

CAN THINNING OF OVERSTOREY TREES AND PLANTING OF NATIVE TREE SAPLINGS INCREASE THE ESTABLISHMENT OF NATIVE TREES IN EXOTIC ACACIA PLANTATIONS IN SOUTH CHINA?

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YUAN SF, REN H, LIU N, WANG J & GUO QF. 2013. Can thinning of overstorey trees and planting of native tree saplings increase the establishment of native trees in exotic *Acacia* plantations in South China? Assessing the effect of thinning of overstorey trees and planting of native trees will be helpful to better understand the vegetation restoration. A stand conversion experiment was conducted in a 12-year-old *Acacia auriculiformis* plantation in 1996. Treatments were thinning and underplanting, underplanting, thinning, and control. Results showed that thinning enhanced the establishment and growth of underplanted and regenerated native seedlings. The thinning and underplanting treatment reduced soil organic matter, soil total nitrogen, soil bulk density and soil water content but increased soil phosphorus and potassium contents. The establishment and growth of underplanted native species depended on their responses to light and soil resources. Thinning increased recolonisation by native species. Since some of the underplanted native trees grow rapidly, the regenerating canopy cover can become dense after thinning, and the density of the new canopy inhibits regeneration of other native tree species. Therefore, moderate thinning should be periodically performed as part of the long-term management of plantation and different thinning intensities can be used to increase spatial variability in the overstorey. The shade tolerance of native species was the most important characteristic in determining the response of the native trees to the treatments.

Keywords: Subtropical areas, photosynthetic parameters, stand conversion, shade tolerance, soil properties

YUAN SF, REN H, LIU N, WANG J & GUO QF. 2013. Dapatkah penjarangan pokok lapis atas dan penanaman anak pokok asli meningkatkan pertumbuhan pokok asli di ladang *Acacia* di China Selatan? Menilai kesan penjarangan pokok lapis atas dan penanaman pokok asli merupakan satu langkah yang berguna untuk memahami penggantian ladang serta pemulihan tanaman di ekosistem hutan yang ternyah gred. Kajian penukaran dirian dijalankan di ladang *Acacia auriculiformis* yang berusia 12 tahun pada tahun 1996. Kajian yang dijalankan ialah (1) penjarangan dan tanam bawah, (2) tanam bawah, (3) penjarangan dan (4) kawalan. Keputusan menunjukkan bahawa penjarangan meningkatkan penubuhan serta pertumbuhan anak pokok tanam bawah dan menggalakkan pertumbuhan semula anak pokok asli. Kajian penjarangan dan tanam bawah mengurangkan kandungan bahan organik tanah, jumlah nitrogen tanah, ketumpatan pukal tanah dan kandungan air tanah. Bagaimanapun, ia meningkatkan kandungan fosforus serta kalium tanah. Penubuhan dan pertumbuhan spesies asli tanam bawah bergantung pada gerak balasnya terhadap cahaya dan sumber tanah. Penjarangan juga meningkatkan pengkolonian semula spesies asli. Memandangkan sesetengah pokok asli tanam bawah tumbuh dengan cepat, kanopi yang terbentuk semula itu mungkin menjadi tebal selepas penjarangan. Kelebatan kanopi baharu ini menghalang pertumbuhan semula spesies pokok asli yang lain. Oleh sebab itu, penjarangan sederhana harus dijalankan secara berkala sebagai usaha pengurusan ladang jangka panjang. Tambahan lagi, kepadatan penjarangan yang berbeza dapat diguna untuk meningkatkan keragaman ruang lapis atas. Ketahanan spesies asli terhadap naungan merupakan ciri paling penting dalam menentukan gerak balas spesies asli terhadap kajian.

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INTRODUCTION

The forest cover in China was about 20.4% and includes 620 million ha of plantations in 2000s. Most plantations in China were tropical and subtropical, and were afforested with exotic, fast-growing pioneer tree species such as *Acacia*, *Eucalyptus* and *Pinus* (Ren et al. 2007b). These pioneer species are initially desirable because early in their development, the fast-growing stands are quite productive, improve the habitat and conditions, and increase biodiversity (Yang et al. 2009). After decades of development, however, the plantations still have a relatively simple structure, provide fewer ecosystem services than natural forests, and are even facing degradation. Moreover, relative to the native mature forests, these exotic plantations are unsustainable. Due to the lack of seed sources of native species, the plantations cannot be colonised by native species and remain in the pioneer stages. Succession to more natural communities is thus inhibited in the first few decades (Wang et al. 2009), although the community can eventually reach climax stages after a prolonged period of time. To maintain health, increase stand stability, improve stand structure and obtain greater ecological and economic benefits in a short period of time, forest managers in many countries are currently attempting to convert exotic, monospecific plantations into more natural broad-leaved forest and mixed forests with native species (Ren et al. 2007a, Heinrichs & Schmidt 2009).

The problem with exotic, monospecific plantations is well exemplified by *Acacia auriculiformis* (Fabaceae). It is a fast-growing evergreen tree native to Australia, Indonesia, and south-eastern Papua New Guinea. In its native area, it grows at latitudes 7° to 20° S and at elevations under 500 m. In 1961, it was introduced into China from South-East Asia by the South China Botanical Garden, Chinese Academy of Sciences. Due to its adaptability to infertile soil and its fast growth rate, this exotic species was widely planted in south-eastern China with the goal of restoring degraded areas (Wang et al. 2010). In the early stages of development, *A. auriculiformis* plantations increased nutrient cycling and the diversity of the plant community beneath the

tree canopy. Since native tree species rarely disperse from outside communities and do not accumulate in the soil seed bank, the seed rain and seed bank are poor sources for the native tree species associated with natural succession in these exotic plantations (Wang et al. 2010). After decades of development, however, these pure and unconverted *A. auriculiformis* plantations are still dominated by pioneer trees and shrubs, and contain few or no native tree characteristics of the zonal climax community (Wang et al. 2009, Duan et al. 2010). To accelerate plant succession and achieve sustainable development for these plantations, ecologists and managers now recognise that forest stand conversion is essential.

The goals of stand conversion are to make full use of local resources and establish a stand with tree species adapted to the local environment. The process includes establishing a mixed forest with native and exotic species and optimal spatial structure and arrangement. Forest stand conversion has become increasingly important worldwide (Lamb et al. 2005). The selection of native species affects the success of stand conversion. Some researchers have suggested that tree species used in stand conversion or forest restoration should be selected based on their ability to survive, grow fast, shade out herbaceous weeds, tolerate shade and attract seed-dispersing wildlife (Yang et al. 2009).

When the canopy of the existing stand is dense, thinning opens the canopy, increases tree growth rate, maintains timber quality, and increases diversity, biomass and cover of understorey vegetation (Maleque et al. 2007). Thinning also increases the survival and growth of underplanted seedlings and regeneration due to the moderation in light, water and nutrient conditions (Chan et al. 2006). Research has demonstrated that periodic thinning increases the establishment and regeneration of both natural and planted tree species (Heinrichs & Schmidt 2009). Increase in the abundance and diversity of understorey species also promotes the development of natural tree regeneration due to increase in habitat heterogeneity and optimal soil water and nutrient conditions or refuge from herbivores that facilitate survival

(Maas-Hebner et al. 2005). However, excessive cover of understorey vegetation may inhibit natural regeneration due to competition (Yang & Guan 2006).

Previous studies have examined how native seedlings such as *Castanopsis chinensis*, *Michelia chapensis* and *Psychotria rubra* grow in the open field or as part of the understorey (with and without litter) in different types of plantations (Wang et al. 2009, Yang et al. 2009). According to these researches, mature trees of *Acacia* species can facilitate the establishment and growth of native species seedlings by buffering temperature, reducing radiation and improving nutrients. The long-term effects of thinning mature *Acacia* trees on native species seedlings have not been examined.

In 1996, 12-year-old plantations of *A. auriculiformis* in the Heshan National Field Research Station, South China were either thinned or unthinned, and then either underplanted or not underplanted with seedlings of about 80 native species. In 2010, we surveyed the *A. auriculiformis* plantations again to answer the following questions: (1) Which of the four treatments resulted in the largest number of native saplings or seedlings and the largest overstorey of *A. auriculiformis*? (2) How did thinning and underplanting affect soil properties, litter quantity and light intensity? (3) Which underplanted native species had the highest regenerating abilities (here the term 'regeneration' meant the development of native plants from naturally recruited seeds produced by mature underplanted trees)? (4) Were the growth and regeneration of native trees affected more by extrinsic factors (the environment) or intrinsic factors (the physiology and ecology of the underplanted trees)?

MATERIALS AND METHODS

Study area

The study was conducted at the Heshan National Field Research Station (22° 40' N, 112° 50' E) in Heshan City, Guangdong, South China. The station is located in a subtropical monsoon climate zone and was established in 1984 for hilly land interdisciplinary research. The mean annual temperature at the station

is 21.7 °C. Annual rainfall is about 1801.8 mm and annual evaporation is 1600 mm. The soil is lateritic, a type of heavy acidic soil with little organic matter, total nitrogen (N) or available phosphorus (P) (Wang et al. 2009).

Stand conversion treatments

Forest restoration at Heshan Station was carried out in 1984 and experimental plantations were started with the planting of *A. auriculiformis* and *A. mangium* seedlings. Stand conversion was initiated in 1996 to introduce native species into the 12-year-old *A. auriculiformis* plantation. Before thinning, the spacing between *A. auriculiformis* trees was 3 m × 3 m, the average stand height was 8.13 ± 0.60 m and the average diameter at breast height (dbh) was 8.83 ± 0.26 cm (Figure 1b). We performed thinning in the fall and winter of 1995 and planting in the next spring. Linear sections of the plantation (without considering the size of the thinned plantation) were harvested along the slope directions. For thinning treatments, logged *A. auriculiformis* individuals including branches and roots were removed. These operations might cause scarification of the forest floor but rarely affected seedbeds and germination of native trees because these plantations had few seeds of native trees before the conversions. About 80 native wood species and 1000 seedlings per ha were planted (see Appendix 1). Effects of thinning and underplanting were assessed with the following four treatments: (1) thinning and underplanting (TP), in which half of the *A. auriculiformis* individuals were logged (uniformly distributed) in the plantation and native species were randomly planted at the thinned points; (2) underplanting (P), in which the native species were randomly planted directly under the canopy in the existing unthinned stand; (3) thinning (T), in which half of the *A. auriculiformis* individuals were logged and no native species were planted; and (4) control (C), in which no trees were logged and no native species were underplanted. In 1997, canopy densities of thinned stands were between 30 and 40%, while in the unthinned stands, the values were above 60% (Cai et al. 2005). There were four separate watersheds (about 3 ha each) in 100 m intervals apart.

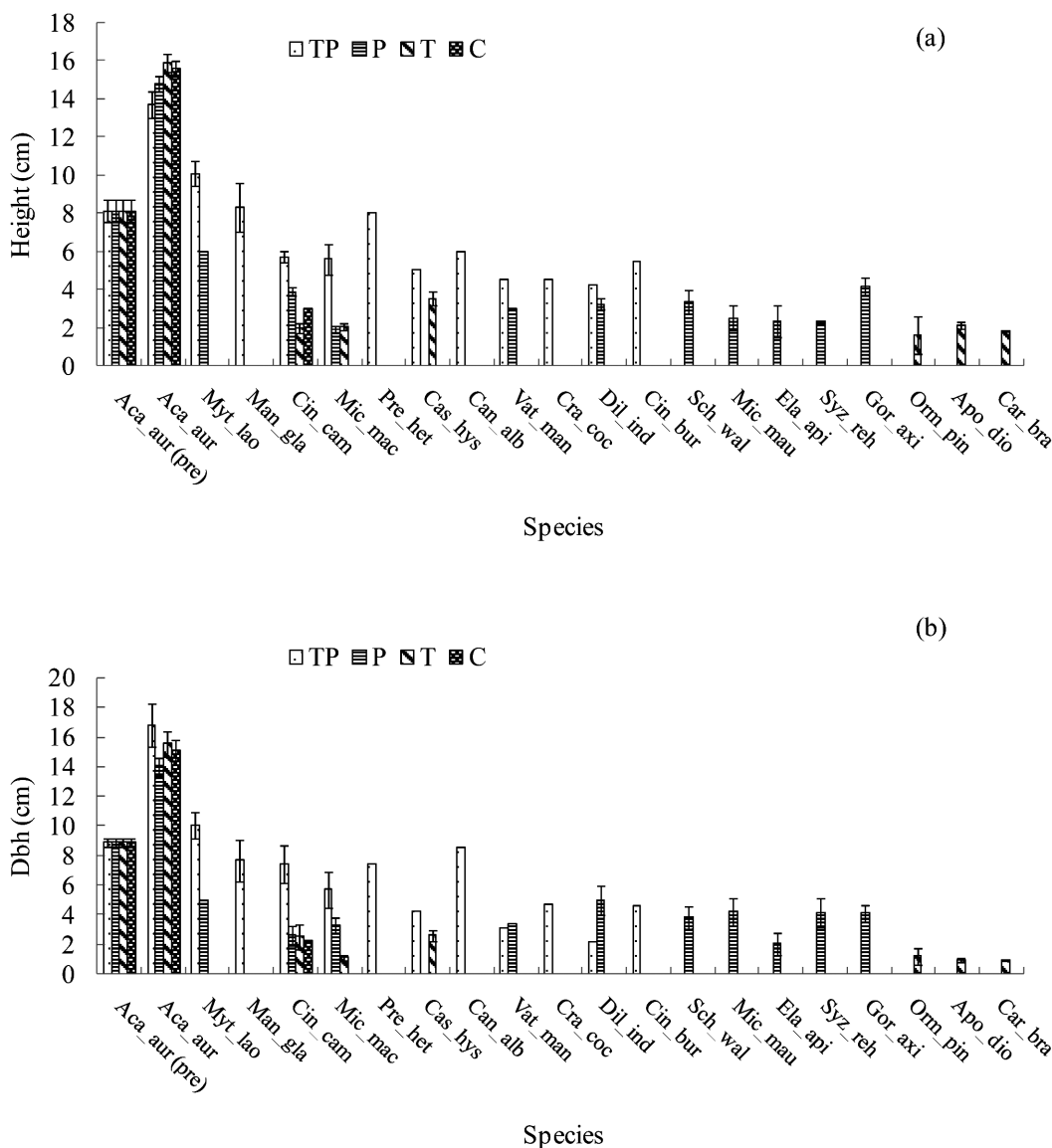


Figure 1 Height (a) and dbh (b) of *Acacia auriculiformis* and underplanted native species in the four treatments; values are means \pm SE; Aca_aur (pre) = *A. auriculiformis* (pre-treatment), Can_alb = *Canarium album*, Cra_coc = *Cratoxylum cochinchinense*, other abbreviations of plant names are provided in Table 1

Three plots of each treatment were established in every watershed with similar topographic and soil conditions.

Seedlings were raised from seeds of native stock, collected from the forest or purchased from local nurseries. All seedlings were grown in containers. The average size of seedlings before planting was 0.2–0.5 cm in basal diameter and 0.4–0.6 m in height. In March and April 1996, the seedlings were planted at thinned points or under the canopy of *A. auriculiformis* individuals in the TP and P stands respectively. The initial seedling size was kept the same among stands. Regular

watering, weeding and antigrazing measures were performed during the first 3 years after planting. Weed treatments (removing the vegetation) were conducted only around the planted native seedlings, each within an area of about 1 m². All seedlings were protected with 0.6-m tall plastic-mesh tubing. The number of native plants surviving in the P and TP stands was recorded 1.5 years after planting.

Assessment of vegetation

In 2010, three replicated plots (each 30 m \times 30 m in size) were selected, established and

sampled randomly from three different slope directions in each watershed. To facilitate the field investigation, nine permanent subplots (10 m × 10 m) within each plot were established for measuring the overstorey conditions (to indicate native trees including the original *A. auriculiformis*). Height and diameter at breast height (dbh) of all native trees were recorded. Within each subplot, forest stand structure was surveyed by recording the identity and abundance of trees, saplings and seedlings. Individuals taller than 5 m or with dbh greater than 2 cm were recorded as trees. Woody plants (trees only) between 1.3 and 5.0 m tall or with dbh between 1.2 and 2.0 cm were recorded as saplings. Woody plant species shorter than 1.3 m or with dbh less than 1.1 cm were recorded as seedlings. Given that 14 years had past since underplanting was performed, we assumed that these native seedlings resulted from seeds that were naturally produced by mature planted trees in the plots.

Leaf area index, litter mass and soil properties

Four points were selected in each subplot, and the LAI-2000 plant canopy analyser was used to measure community leaf area indices (LAI) from eight directions, namely, N, NE, E, SE, S, SW, W and NW at 3 p.m. for three continuous days in May and October 2010. Litter depth was measured with a ruler randomly positioned at 25 points and then averaged for each plot. All litter from six areas each measuring 1 m × 1 m was then removed and dried at 65 °C for 48 hours for the determination of dry weight. Mean litter mass for each plot was estimated in tonnes per hectare. In each plot, soil samples were collected from 12 random points using a 5-cm diameter soil corer inserted to a depth of 10 cm after removal of the litter and humus layer. Soil samples were air dried, passed through a sieve and then analysed for chemical characteristics (CAS 1978). Another three soil samples were collected from each plot by inserting a cutting ring (volume 100 cm³) into the soil. The collected soil was weighed moist and weighed again after drying at 105 °C for 24 hours before its bulk density and water content were calculated.

Gas exchange and photosynthetic parameters

In September 2010, we measured gas exchange on sun-exposed mature leaves of 1.5 m saplings of all 12 native species under full sun conditions. Three replications of each species were sampled in each plot. The photosynthetic light response curve was measured at different light intensities (1500, 2000, 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 50, 20, 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$) using a portable infra red gas analyser. The 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light level was set before the 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ level to prepare the chamber for light-response curves in C3 plants. Photosynthetic parameters were derived from each light-response curve by fitting a linear regression line between the 0 and 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light range, with the light compensation point ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) determined when $y = 0$ and the dark respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) determined when $x = 0$. Apparent quantum efficiency was calculated as the initial slope of the curve. The light-saturated photosynthetic rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) was estimated for each plant as the asymptote of the light-response curve, while the light level was the light saturation point ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). Before the photosynthetic light response value was determined, each plant was maintained at maximum irradiance until the net photosynthetic rate became constant, a process requiring 25 to 30 min.

Data analysis

All data were summarised and analysed at the plot level. We compared the total number of mature trees, saplings and seedlings of all native species between the four treatments (TP, P, T and C). Sample normality and homogeneity of variances were checked using the Kolmogorov–Smirnov and Cochran tests respectively (Bortz et al. 1990). The Kruskal–Wallis nonparametric H-test was used because most data were not normally distributed. This test is equivalent to the one-way ANOVA that compared different groups with regard to the ordinal variables. Pairwise comparisons were performed with the Mann–Whitney U-test. One-way ANOVA was carried out to

compare differences in dbh and height of overstorey plants, litter mass, litter depth and soil variables between the different treatments. Least significant difference (LSD) tests were used for post-hoc multiple comparison. In addition, we used canonical correspondence analysis (CCA) to analyse the relative effects of environmental variables on the distribution of native trees. Data were either arcsine (percentages) or log transformed to minimise kurtosis. The total variation explained was the ratio between the sum of all constrained eigenvalues and the total inertia of the data set. The sum of all canonical eigenvalues or trace was used to build the F-ratio statistic (Legendre & Anderson 1999). All statistical analyses were performed using SPSS (version 17.0) and CANOCO 4.5 for Windows.

RESULTS

Height and dbh of *A. auriculiformis*

Height ($F_{23} = 2.705$, $p = 0.047$) and dbh ($F_{23} = 5.321$, $p = 0.002$) of overstorey trees differed significantly between treatments. The T treatment led to the increase of dbh in *A. auriculiformis* but the P treatment decreased the height of tree. Tree height was greater in the T and C plots than in the TP and P plots, and dbh values were greater in the TP and T plots than in the P and C plots (Figure 1). Growth rates were 30.1, 44.2, 31.0 and 32.0% for height and 45.5, 33.4, 39.1 and 24.7% for dbh in the TP, P, T and C plots respectively, 14 years after the conversion.

Overall survival, height and dbh of native species

One and half years after planting, the survival rate of the underplanted native seedlings was about 86% (Cai et al. 2005). In 2010, the numbers of native species were 11, 10, 6 and 1 in the TP, P, T and C plots respectively (Figure 1). Differences in height and dbh between treatments were apparent for each species (Figure 1). The height and dbh of some common species such as *Mytilaria laosensis*, *Cinnamomum camphora* and *Michelia*

macclurei were significantly greater in TP than P plots ($F_{\text{height } 23} = 17.802$, $F_{\text{dbh } 23} = 5.230$, $p < 0.05$). *Dillenia indica* was taller but had lower dbh values in TP than in P plots. Other species in the TP plots such as *Manglietia glauca*, *Pterospermum heterophyllum* and *Canarium album* also had substantial height and dbh.

Establishment of native species

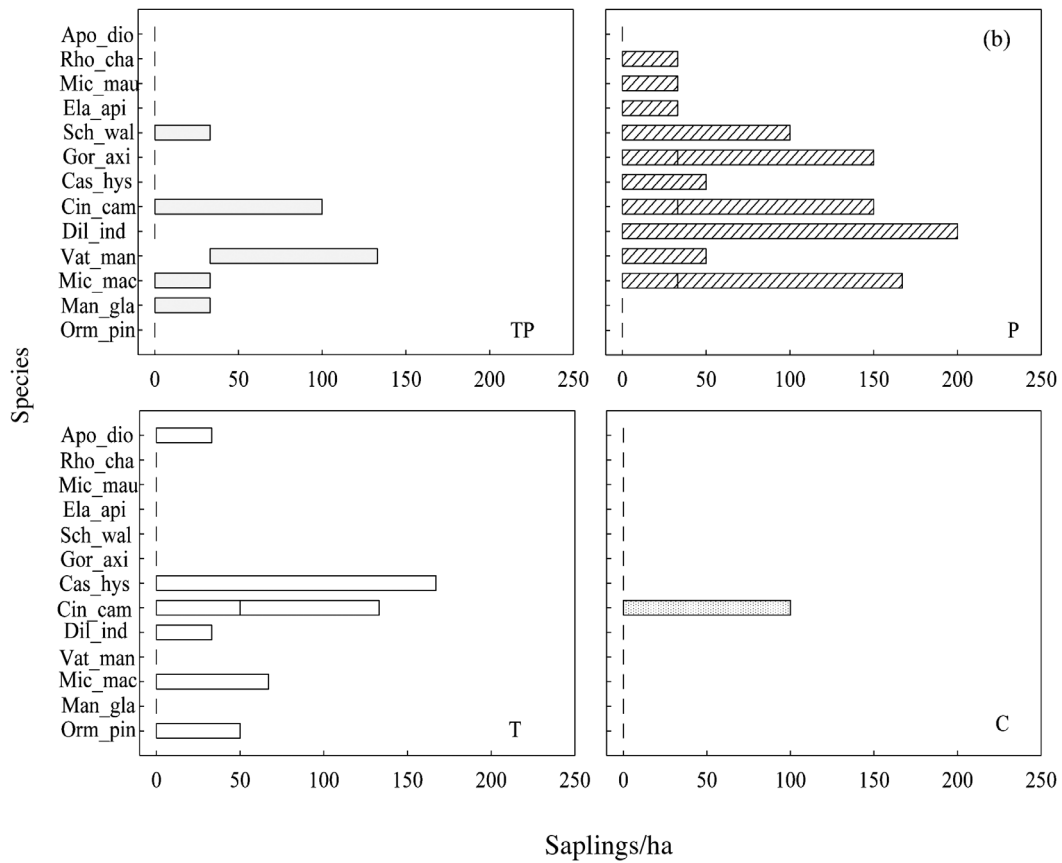
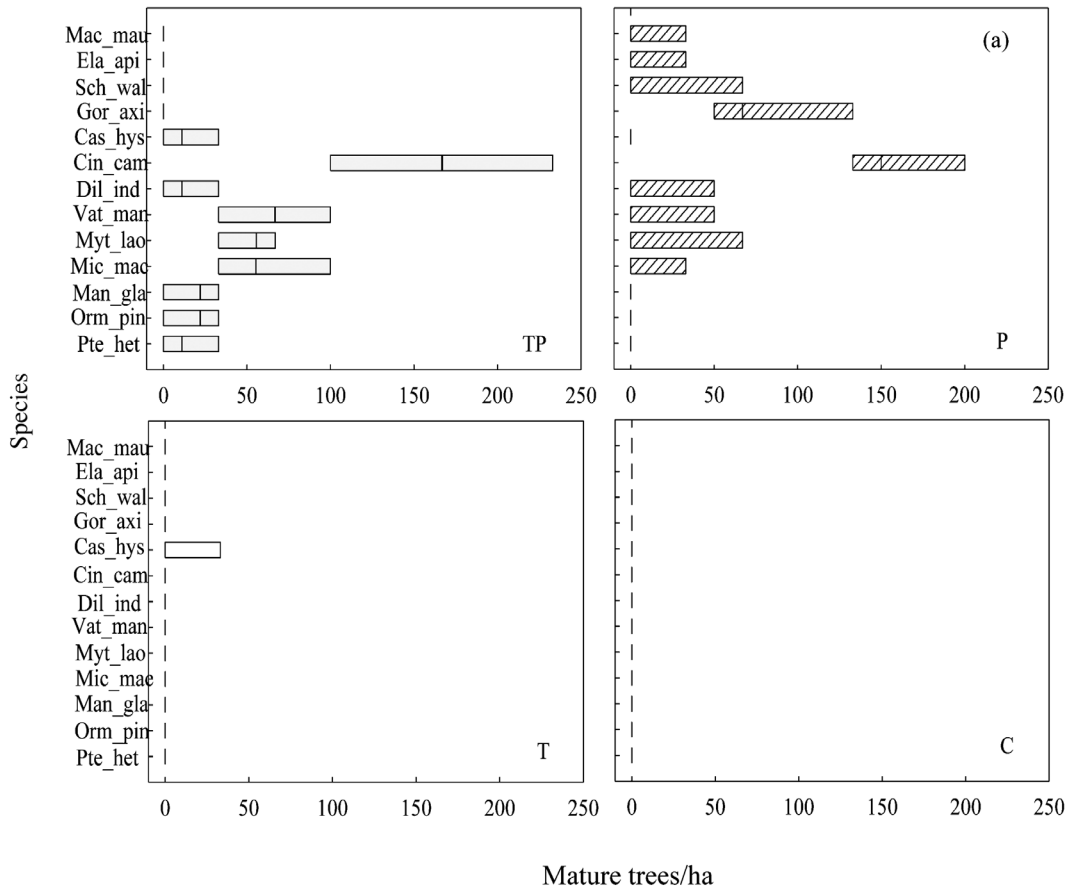
Mature trees

A total of 13 species of native mature trees were recorded in the study (Figure 2a). Species with fewer than three individuals per subplot were omitted from Figure 2a. There were no mature native trees in C plot. The only native species with mature individuals in TP, P and T plots was *Castanopsis hystrix*. Nine species were found in the TP and P plots, six of them in both TP and P plots. The abundance of all native mature trees showed significant differences between the treatments ($F_{11} = 30.917$, $p = 0.000$). The abundances of 5 of the 13 species (i.e. *M. macclurei*, *M. laosensis*, *Vatica mangachapoi*, *C. camphora* and *Gordonia axillaris*) significantly differed between TP and P plots (Figure 2a, Table 1).

Saplings

The P plot contained the largest number of saplings. Most of the important native species were present but *Ormosia pinnata*, *M. glauca* and *Aporosa dioica* were absent from the P plot. Native saplings were less abundant than native mature trees in TP plot but the opposite was true in T plot. Saplings of *C. camphora* were present (although unevenly distributed) in C plot (Figure 2b). The results of non-parametric H- and U-tests are given in Table 1.

Similar to the mature trees, abundance of all native saplings also showed significant differences between treatments ($F_{11} = 7.815$; $p = 0.009$). For species, the abundance of *C. camphora* saplings did not differ significantly between treatments. *Vatica mangachapoi* saplings were more abundant in TP than in P plots (H-test, $p = 0.04$). Although *D. indica* saplings tended to be more abundant in P than in



(continued)

Figure 2 (continued)

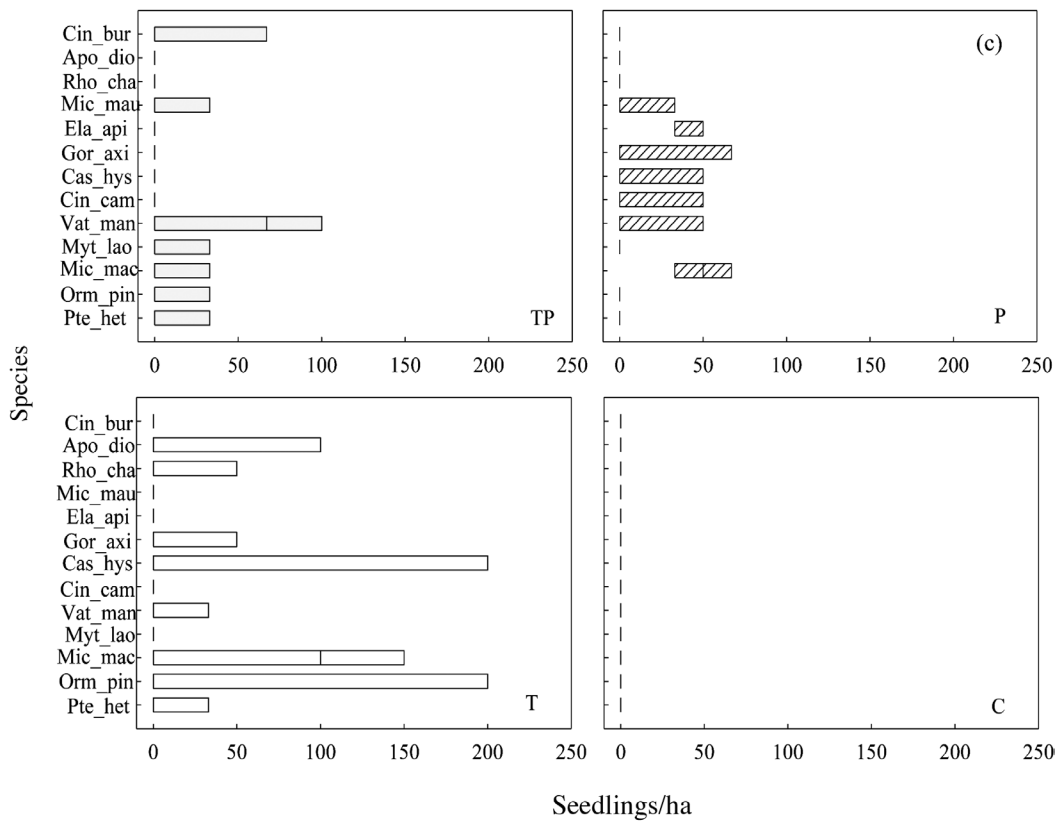


Figure 2 The abundance of mature trees (a), saplings (b) and seedlings (c) of native species in the four treatments: thinning and underplanting (TP), underplanting (P), thinning (T) and control (C); bars represent the 25–75% percentile, with 50% of the data distributed in this area; line among the bars means median or 50% four digits, and two lines among the bars mean the maximum and minimum values after removing the abnormal values

T plots, the difference was not significant. Interestingly, saplings of *A. dioica* and *O. pinnata* were absent in TP, P and C plots but they were present in the T plot. Saplings of four native species were found in the P plot, namely, *G. axillaris*, *E. apiculatus*, *M. maudiae* and *Rhodoleia championii*. Saplings of *M. glauca* and *Schima wallichii* only appeared in the TP plot.

Seedlings

As noted earlier, we assumed that the seedlings present in 2010 could not be those planted in 1996 (i.e. they could not remain as seedlings for 14 years) but were derived from seeds that were naturally produced in the plots. A total of 13 species of native seedlings were found,

with 8 species in the T plot and 7 species in the TP and P plots (Figure 2c). Seedlings of *V. mangachapoi* and *M. macclurei* were found in all treatments but the latter were more abundant in the T plot compared with TP and P plots. The former were more abundant in the TP plot than in the P and T plots. *Ormosia pinnata* and *C. hystrix* seedlings were more abundant in the T plot than in the TP or P plot. *Pterospermum heterophyllum* seedlings were equally abundant in the TP and P plots. *Mytilaria laosensis* and *C. burmanni* only occurred in the TP plot. Similarly, *R. championii* and *A. dioica* only occurred in the T plot while *E. apiculatus* and *C. camphora* seedlings were only found in the P plot. The abundance of all native seedlings showed significant differences between treatments ($F_{11} = 4.349$, $p = 0.045$).

Table 1 Abundance of mature trees, saplings and seedlings of native tree species as affected by four treatments

Species	Abbreviation	H-test (p-value)	TP	P	T	C
Mature trees						
<i>Pterospermum heterophyllum</i>	Pre_het	0.392	a	-	-	-
<i>Ormosia pinnata</i>	Orm_pin	0.086	a	-	-	-
<i>Manglietia glauca</i>	Man_gla	0.086	a	-	-	-
<i>Michelia macclurei</i>	Mic_mac	0.037	a	b	-	-
<i>Mytilaria laosensis</i>	Myt_lao	0.050	a	b	-	-
<i>Vatica mangachapoi</i>	Vat_man	0.040	a	b	-	-
<i>Dillenia indica</i>	Dil_ind	0.530	a	a	-	-
<i>Cinnamomum camphora</i>	Cin_cam	0.024	a	b	-	-
<i>Castanopsis hystrix</i>	Cas_hys	0.532	a	-	a	-
<i>Gordonia axillaris</i>	Gor_axi	0.013	-	a	-	-
<i>Schima wallichii</i>	Sch_wal	0.392	-	a	-	-
<i>Elaeocarpus apiculatus</i>	Ela_api	0.392	-	a	-	-
<i>Michelia maudiae</i>	Mic_mau	0.392	-	a	-	-
<i>Pterospermum heterophyllum</i>	Pre_het	0.392	a	-	-	-
<i>Ormosia pinnata</i>	Orm_pin	0.086	a	-	-	-
<i>Manglietia glauca</i>	Man_gla	0.086	a	-	-	-
<i>Michelia macclurei</i>	Mic_mac	0.037	a	b	-	-
<i>Mytilaria laosensis</i>	Myt_lao	0.050	a	b	-	-
<i>Vatica mangachapoi</i>	Vat_man	0.040	a	b	-	-
<i>Dillenia indica</i>	Dil_ind	0.530	a	a	-	-
<i>Cinnamomum camphora</i>	Cin_cam	0.024	a	b	-	-
<i>Castanopsis hystrix</i>	Cas_hys	0.532	a	-	a	-
<i>Gordonia axillaris</i>	Gor_axi	0.013	-	a	-	-
<i>Schima wallichii</i>	Sch_wal	0.392	-	a	-	-
<i>Elaeocarpus apiculatus</i>	Ela_api	0.392	-	a	-	-
<i>Michelia maudiae</i>	Mic_mau	0.392	-	a	-	-
Saplings						
<i>Ormosia pinnata</i>	Orm_pin	0.392	-	-	a	-
<i>Manglietia glauca</i>	Man_gla	0.392	a	-	-	-
<i>Michelia macclurei</i>	Mic_mac	0.407	a	a	a	-
<i>Vatica mangachapoi</i>	Vat_man	0.040	a	b	-	-
<i>Dillenia indica</i>	Dil_ind	0.266	-	a	a	-
<i>Cinnamomum camphora</i>	Cin_cam	0.788	a	a	a	a
<i>Castanopsis hystrix</i>	Cas_hys	0.530	-	a	a	-
<i>Gordonia axillaris</i>	Gor_axi	0.088	-	a	-	-
<i>Schima wallichii</i>	Sch_wal	0.530	a	a	-	-
<i>Elaeocarpus apiculatus</i>	Ela_api	0.392	-	a	-	-
<i>Michelia maudiae</i>	Mic_mau	0.086	-	a	-	-
<i>Rhodoleia championii</i>	Rho_cha	0.392	-	a	-	-
<i>Aporosa dioica</i>	Apo_dio	0.392	-	-	a	-
Seedlings						
<i>Pterospermum heterophyllum</i>	Pre_het	0.532	a	-	a	-
<i>Ormosia pinnata</i>	Orm_pin	0.530	a	-	a	-
<i>Michelia macclurei</i>	Mic_mac	0.131	a	a	a	-
<i>Mytilaria laosensis</i>	Myt_lao	0.392	a	-	-	-
<i>Vatica mangachapoi</i>	Vat_man	0.293	a	a	a	-
<i>Cinnamomum camphora</i>	Cin_cam	0.392	-	a	-	-
<i>Castanopsis hystrix</i>	Cas_hys	0.530	-	a	a	-
<i>Gordonia axillaris</i>	Gor_axi	0.530	-	a	a	-
<i>Elaeocarpus apiculatus</i>	Ela_api	0.013	-	a	-	-
<i>Michelia maudiae</i>	Mic_mau	0.214	a	a	-	-
<i>Rhodoleia championii</i>	Rho_cha	0.392	-	-	a	-
<i>Aporosa dioica</i>	Apo_dio	0.392	-	-	a	-
<i>Cinnamomum burmanni</i>	Cin_bur	0.392	a	-	-	-

TP = thinning and underplanting, P = underplanting, T = thinning and C = control; within a row, different letters indicate significant differences between treatments; - indicates the absence of the species in the treatment

Among the 13 species, only the abundance of *E. apiculatus* significantly differed between the four treatments (H-test, $p = 0.013$).

Soil properties, canopy LAI and litter mass

Soil organic matter, soil organic carbon and total N were significantly reduced in the TP and P plots compared with that in C plot (Table 2). Total phosphorus was also significantly lower in the P and T plots than that in the TP plot, but did not differ between the C plot and the rest of the plots. Soil water content was significantly lower in P plot than in the rest of the plots ($F_{23} = 6.849$, $p = 0.002$). Available P, available K and soil bulk density did not significantly differ between treatments ($p > 0.05$).

Canopy LAI was significantly greater in the TP plot than P, T and C plots ($F_{31} = 46.095$, $p = 0.000$, Figure 3a). Litter mass was significantly greater in TP plot compared with P, T and C plots ($F_{28} = 3.685$, $p = 0.022$). Litter depth was also significantly greater in TP plot than in P and C plots ($F_{104} = 3.782$, $p = 0.013$, Figure 3b).

Relationship between native tree distribution and environmental factors

The CCA model was significant ($p < 0.05$), suggesting that environmental factors explained the native tree distribution. The model explained 80.6% of the total variation. The eigenvalues (1, 2 and 3) of the corresponding extracted axes were 0.474, 0.376 and 0.28 respectively (F-ratio = 2.10, $p = 0.002$). As shown in Figure 4, total K was the most important determinant of axis I, whereas LAI was the most important determinant of axis II. The next most important environmental factors determining the distribution of native trees were soil water content, available P and soil bulk density. *Pterospermum heterophyllum*, *M. laosensis*, *V. mangachapoi* and *M. glauca* tended to occur in locations with high LAI and high total P. *Ormosia pinnata* tended to occur in locations with high soil water content and high available P. The distribution of *M. macclurei*, *M. glauca*, *O. pinnata*, *E. apiculatus* and *S. wallichii* was strongly affected by soil properties but weakly and negatively affected by LAI. *Aporosa dioica* was quite isolated from other species,

which might be related to the high soil organic matter (Figure 4).

Gas exchange and photosynthetic parameters

Light saturation point ($F_{23} = 40.19$, $p = 0.000$), light compensation point ($F_{23} = 8.53$, $p = 0.000$), dark respiration rate ($F_{23} = 17.46$, $p = 0.000$) and light-saturated photosynthetic rate ($F_{23} = 25.33$, $p = 0.000$) values significantly differed between the 12 native species, but not for apparent quantum efficiency ($F_{23} = 1.10$, $p = 0.412$) values. There were no significant treatment effects on gas exchanges (data not show). The light saturation point of native species ranged from 199 to 1134 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and was highest for *C. camphora* and lowest for *M. laosensis*. Light saturation point values were greater than 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for two-thirds of the 12 species that were measured. *Cinnamomum camphora* also had the highest light compensation point, light-saturated photosynthetic rate and dark respiration rate among the 12 native species. Light compensation point of native species ranged from 6 to 27 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and was lowest for *G. axillaris*. Apparent quantum efficiency was highest (0.09) for *G. axillaris* and lowest (0.02) for *E. apiculatus*. The dark respiration rate varied widely between the 12 species and was highest (1.91) for *C. camphora* and lowest (0.38) for *G. axillaris*. Light-saturated photosynthetic values ranged from 3.61 to 12.82 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 3).

DISCUSSION

Survival and growth of tree species

Relative to the control, the thinning treatment increased overstorey canopy development, accelerated the growth of the underplanted native seedlings and benefited the regeneration of native species. Large changes in overstorey structure persisted for at least 14 years after thinning was performed.

The height and dbh of underplanted native species were greater in TP than in P plots and the dbh of the underplanted native species was greater in the TP and T plots than in the unthinned plots. Compared with the

Table 2 Soil properties in the four treatments

Soil property	Treatment				F test	df	p value
	TP	P	T	C			
Organic matter (%)	4.73 ± 0.12 a	5.01 ± 0.24 a	5.41 ± 0.08 b	5.95 ± 0.29 b	6.742	23	0.003
Organic carbon (%)	2.75 ± 0.07 a	2.91 ± 0.14 a	3.14 ± 0.05 b	3.45 ± 0.17 b	6.746	23	0.003
Total N (%)	0.194 ± 0.00 a	0.208 ± 0.01 a	0.223 ± 0.00 b	0.243 ± 0.01 b	6.065	23	0.004
Total P (%)	0.018 ± 0.00 a	0.015 ± 0.00 b	0.016 ± 0.00 b	0.017 ± 0.00 ab	4.209	23	0.018
Total K (%)	1.30 ± 0.04 a	1.30 ± 0.01 a	1.00 ± 0.01 b	1.27 ± 0.06 a	15.11	23	0.000
Available P (mg/kg)	3.31 ± 0.13 (ab)	2.96 ± 0.14 (b)	3.76 ± 0.39 (a)	3.31 ± 0.13 (ab)	2.487	23	0.090
Available K (mg/kg)	36.4 ± 2.73 (a)	36.2 ± 2.39 (a)	31.9 ± 2.05 (a)	36.2 ± 1.79 (a)	0.916	23	0.451
Bulk density (g/cm ³)	1.09 ± 0.03 (ab)	1.12 ± 0.05 (a)	0.988 ± 0.03 (b)	1.11 ± 0.039 (a)	2.511	23	0.088
Soil water content (%)	34.0 ± 1.10 a	27.9 ± 1.46 b	37.5 ± 1.99 a	35.9 ± 1.74 a	6.849	23	0.002

TP = thinning and underplanting, P = underplanting, T = thinning and C = control; values are means ± SE; means in a row followed by different letters are significantly different

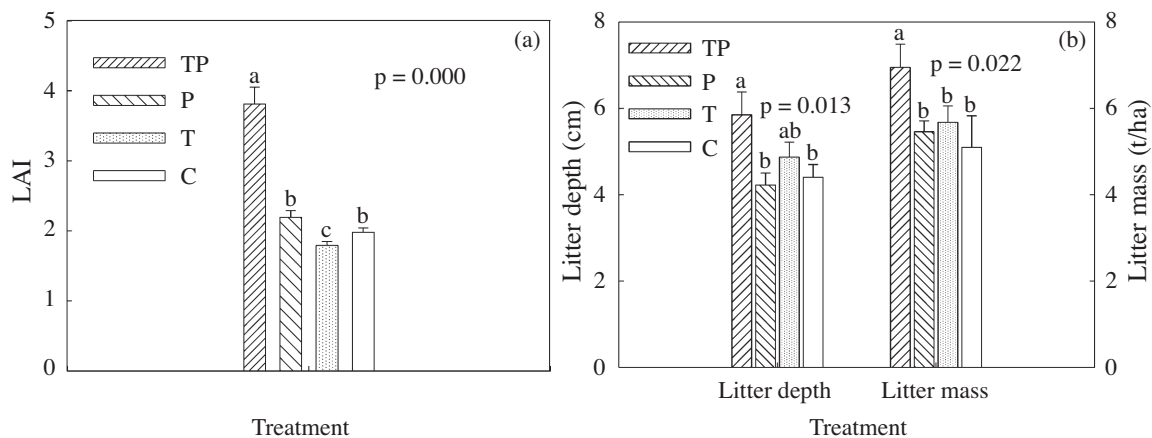


Figure 3 Leaf area index (LAI) and litter characteristic following four treatments (thinning and underplanting (TP), underplanting (P), thinning (T), and control (C)); values are means (± SE); values with different letters are significantly different

same species in sparse canopy sites, there was significant delay in the growth of diameter, marketable volume and height of planted natives in the dense overstorey canopy (Piotto 2007). Therefore, the growth of several native species such as *M. laosensis*, *M. glauca*, *C. camphora*, *P. heterophyllum* and *Canarium album* may be increased by thinning of the overstorey trees.

Stand management significantly affects the establishment and development of native species. There are few native seeds in this exotic plantation (Wang et al. 2010). Native species were present not only in plots where they were planted (TP and P plots) but also in plots where they were not planted (T plot).

Native species, however, were rare in the C plot. Most of established native species such as *G. axillaris*, *M. macclurei*, *O. pinnata*, *M. glauca*, *C. hystrix*, *C. burmanni* and *C. camphora* produced fruits and seeds. Thus, the seeds of native species came from mature trees. Seedlings were not abundant in the P and TP plots, indicating that germination and establishment of seedlings of native species might have been inhibited by the dense canopy in these plots (the differences in LAI in Figure 3a). In the T plot, however, germination and establishment of native tree species apparently benefited from the long-term effect of thinning, i.e. native species showed significant regeneration potential. Evidence for the regeneration

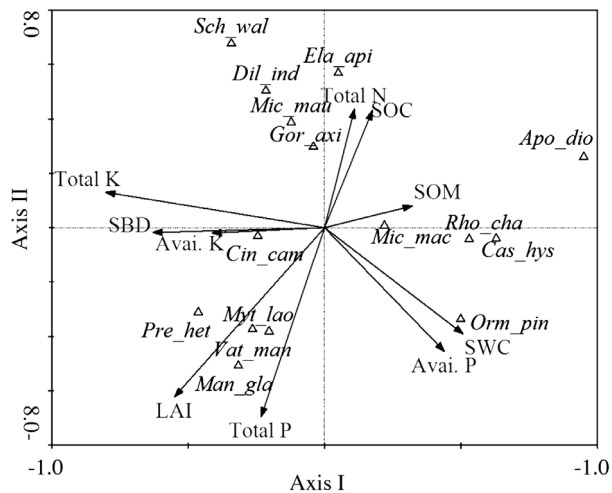


Figure 4 Canonical correspondence analysis (CCA) of biplot of native tree abundance vs environmental factors; species abbreviations are given in Table 1; abbreviated environmental factors are LAI = leaf area index, SOC = soil organic carbon, SOM = soil organic matter, SWC = soil water content, SBD = soil bulk density, Avai. K = available potassium

potential in the thinned plots was indicated by the presence of large numbers of seedlings of *O. pinnata*, *C. hystrix* and *M. macclurei*.

Few native seedling species occurred in C plot probably because of the shortage of seed sources of native species and because of inhibition from the dense understorey canopy. With the same seed sources and spread conditions, seedling establishment usually depended on the plot status. Thus, the denser canopies (covered by *Dicranopteris linearis* ferns and *Smilax setosa* vines) had inhibited the spreading of seeds, their germination and seedling establishment of native species. In addition, the relatively high abundance of saplings in the P plot was probably due to insufficient resources such as light, which would retard the development of saplings into mature trees. This result agreed with the findings of Nagai and Toshiya (2006).

Soil, litter and light properties

Acacia auriculiformis has a large N-fixation capability that increases soil N and causes a

shift from low to high N cycling in ecosystems (Yelenik et al. 2004). Thus, removal of N fixers greatly affects N cycling (Jovanovic et al. 2009). Forest clearing can increase N losses and decrease mineral N in ecosystems. In the current study, thinning of *A. auriculiformis* reduces total N, organic matter and organic carbon in soil. These reductions can be explained by the reduced abundance of N-fixing trees. In addition, thinning increases the abundance of native seedlings and saplings in the understorey and these seedlings and saplings may have removed significant quantities of N and other nutrients from the soil.

Our results suggested that thinning and underplanting can significantly increase litter mass and litter depth in *A. auriculiformis* plantations (Figure 3b). Litter properties in a plantation are affected by the community structure (Facelli 1991). In the current study, species composition significantly differed between treatments and this apparently affected litter properties. Moreover, *M. laosensis*, *M. glauca*, *C. camphora*, *C. hystrix* and *M. macclurei* produce large quantities of litter relative to other underplanted native species (Zhang & Zhuang 2008).

The thinning treatment removed half the trees in the *A. auriculiformis* plantation. This left the canopy significantly more open than the control plot in the years immediately following the treatment (Chan et al. 2006). According to the initial records, the canopy interception ratio of photosynthetically active radiation was about 0.50 ± 0.03 after the thinning treatment in 1997 (Cai et al. 2005). Thinning may also increase the availability of under-canopy and belowground resources such as nutrients and water which can affect understorey plant abundance and accelerate growth rates of planted saplings.

Environmental factors and species physiology

Our results showed that growth and establishment varied considerably between species and treatments. Responses of native tree species to environmental conditions are species-specific (Baraza et al. 2010). According to the CCA, soil total K was the most important environmental factor affecting the distribution of native

Table 3 Photosynthetic characteristics of the 12 native species in the stand conversion experiment

Species	LSP ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	LCP ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	AQE	R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
Cin_cam	1134 ± 19.76	27 ± 5.81	0.08 ± 0.03	-1.91 ± 0.25	12.8 ± 0.76
Mic_mac	712 ± 53.02	13 ± 1.34	0.04 ± 0.01	-0.6 ± 0.15	9.67 ± 0.6
Apo_chi	693 ± 17.48	12 ± 0	0.06 ± 0	-0.65 ± 0.05	9.86 ± 0.35
Sch_wal	634 ± 28.22	13.67 ± 1.33	0.04 ± 0.01	-0.73 ± 0	7.45 ± 0.19
Gor_axi	596 ± 15.68	6 ± 1.15	0.09 ± 0.02	-0.38 ± 0.06	5.87 ± 0.26
Ela_api	596 ± 12.03	20 ± 1.02	0.02 ± 0	-0.45 ± 0	5.46 ± 0.25
Pte_het	545 ± 76.69	9.32 ± 1.34	0.05 ± 0	-0.45 ± 0	8.9 ± 1.28
Mic_mau	543 ± 138.45	10.66 ± 3.53	0.06 ± 0.01	-0.65 ± 0.2	8.64 ± 1.58
Mag_gla	348 ± 40.46	12 ± 2.31	0.05 ± 0.01	-0.55 ± 0.06	4.46 ± 0.3
Vat_man	320 ± 9.19	12 ± 0	0.05 ± 0.01	-0.6 ± 0.08	4.19 ± 0.18
Cas_hys	296 ± 62.83	24 ± 2.31	0.05 ± 0	-1.05 ± 0.05	3.61 ± 0.28
Myt_lao	199 ± 45.86	11 ± 1.33	0.07 ± 0.01	-0.62 ± 0.15	4.24 ± 0.79

LSP = light saturation point, LCP = light compensation point, AQE = apparent quantum efficiency, R_d = dark respiration rate, A_{max} = light-saturated photosynthetic rate

trees although the detailed mechanism needed further research. In addition, the distribution of *M. macclurei*, *M. glauca*, *O. pinnata* and *S. wallichii* were mainly related to soil properties. Some species (*P. heterophyllum*, *M. laosensis*, *V. mangachapoi* and *M. glauca*) were more common in locations with high LAI, while other species (*A. dioica* and *E. apiculatus*) were restricted to areas with low LAI. On the other hand, high LAI in 2010 was responsible for the self-regeneration and high abundance of *P. heterophyllum*, *M. laosensis*, *V. mangachapoi* and *M. glauca* although past disturbances, species silvics, climate change and stand dynamics might also have influences.

Previous research showed that seedlings performed well under a maximum relative irradiance of about 40% of full radiation (Johnson et al. 1997). The purpose of thinning the pioneer *A. auriculiformis* plantation was to provide an optimal light environment for the growth of underplanted native species. This process led to the development of more structurally complex stands (Chan et al. 2006). After thinning, about 50% of sunlight radiation reached the understorey and thinning also resulted in air temperature and relative humidity that favoured the growth of underplanted native species (Cai et al. 2005). Thus, most underplanted native species that were taller and larger in canopy size at the TP plot might be due to better growth conditions created from thinning as thinning increased the sunlight

reaching the understorey. However, excessive sunlight can also reduce seedling growth (i.e. *V. mangachapoi*) through photoinhibition (Aranda et al. 2000). In addition to being affected by light, the growth and performance of native species (such as *M. macclurei* and *O. pinnata*) are also linked to soil water content (Climent et al. 2006).

The significant increases in litter in the TP plot may affect soil nutrients and in turn change the composition of the underplanted community. Litter affects seedling establishment in many ways. Litter shades seeds and young seedlings, represents a physical barrier to emerging seedlings, and increases fungal and bacterial pathogens (Facelli 1991). As a result, litter tends to depress germination and establishment (Stevens et al. 2004). It is suggested that the dominant tree, *M. laosensis*, markedly decreased the regeneration of other species by producing deep shade and thick litter layer in the understorey (Figure 3).

As stated above, understorey plantations are spatially heterogeneous in light/irradiance, soil resources and litter characters owing to the different conversion treatments and species-specific seedling growth. The establishment responses to resource levels could influence biodiversity, community structure and function. Thus, to accelerate the restoration process or to enhance the conversion, effective plantation managements should provide better microconditions for germination and establishments of native species.

Shade tolerance can greatly influence the growth and establishment of native species (Yang et al. 2009). Since the level of shading differed between the four treatments and because the understorey trees differed in shade tolerance, growth and performance of the understorey trees differed between species and between treatments. The 12 native species differed in the following photosynthetic characteristics: light saturation point, light compensation point, dark respiration rate and light-saturated photosynthetic rate. The parameters apparent quantum efficiency and light compensation point are key indicators of low light-utilisation efficiency for plants (Wu et al. 2006). Heliophobic species such as *M. laosensis*, *G. axillaris*, *M. glance* and *V. mangachapoi* had low light saturation point and light compensation point and high apparent quantum efficiency. Therefore, these species tended to occur in locations with high LAI conditions. These species may be suitable for conversion of dense stands. Relative to heliophobic plants, heliophilous plants have higher light saturation point, light compensation point, dark respiration rate and light-saturated photosynthetic rate but lower apparent quantum efficiency. No heliophilous plants were detected in our study. *Cinnamomum camphora* might be characterised as heliophilous with highest light saturation point, light compensation point, dark respiration rate and light-saturated photosynthetic values but its apparent quantum efficiency indicated a relatively high efficiency for utilisation of low light. Species such as *C. camphora* may be suitable for conversion of both dense and thin plantations stands. As indicated by their light compensation point, apparent quantum efficiency and light-saturated photosynthetic values, the rest of the species in this study were semi-heliophilous (*M. macchurei*, *S. wallichii* and *E. apiculatus*) or semi-heliophobic (*P. heterophyllum* and *M. maudiae*), and their distribution corresponded with the light conditions in the plots.

Although our results offer insights into the effectiveness of the various treatments, monitoring over longer periods is needed to increase our understanding of forest dynamics. Parameters that should be assessed over the long term include growth rate, canopy

structure, time to fruiting, fruit yield and attractiveness to wildlife. For example, time to fruiting is particularly important because fruit attracts seed-dispersing animals. Structural diversity within the regenerating forest canopy is beneficial to forest restoration because it provides more niches for seed-dispersing wildlife.

CONCLUSIONS

Our results suggested that selective thinning and underplanting of native species were effective for stand conversion in *A. auriculiformis* plantations in South China. However, the natural regeneration of native tree species was hampered by the dense canopy and substantial litter that developed in the thinned and underplanted plots. Moreover, thinning and underplanting reduced soil N, probably because the number of N-fixing plant (*A. auriculiformis*) was reduced and the underplanted species removed N from the soil. It follows that the conversion of exotic *A. auriculiformis* plantations into mixed native forests may require periodic thinning and underplanting. The periodic creation of small gaps could facilitate the establishment of native shade-tolerant species such as *M. laosensis* and *G. axillaris*. Variation in thinning intensity could also increase the variability in canopy structure and thereby increase the niches available for native trees.

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Appendix 1 List of native species underplanted in *Acacia auriculiformis* plantation, *A. mangium* plantation and mixed *A. auriculiformis* and *A. mangium* plantation

Family	Species	Survival (in 2010)
Podocarpaceae	<i>Podocarpus nagi</i>	
Magnoliaceae	<i>Michelia macclurei</i>	○△
	<i>Manglietia glauca</i>	○△
	<i>M. maudiae</i>	○△
	<i>Tsoongiodendron odorum</i>	△
Lauraceae	<i>Cryptocarya chinensis</i>	△
	<i>C. concinna</i>	△
	<i>Machilus chinensis</i>	△
	<i>Lindera chunii</i>	
	<i>Cinnamomum burmanni</i>	○△
	<i>C. camphora</i>	○△
	<i>Lindera communis</i>	
Dilleniaceae	<i>Dillenia indica</i>	○△
Thymelaeaceae	<i>Aquilaria sinensis</i>	
Proteaceae	<i>Helicia cochinchinensis</i>	△
	<i>H. reticulata</i>	△
Burseraceae	<i>Canarium album</i>	○
	<i>C. pimela</i>	
Myrtaceae	<i>Syzygium levinei</i>	
	<i>S. rehderianum</i>	△
	<i>Acmena acuminatissima</i>	△
	<i>Syzygium cumini</i>	△
Theaceae	<i>Schima superba</i>	△
	<i>Gordonia axillaris</i>	○
	<i>Schima wallichii</i>	○△
Hypericaceae	<i>Cratoxylum cochinchinense</i>	○
Rhizophoraceae	<i>Carallia brachiata</i>	○
Guttiferae	<i>Garcinia oblongifolia</i>	△
	<i>G. multiflora</i>	
Elaeocarpaceae	<i>Elaeocarpus sylvestris</i>	
	<i>Sloanea sinensis</i>	
	<i>Elaeocarpus apiculatus</i>	○
Sterculiaceae	<i>Pterospermum heterophyllum</i>	○
	<i>Sterculia lanceolata</i>	△
Euphorbiaceae	<i>Aporosa dioica</i>	○
	<i>Endospermum chinense</i>	
	<i>Sapium discolor</i>	△
	<i>Microdesmis caseariiifolia</i>	
	<i>Aporosa yunnanensis</i>	
	<i>Bischofia polycarpa</i>	
	<i>Cleidiocarpon cavaleriei</i>	△
Rosaceae	<i>Pygeum topengii</i>	
	<i>Laurocerasus phaeosticta</i>	
Mimosaceae	<i>Abarema clypearia</i>	△
	<i>A. lucida</i>	
	<i>Ormosia glaberrima</i>	
	<i>O. pinnata</i>	○△
Caesalpiniaceae	<i>Cassia siamea</i>	
	<i>Erythrophleum fordii</i>	△
Papilionaceae	<i>Dabergia odorifera</i>	△

(continued)

Appendix 1 (continued)

Family	Species	Survival (in 2010)
Hamamelidaceae	<i>Exbucklandia populnea</i>	
	<i>Mytilaria laosensis</i>	○△
	<i>Rhodoleia parvipetala</i>	
Fagaceae	<i>Castanopsis chinensis</i>	△
	<i>C. hystrix</i>	○△
	<i>C. kawakamii</i>	△
	<i>Lithocarpus glaber</i>	△
	<i>Castanopsis eyrei</i>	
Ulmaceae	<i>Gironniera subaequalis</i>	△
Moraceae	<i>Artocarpus styracifolius</i>	△
	<i>Ficus altissima</i>	
	<i>F. variegata var. chlorocarpa</i>	
	<i>Artocarpus hypargyreus</i>	△
	<i>A. lingnanensis</i>	△
Rutaceae	<i>Acronychia pedunculata</i>	△
Meliaceae	<i>Swietenia macrophylla</i>	
	<i>S. mahagoni</i>	
	<i>Chukrasia tabularis</i>	△
Anacardiaceae	<i>Dracontomelon duperreanum</i>	
Araliaceae	<i>Schefflera octophylla</i>	△
	<i>Heteropanax fragrans</i>	
Ebenaceae	<i>Diospyros morrisiana</i>	△
Symplocaceae	<i>Symplocos lancifolia</i>	△
	<i>S. cochinchinensis</i>	
	<i>S. chunii</i>	
	<i>Engelhardtia fengelii</i>	
	<i>E. roxburghiana</i>	
Alangiaceae	<i>Alangium chinense</i>	
Oleaceae	<i>Osmanthus matsumuranus</i>	
Rubiaceae	<i>Tricalysia dubia</i>	
Palmae	<i>Caryota ochlandra</i>	
Dipterocarpaceae	<i>Vatica mangachapoi</i>	○

○, △ and ○△ represent the species that survived in *A. auriculiformis* plantations, in *A. mangium* plantations and in both until 2010 respectively