year 2. While in year 3, when the canopy of *S. superba* covered *R. tomentosa* in the CS treatment, G_s of *R. tomentosa* was much lower ($p < 0.05$) in CS than in OS. G_s for *C. fissa* and *M. macclurei* did not differ significantly between CS and OS in year 3.

Changes of leaf antioxidant capacity

In year 2, all five species had lower DPPH-scavenging capacity in CS than in OS, although the differences were not significant for *P. elliotii* and *C. fissa* (Figure 2d). The largest difference occurred with *S. superba*, in which the DPPH-scavenging capacity in CS was 47.5% that of OS (Figure 2d). In year 3, DPPH-scavenging capacities of *P. elliotii* and *C. fissa* were significantly lower ($p < 0.05$) in CS than in OS but were significantly higher ($p < 0.05$) in CS than in OS for *S. superba* and *R. tomentosa*.

DISCUSSION

Changes in interactions between target tree species and shrub nurse plants

As revealed in Yang et al. (2010), the establishments of transplanted target tree species seedlings were facilitated by the shrub *R. tomentosa*, so the commensal relationship (+0) between the

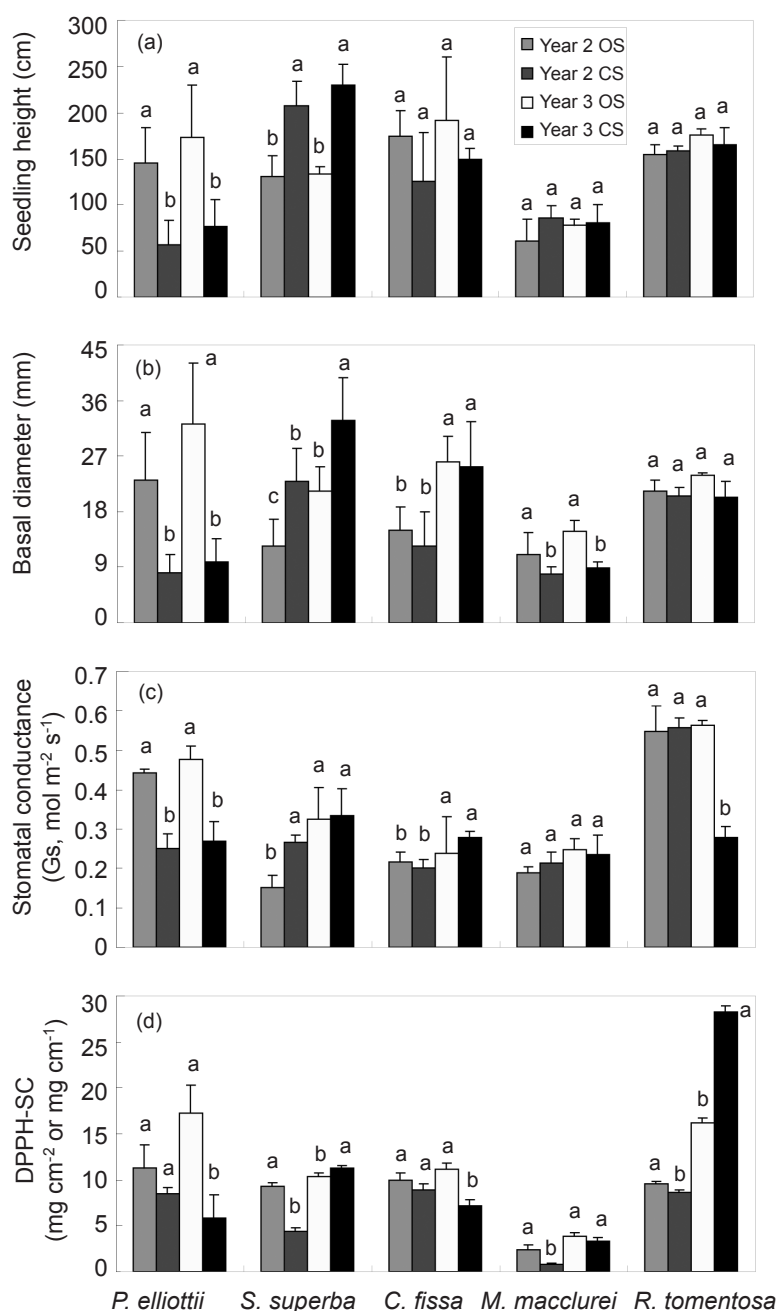


Figure 2 (a) Plant height, (b) basal diameter, (c) leaf stomatal conductance and (d) DPPH-scavenging capacity of target species (*Pinus elliotii*, *Schima superba*, *Castanopsis fissa* and *Michelia macclurei*) growing in open site (OS) or canopy site (CS) in years 2 and 3; results are also shown for the nurse plant (*Rhodomyrtus tomentosa*) growing adjacent to *S. superba* (CS) or separate from all target species (OS); values are means $\pm$ SD; for each plant species, values with different letters are significantly different in year 2 or 3; DPPH-SC = DPPH-scavenging capacity (mg cm⁻² for broadleaved species or mg cm⁻¹ for pine needles)

nurse and nursed species was set up in year 1. As the experiment progressed to year 2, the effect of the shrub on seedling growth of *P. elliotii* and *C. fissa* was negative, indicating that the commensal relationship (+0) between target tree species and shrub nurse plant turned to an amensal relationship (-0), which was also

maintained in year 3. For the target tree species *M. macclurei*, effect from shrub was positive in year 2 but changed to negative (amensal) by year 3. Obviously, the positive effect from *R. tomentosa* on *S. superba* documented in year 1 by Yang et al. (2010) continued into years 2 and 3. For the retroaction from target tree species to

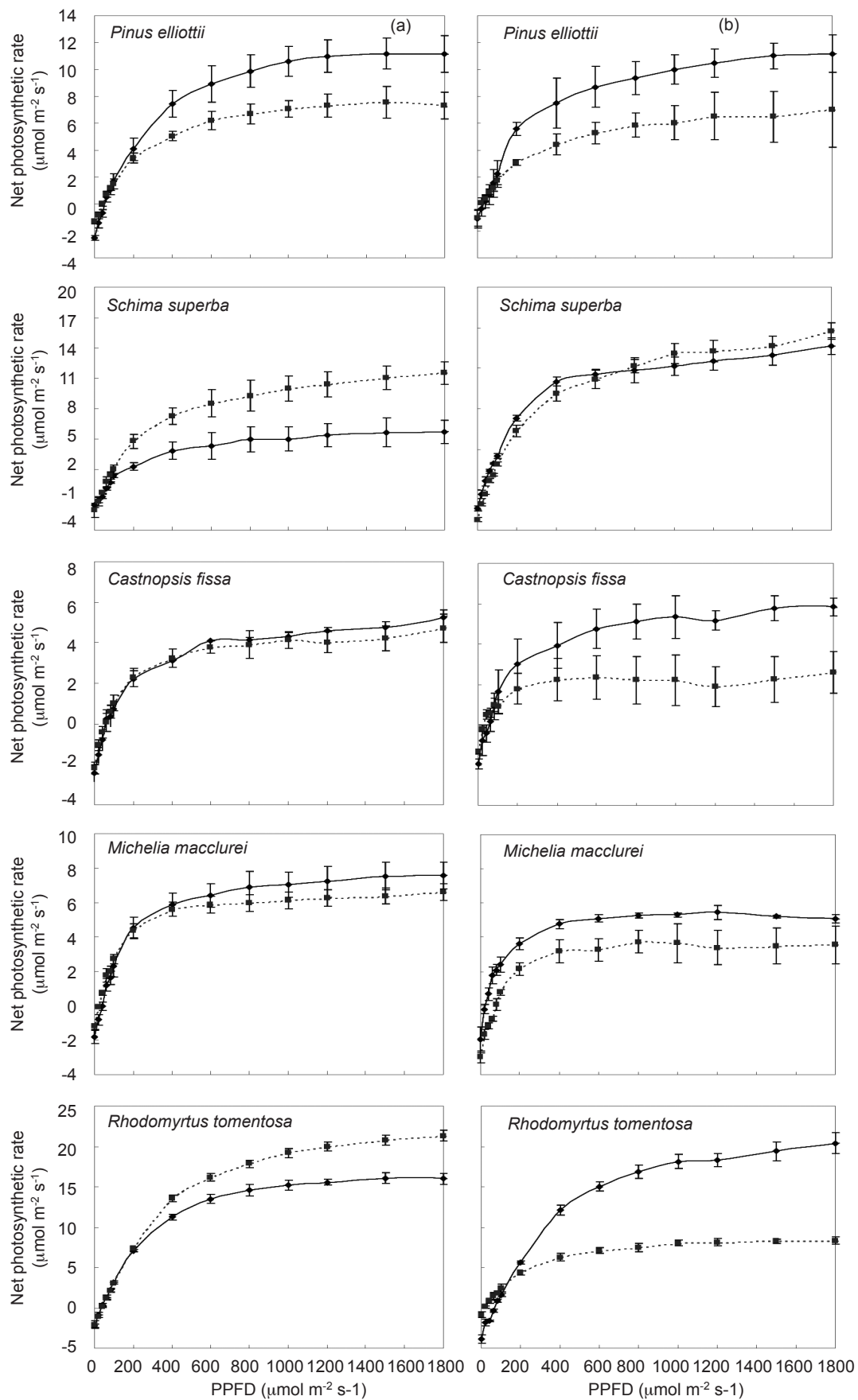


Figure 3 Photosynthesis–light response (A–PPFD) curves of target species (*Pinus elliotii*, *Schima superba*, *Castnopsis fissa* and *Michelia macclurei*) and nurse plant (*Rhodomyrtus tomentosa*) growing in open site (OS) (solid line) or canopy site (CS) (dash line) in years (a) 2 and (b) 3

nurse plant, we found that by the end of year 2, *S. superba* had grown taller than the shrub, suggesting that this target tree species could significantly affect subsequent growth of the shrub. However, negative effects of *S. superba* on *R. tomentosa* (antagonism, +-) were not evident in year 2 but evident in year 3.

Physiological performances suggest the mechanisms underlying plant interactions

Yang et al. (2010) showed that the canopy and litter of shrub *R. tomentosa* buffered the microenvironment below it, resulting in lower photo-oxidative stress, higher water retention and greater soil structural stability, all of which favoured biomass accumulation of target tree seedlings. However, as target tree species developed, the negative effects from shrub might impair the performance of understorey plants through competition by reducing light availability (Valladares & Pearcy 2002). In our study, the canopy of *R. tomentosa* generated low light stress for *P. elliptii*, which was typically heliophytic, as evidenced by reduced stomatal conductance, low $A_{\max}$ and thus reduced growth. The data in the current study also showed that photosynthetic rates for *C. fissa* and *M. macclurei*, which were not affected by the shrub in year 2, were reduced by the shrub in year 3, leading to some reductions in seedling height and basal diameter. Clearly, the negative effects from shrubs offset positive effects on seedlings along with ontogenetic development of target tree species which caused shifts in their interactions.

Adult shrubs form multi-stemmed canopies and effectively protect target tree species below against excessive radiation, thermal stress and soil water deficiency (Pugnaire et al. 2004). In year 2, $A_{\max}$ of *S. superba* seedlings was significantly higher when grown with the shrub than without. This phenomenon could be explained by the reduction of oxidative stresses in leaves, as indicated by the reduced DPPH-scavenging capacity under shrub facilitation (Liu et al. 2009a). With respect to photosynthesis, *S. superba* made better use of the favourable microclimate produced by the shrub than the other target tree species. Shade from neighbours can further protect plants from photoinhibition, reducing plant transpiration and improving water status of the understorey species (Gasque & García-Fayos 2004). By the end of year 2, *S. superba* had grown

taller than the shrub, suggesting that this target tree species could significantly affect subsequent growth of the shrub. The canopy of *S. superba* reduced sunlight irradiation and therefore reduced the accumulation of reactive oxygen species and oxidative stress in *R. tomentosa*, which was indicated by a reduced DPPH-scavenging capacity. This agreed with earlier findings by Liu et al. (2009a) and Yang et al. (2010).

In year 3 of the experiment, *S. superba* had grown substantially taller than the shrub and the *S. superba* canopy covered much of the CS. At this time, RNE value was positive for *S. superba* but negative for *R. tomentosa*. As a pioneer species on degraded hilly slopes, *R. tomentosa* is strongly heliophytic. It was apparently negatively affected by the low light environment generated by the fast expanding *S. superba* canopy. Plants grown in permanent shade often suffer from deficient Rubisco content, low photosynthetic electron transport rate and reduced CO₂ fixation capacity (Stitt & Schulze 1994). During most hours of the day time, sunlight penetrating the *S. superba* canopy could not reach the light compensation point of *R. tomentosa*. The reduced $A_{\max}$ and Gs values of the shrub demonstrated that it was experiencing shade stress. The elevated DPPH-scavenging capacity in shaded shrub leaves is probably related to the carotenoid and anthocyanin accumulations that occur with senescence (Liu et al. 2009b). Shrub when grown with *S. superba* in year 3 showed senescence, as indicated by decrease in leaf area, Gs, reduction in leaf photosynthetic parameters and an obvious leaf fall (from observation). The relationship between *S. superba* and *R. tomentosa* reversed in year 3. The shrub continued to have positive nurse effect on *S. superba* but *S. superba* was affecting the shrub negatively.

Possible community dynamics and implications for forest restoration on degraded shrubland

Facilitation is a bidirectional process (Gasque & García-Fayos 2004) as the balance between positive and negative drivers may change temporally throughout the life of the nurse and nursed plants (Rousset & Lepart 2000, Valiente-Banuet & Verdú 2008). In accordance with this finding, effects from the shrub *R. tomentosa* on *P. elliptii* and *M. macclurei* changed from positive to negative from year 1 to year 2. By the end of year

3, seedling height of *P. elliotii* and *M. macclurei* remained lower than the nurse plant. The limited seedling growth probably eliminated this species from the community and these two species were not useful for forest restoration programme in the context of nurse plant technique.

At the end of year 3, the relationship between *C. fissa* and the shrub *R. tomentosa* seemed to be mutualistic. At the community level, mutualistic interactions between neighbouring plants are believed to be the main force explaining the coexistence of species in clumps of vegetation (Eccles et al. 1999). The mutualistic community tends to compose positive complex relationships in an existed community (Okuyama & Holland 2008, Valiente-Banuet & Verdú 2008). Even without strong evidence, the mutualistic relationships set up between *C. fissa* and *R. tomentosa* may produce more diverse communities with complex species composition. However, this process could increase biodiversity in a regional community but opposed our initial purpose of accelerating forest restoration by planting tree species under nurse plant coverage.

The interactions between *R. tomentosa* and *S. superba* support the use of this shrub as a nurse plant in reforestation of degraded shrubland in South China. When nursed by *R. tomentosa*, the target tree species *S. superba* was able to replace *R. tomentosa*, thereby contributing to the succession of this degraded shrubland to native forest. Rather than using traditional reforestation tactics such as clear cutting or pure burning, forest managers should be able to use the relationship between *S. superba* seedlings and the shrub *R. tomentosa* to accelerate natural forest restoration.

Since light is one of the most important factors affecting the relationship between target tree species and the nurse plant *R. tomentosa* on degraded shrubland, light should be considered when nurse plants are used for forest restoration. With this in mind, we provide three recommendations for use of the nurse plant technique on degraded shrubland. Firstly, forest managers should select target tree species such as *S. superba* that are adapted to a wide range of light intensity. Secondly, artificial methods such as moderate lopping of the shrub should be used when needed to provide an appropriate light environment for tree seedling establishment and growth. Thirdly, rather than planting seeds or small seedlings, managers should plant saplings that are as tall as the shrub

R. tomentosa (about 1.0–1.5 m) in the shrubland at the beginning of forest restoration. The buffered microenvironment under the shrub together with the high light intensity above the shrub canopy should accelerate the succession of the shrubland to zonal native forest.

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