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REGULAR ARTICLE

Seedling growth and soil nutrient availability in exotic and native tree species: implications for afforestation in southern China

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Abstract

Background and aims The relationship between tree species and soil nutrient availability is critical for evaluating plantation succession and promoting forest restoration. This study was conducted to evaluate the impact of exotic and native tress species on soil nutrient availability.

Methods Four exotic species (Eucalyptus urophylla, E. tereticornis, Acaia auriculaeformis, A. mangium) and four native species (Castanopsis fissa, Schima superba, C. hystrix, Michelia macclurei) were planted

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W. Zhu Department of Biological Sciences, State University of New York-Binghamton, Binghamton, NY 13902, USA

D. A. Neher Department of Plant and Soil Science, University of Vermont, Burlington, VT 05405, USA and grown for one-year. Soil solution (DOC, DON, NH_4-N , NO_3-N) was sampled and analyzed during the study. After the experiment, soil properties were determined, and plant tissues were analyzed.

Results DOC levels were greater in soils with trees planted than controls without trees. Compared to native species, exotic species had much faster growth rates and greatly reduced DON and NO₃–N concentrations. Exotic species always had less P concentrations in leaves and stems than native species. Furthermore, N-fixing *A. auriculaeformis* led to greater soil available P compared to other species.

Conclusions Based on these findings, we provide some recommendations for afforestation practice. This study highlights that a better understanding of the pros and cons of exotic species would be beneficial to advance afforestation in China and the world.

Keywords Soil solution · Nutrient availability, exotic species · Native species · Afforestation, South China

Abbreviation

DOCDissolved organic CDONDissolved organic N.

Introduction

In subtropical and tropical areas, millions of hectares of forests are being deforested or degraded due to human activities (FAO 2011; Lamb et al. 2005). Author's personal copy

Restoration at both regional and global scales, thus, is critical for the sustainability of the global ecosystem (Gardiner et al. 2003). Afforestation of former agricultural land, rehabilitation of degraded natural ecosystems, and conversion of single-species to mixedspecies plantations are among the major types of restoration practices currently being implemented throughout the world (Lamb 1998; Lamb et al. 2005).

Much of the plantations in tropical and subtropical regions were established with exotic species from a small selection of genera (e.g., Eucalyptus, Acacia, *Pinus*). For example, there were $39,700 \text{ km}^2$ Eucalyptus and Acacia plantations in southern China until 2011 (China Eucalypt Center 2011). Although these exotic species usually are very productive, use of these exotic species is in great dispute (Lamb 1998), mostly due to their inferior ecological services compared to native species in the original forests. To improve ecological services (i.e., biodiversity, soil and water conservation), the practice of planting native tree species has increased in the past several decades in many tropical and subtropical regions, including Malaysia, Australia, Costa Rica, Vietnam (Lamb et al. 2005) and southern China (Zhou and Yan 2000; Wang et al. 2008; Ren et al. 2007). Since the 1990s, the coverage of ecological forests, mainly planted with native species, has been increasing due to the encouragement by local governments in southern China (Zhou and Yan 2000).

During the last three decades, China has established the largest area of plantation in the world, covering 616,884 km² (National Bureau of Statistics of China 2011). Most of these plantations were established in southern China, located in the tropical and subtropical regions. As part of a large-scale afforestation campaign launched in the 1980s, more than 20 tree species were planted initially to evaluate their suitability to the regional climate and soils (Li et al. 2001). Based on the initial experimental results, the most common species used today are exotic species Eucalyptus urophylla, Eucalyptus tereticornis, Eucalyptus citriodora, Eucalyptus exserta, Acacia auriculaeformis (N-fixing), Acacia mangium (Nfixing), and native species Castanopsis fissa, Schima superba, Castanopsis hystrix, Michelia macclurei (Li et al. 2001; Wang and He 2006). This choice was based on their biological characteristics (Qin et al. 2007; Zhao et al. 1995), stand qualities or yields (Chen et al. 1998; Lu et al. 2004), and readiness for forest management (Lin 2002; Wang and He 2006; Zhu 2006). Only a few researchers have studied the impacts of these species on nutrient cycling in soils such as litter decomposition (Chen 2001; Li et al. 2003) and nitrogen mineralization (Li et al. 2003; Schlesinger and Lichter 2001). However, assessing the impact of plant species on soil nutrient availability is of particular importance for forest restoration (Rhoades and Binkley 1996). In particular, the specific knowledge in terms of the effects of exotic and native species on soil properties is limited. A detailed understanding on the plant-soil interactions between exotic and native species is critical and imperative for evaluating the function of different tree species in the production and succession of plantations, designing more sustainable agroforestry systems, and promoting restoration on degraded lands (Russell et al. 2007).

In this present study, we designed a one-year common garden experiment in a homogeneous soil in southern China to focus on species-specific effects of exotic and native tree species on soil nutrient availability and nutrient uptake. The species selected in this study were the most commonly used trees in forestry programs of southern China (Li et al. 2001; Wang and Lin 2001). The specific aims of this study were to: 1) evaluate the impact of these exotic and native species (with contrasting growth rates) on soil N and P availability; and quantify the growth of plants in relationship to the availability of soil nutrients; and 2) provide management recommendations for afforestation in this region. We hypothesized that 1) exotic species, due to their faster growth rates, would lower soil N and P availabilities than native species and lead to nutrientlimitation on plant growth; 2) N-fixing species could alleviate the N limitation due to their N-fixing capability.

Materials and methods

Experimental design

Four exotic species (Eucalyptus urophylla, Eucalyptus tereticornis, Acaia auriculaeformis, Acaia mangium) and four native species (Castanopsis fissa, Schima superba, Castanopsis hystrix, Michelia macclurei) were chosen for this study. Of these eight species, only the two Acacia species are capable of N-fixation. All eight species were heliophilous plants, and their seedlings were germinated from seeds in nutrient cups. One seedling of each of the tree species (initial height 30–40 cm) was planted per pot. In the planting, the original soils adhering in seedlings' roots were carefully washed out with water. Each plant species was replicated in five separate pots. Unplanted pots served as controls, also replicated five times.

Soil and pot installation

Soil was obtained from a forested land located in the Heshan National Forest Research Station (112°540 E, 22°410 N), Chinese Academy of Science, in Guangdong Province, China. The surface soil (0-20 cm) was collected, air-dried, sieved to remove gravel and debris >5 mm, and mixed thoroughly. The soil was an Acrisol, with a silt loam texture. The average soil pH was 4.54, soil organic carbon (SOC) was 1.63 %, and soil total N was 0.83 g/kg. A polyvinyl-chloride pot (height: 40 cm, diameter: 30 cm) was used as the container and filled with air-dried soil (25 kg/pot) without any fertilizer addition. All pots were maintained in an open area in South China Botanical Garden, Guangzhou. The monthly rainfall and mean air temperature in the experimental site were recorded (Fig. 1). All pots were watered biweekly. Any weeds that were germinated in pots were removed regularly by hand.

A soil solution sampler with four silicon suctioncups was installed in each pot at the depth of 10 cm under the soil surface. The four suction-cups in each sampler were distributed in a square at equidistance (10 cm) to the planted seedling which was located at the center of the pot.

Analyses of soil and plant materials

Seedlings were planted in October 2006, and soil solution samples were collected four times in the



Fig. 1 The monthly rainfall and mean air temperature in the experiment site, Guangzhou, Guangdong, China

one-year study (December 2006, April 2007, July 2007 and October 2007). Soil solutions were sampled at 24 h after a saturated watering. In total, 180 samples were obtained and analyzed for the following parameters: dissolved organic carbon (DOC), total dissolved N (TDN), ammonium N (NH₄-N), and nitrate N (NO_3-N) . DOC and TDN were determined using a TOC analyzer (TOC-VSCH, Shimadzu Corp., Japan). NH₄-N was determined colorimetrically by the salicylate-nitroprusside method on a Flow-Injection Autoanalyzer (FIA, Lachat Instruments, USA). NO₃-N was determined colorimetrically after cadmium reduction using the same FIA. Dissolved organic nitrogen (DON) was calculated as the difference between the TDN concentration and the combined NH₄-N and NO₃-N concentration (DIN).

At the end of the experiment, the surface soil (0-20 cm) in each pot was sampled to analyze the following soil properties: soil extractable ammonium N (NH₄-N) and nitrate N (NO₃-N), soil organic matter (SOM), total N (TN), total P (TP) and available P. NH₄-N and NO₃-N were extracted from 10 g of fresh homogenized soil without roots using 50 ml of 2 M KCL. Concentrations of extractable NH₄-N and NO₃-N were determined by the FIA (Lachat Instruments, USA). The remaining soil was air-dried and ground to pass through a 2-mm sieve. Soil available P was extracted by Bray solution (Bray and Kurtz 1945), and determined by Mo-Sb Spectrochemistry. Soil samples for TN,TP and TOC analysis were ground to pass through a finer, 0.25-mm sieve. TN and TP contents were determined by the micro-Kjeldahl digestion procedure (Bremmer and Mulvaney 1982) followed by colorimetric determinations using the FIA. Organic C content was determined by wet combustion method (Liu et al. 1996). Soil gravimetric water content was determined by drying samples at 105 °C oven for 24 h.

The height of each seedling was measured through the study. After one-year growth, all seedlings were harvested. Each plant was separated into root, stem and leaf parts to determine the biomass and nutrient concentrations of different tissues. All plant samples were dried and weighed. A sub-sample of each plant tissue was grounded in preparation for the analysis of nutrient content. Plant organic C was measured by wet combustion (Liu et al. 1996). Plant N and P concentrations were determined by colorimetry using FIA, after micro-Kjeldahl digestion.

Statistical analysis

Repeated measures analysis of variance (RM-ANOVA) was performed to determine the effect of tree species on soil solution chemistry through time. In the RM-ANOVA analyses, sampling time (n=4) and its interaction with species were included in the within-subjects model. An orthogonal contrast analysis was used to compare the different performance of exotic species versus native species, and planted treatments versus unplanted control. One-way ANOVA was performed to determine the effect of tree species on plant and soil properties (plant N and P concentrations in different tissues, and general soil properties like soil extractable inorganic N, soil total N and soil organic C), followed by the orthogonal contrast analyses. Homoscedasticity was tested using the Levene's test. Pearson's correlation analysis was used to analyze the relationship between plant growth and soil nutrient availability, and a partial correlation with plant growth as a controlling factor was used to detect the relationship between soil nutrient availability and plant N and P properties. All statistical procedures were performed using SPSS Version 18.0 software (SPSS Inc., USA).

Results

Plant species effects on soil solution chemistry

RM-ANOVA showed that plant species significantly affected the concentration of soil DOC (P=0.03, Table 1 and Fig. 2a). However, there was no significant difference between the exotic and native species (P=0.124). The unplanted soils maintained significantly lower DOC than planted soils (P=0.029). The concentration of soil DOC under plants steadily increased

through time (P<0.002, Table 1 and Fig. 2a). For example, in October 2006, both planted soils and unplanted controls had the similar low DOC concentrations (the mean concentration of DOC under plants: 4.97 mg/L, control: 4.91 mg/L). However, after 1 year's growth, the level of DOC under plants (all planted pots) was 12.3 mg/L, 50 % higher than that in unplanted soils (Control: 8.22 mg/L), with the highest level of DOC found under exotic *E. urophylla* (18.7 mg/L).

DON concentration was also affected by plant species (P < 0.001, Table 1). In both December 2006 and April 2007, 2 months and 6 months after the planting experiment, the largest values of DON concentration were found in the unplanted controls (Fig. 2b), while the exotic species had lower DON concentration than the native species (P < 0.001). The temporal pattern of soil DON contrasted that of DOC. In April 2007, DON increased 1–2 mg/L in exotics and up to 20 mg/L in control in comparison to that in December 2006 (Fig. 2b). Thereafter, DON concentrations in both July and October 2007 were substantially lower than the previous two sampling dates (P < 0.001, Table 1).

The NH₄–N concentration in soil solution was also influenced by plant species (P=0.043, Table 1), but there was no difference between exotic and native plants (P=0.83). However, a strong temporal variation was observed (P<0.001, Table 1, Fig. 2c). Solution NH₄–N was the greatest at the first sampling (5.0 mg/ L) and decreased rapidly through time, reaching values less than 1 mg/L in exotic plant treatments, and 1– 2 mg/L in control and native species treatments by April 2007 (Fig. 2c and Fig. S1).

Opposite of NH₄–N, concentration of NO₃–N in soil solution varied significantly by plant species (P <0.001, Table 1, Fig. 2d). The highest values of NO₃–N concentration were all in soil-only controls,

	DOG		DON				NON	
Source	DOC		DON		NH ₄ -N		NO ₃ -N	
	F	Р	F	Р	F	Р	F	Р
Time [*]	31.4	< 0.001	60.4	< 0.001	2039	< 0.001	113	< 0.001
Time \times species [*]	2.03	0.07	6.95	< 0.001	11.1	< 0.001	11.9	< 0.001
Species	3.68	0.03	9.53	< 0.001	2.29	0.043	33.0	< 0.001

Table 1 The RM-ANOVA analysis of soil solution variables (n=180)

Time was regarded as a within-subjects factor in the RM-ANOVA, and the statistic values of time effects and the interaction between time and species were tested with Lower-bound method due to the denying of Mauchly's Test of Sphericity

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Fig. 2 Concentrations of DOC (a), DON (b), Ammonium N (c), and Nitrate N (d) in soil solution under different tree species and Control in four sampling events (Data are means +1SE, n=5). Statistical results are shown in Table 1. Only 4 species were shown in this figure, the full version (8 species plus Control) was shown in supplementary material Figure S1



and NO₃–N concentrations under native species were greater than those under exotic species (P<0.001). However, among the four native species, NO₃–N concentrations also varied greatly: *C. fissa* had a NO₃–N concentration similar to the four exotic species and less than the remaining three native species (i.e., *S. superba*, *C. hystrix* and *M. macclurei*) (Fig. S1). The temporal pattern of NO₃–N depended on plant species (P<0.001, Table 1). For example, in April 2007, as much as 4.0 mg/L NO₃–N was accumulated in the control and native species treatments relative to the previous sampling in December (Fig. 2d and Fig. S1), while in the four exotic species treatments, the NO_3 -N concentration was constant through time and then decreased to less than 0.03 mg/L in July and October 2007.

Effects of plant species on soil properties

One-way ANOVA showed that plant species affected soil organic carbon (SOC), soil C/N ratios, soil NO₃–N and available P (P<0.05, Table 2) after the 1-year study, but had no effect on soil total N (TN),

Table 2 Description of chemical properties for soils influenced by eight trees species commonly used in southern China plantations. Values represent soil properties after 1 year of tree growth in pots (Data are represented as means ± 1 SE, n=5)

Species	TN (g/kg)	TP (g/kg)	SOC (%)	C/N	NH ₄ -N (mg/kg)	NO ₃ -N (mg/kg)	Available P (mg/kg)	Soil pH
EU	$0.91 {\pm} 0.06$	$0.18 {\pm} 0.01$	$1.54^{ab} {\pm} 0.02$	17.2 ^{ab} ±1.29	1.33±0.17	$0.82^{bc} \pm 0.04$	$0.91^{b} {\pm} 0.04$	$4.3^{d} {\pm} 0.04$
ET	$0.92 {\pm} 0.04$	$0.20{\pm}0.01$	$1.59a^b\pm0.03$	$17.4^{ab}{\pm}0.73$	$1.06 {\pm} 0.08$	$0.51^{\circ} \pm 0.12$	$1.09^{ab}{\pm}0.05$	$4.3^d{\pm}0.01$
AA	$1.13 {\pm} 0.05$	$0.21 {\pm} 0.01$	$1.46^{b} \pm 0.06$	$13.0^{b} {\pm} 0.63$	$1.04 {\pm} 0.04$	$0.60^{c} \pm 0.02$	$1.28^{\mathrm{a}} {\pm} 0.08$	$4.3^{cd} \pm 0.01$
AM	$0.87{\pm}0.02$	$0.18{\pm}0.01$	$1.34^b{\pm}0.06$	$15.6^{ab} \pm 1.03$	$1.18 {\pm} 0.09$	$0.66^{c} \pm 0.03$	$0.99^{ab}{\pm}0.03$	$4.5^{ab} {\pm} 0.04$
CF	$0.83 {\pm} 0.05$	$0.17 {\pm} 0.01$	$1.57^{ab}{\pm}0.02$	$19.1^{a}{\pm}1.32$	$1.12{\pm}0.07$	$0.63^{c} \pm 0.02$	$0.90^b{\pm}0.05$	$4.4^{cd}\pm0.02$
SS	1.03 ± 0.01	$0.19{\pm}0.02$	$1.41^{b}{\pm}0.09$	$16.6^{ab}{\pm}0.87$	$1.36 {\pm} 0.09$	$0.93^{bc} \pm 0.11$	$0.96^b{\pm}0.05$	$4.6^a{\pm}0.07$
СН	$0.85 {\pm} 0.04$	$0.17 {\pm} 0.01$	$1.48^{ab}{\pm}0.05$	$14.9^{ab} \pm 1.32$	$1.30 {\pm} 0.12$	$1.29^{b} \pm 0.19$	$1.04^{ab}{\pm}0.07$	$4.5^{ab}{\pm}0.03$
MM	$0.98{\pm}0.02$	$0.19{\pm}0.00$	$1.90^{a} \pm 0.17$	$19.4^{a}{\pm}1.77$	$1.13 {\pm} 0.06$	$0.67^{c} \pm 0.02$	$1.07^{ab}{\pm}0.07$	$4.4^{bc} \pm 0.02$
Control	$0.93 {\pm} 0.04$	$0.19{\pm}0.01$	$1.53^{ab}{\pm}0.06$	$16.5^{ab}{\pm}0.61$	$1.33 {\pm} 0.07$	$2.83^{a} \pm 0.26$	$1.05^{ab}{\pm}0.05$	$4.4^{cd}{\pm}0.01$
P values	ns	ns	< 0.05	< 0.05	ns	< 0.05	< 0.05	< 0.01

Different lowercase letters indicate significant (LSD, P<0.05) difference. EU Eucalyptus urophylla, ET Eucalyptus tereticornis, AA Acaia auriculaeformis, AM Acaia mangium, CF Castanopsis fissa, SS Schima superba, CH Castanopsis hystrix, MM Michelia macclurei

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Table 3 Nitrogen, P concentration and N.P ratio in different parts of plant (Data are represented as means ± 1 SE, n=4)

total P (TP) and extractable NH₄-N. The lowest C/N ratio (13.0) was found in the N-fixing exotic A. auriculaeformis, associated with the highest value of TN (1.13 g/kg), and the C/N ratio under A. auriculaeformis was less than that under the native C. fissa and M. macclurei (P<0.05, Table 2). Soil extractable NO₃-N concentration in unplanted controls (2.83 mg/kg) was greater than those in planted soils (P < 0.05, Table 2). This pattern was consistent with the trend of NO₃-N concentration in soil solution (Fig. 2d). Moreover, a correlation (r=0.93, P=0.001) was found between soil extractable NO₃-N and soil solution NO₃-N in the last sampling. Acacia auriculaeformis maintained the greatest available P in the soil (1.28 mg/kg), and was greater than those under C. fissa, S. superba and E. urophylla (P < 0.05).

Plant growth and N and P distribution

The concentration of N and P in each type of plant tissue differed among plant species (Table 3). The highest values of root N concentration in N-fixing Acacia species (19.5-21.4 mg/g) were twice as much as those in the native species, and 400 % higher than those in the *Eucalyptus* species (3.88-5.74 mg/g). Eucalyptus had consistently low N concentrations in each plant parts in comparison to other species (P <0.05, Table 3), while the *Acacia* plants had the highest. Compared to exotic species, native species tended to have greater concentrations of P in stem (P=0.001), and leaf (P=0.006), but not in root (P=0.722). The N/ P ratios in all plant parts were greatest in A. auricu*laeformis*, higher than all other species (P < 0.05). The E. urophylla had the smallest N/P in leaves $(7.27 \pm$ 0.36) and roots (12.4 ± 3.86) , while S. superba had the smallest N/P (10.7±2.70) in stems.

The two exotic *Eucalyptus* and two exotic *Acacia* species had much faster growth rates than the four native species, resulting in taller plants (P<0.001, Fig. 3). In December 2006, only 2 months after the initial planting, the height of four exotic species have increased 6–8 cm, while in four native species there were almost no change in height (Fig. 3). The fastest growth rate was measured for *E. tereticornis* and *A. auriculaeformis*, whose heights had increased more than 80 cm in 1 year (Fig. 3). *Castanopsis fissa* had the fastest growth rate among native species, which increased in height by 31.6 cm in 1 year (Fig. 3); for other three native plants, height increase was less than 22.8 cm.

Species	N concentration	t (mg/g)		P concentration (1	mg/g)		N:P		
	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
EU	$9.32^{d}\pm0.14$	$4.98^{cd}\pm0.27$	$5.74^{d}\pm0.42$	$1.30^{cd}\pm0.07$	$0.30^{b}\pm0.04$	$0.62^{ m ab}{\pm}0.20$	7.27 ^c ±0.36	17.7 ^{cd} ±2.85	12.4 ^c ±3.86
ET	$12.3^{cd}\pm1.09$	$3.37^{\rm d}\pm0.22$	$3.88^{\rm d}{\pm}0.16$	$1.23^{\circ}\pm0.06$	$0.25^{\rm b} \pm 0.04$	$0.23^{b}\pm0.01$	$9.99^{b}\pm0.39$	$14.4^{cd} \pm 1.65$	$17.2^{c}\pm1.19$
AA	$22.6^{a}\pm0.68$	$9.15^{a}\pm0.56$	$21.36^{a}\pm0.88$	$1.40^{\circ}\pm0.11$	$0.18^{\mathrm{b}}\pm0.01$	$0.33^{\rm ab}{\pm}0.02$	$16.4^{\rm a}{\pm}0.97$	$50.7^{a}\pm 3.51$	$64.6^{a}\pm4.32$
AM	$21.3^{\mathrm{ab}}\pm0.81$	$7.44^{\mathrm{ab}}\pm0.74$	$19.51^{a}\pm1.41$	$2.39^{\rm ab}{\pm}0.34$	$0.32^{b}\pm0.12$	$0.47^{\mathrm{ab}}\pm0.10$	$9.31^{\mathrm{bc}}\pm0.86$	$29.4^{b}\pm 5.24$	$44.6^{b} \pm 5.52$
CF	$16.7^{\mathrm{bc}}\pm0.99$	$6.47^{\mathrm{bc}}\pm0.62$	$10.23^{bc}\pm0.43$	$1.78^{\mathrm{cd}}\pm0.27$	$0.29^{\rm b}\pm 0.05$	$0.24^{\rm b}\pm0.002$	$9.81^{ m b} \pm 0.84$	24.7 ^{bc} ±4.78	$43.0^{b} \pm 4.62$
SS	$21.0^{ab}\pm1.91$	$7.51^{\rm ab}{\pm}0.29$	$7.60^{cd}\pm0.95$	$2.86^{a}\pm0.20$	$0.86^{a}\pm0.21$	$0.37^{\rm ab}{\pm}0.09$	$7.31^{\circ}\pm0.28$	$10.7^{d}\pm 2.70$	$22.5^{\circ}\pm 2.48$
CH	$17.2^{\rm bc} \pm 1.25$	$7.15^{ab}{\pm}0.36$	$9.25^{\mathrm{bc}}\pm0.89$	$1.78^{\mathrm{cd}}\pm0.20$	$0.44^{\mathrm{ab}}\pm0.17$	$0.26^{\rm b}\pm0.03$	$10.2^{b} \pm 1.58$	$22.4^{bc}\pm5.56$	$37.0^{b} \pm 4.76$
MM	$16.8^{bc}\!\pm\!1.29$	$6.36^{\mathrm{bc}}\pm0.36$	$12.56^{b}\pm1.78$	$2.02^{abc}{\pm}0.13$	$0.55^{\mathrm{ab}}\pm0.05$	$0.70^{\rm a}{\pm}0.07$	$8.31^{\mathrm{bc}}\pm0.30$	$11.8^{\mathrm{cd}}\pm0.66$	$18.7^{c}\pm 3.71$
Ρ	<0.001	<0.001	<0.001	<0.001	<0.01	<0.01	<0.001	<0.001	<0.001
Different 1 Castanons	owercase letters in is fissa SS Schima	dicate significant (L <i>superba</i> , <i>CH</i> Cast	SD, P<0.05) differ anonsis hystrix. MM	ence. EU Eucalyptus 1 Michelia macchurei	t urophylla, ET Euc	alyptus tereticornis,	AA Acaia auriculae	eformis, AM Acaia	mangium, C



Fig. 3 Plant growth rates (plant height increment) at the four sampling times (Data are means +1 SE, n=5)

Plant height is associated positively with plant biomass (r=0.891, P<0.001). There was no significant difference among individual seedlings on height at the beginning of the experiment. Therefore, we assumed that the biomass in the original seedlings were the same among species. The biomass of exotic plants were greater than the native species (P < 0.001, Fig. 4a). Furthermore, total N amount in the two N-fixing species (A. auricu*laeformis*: 3,500 mg/plant and A. mangium: 2,500 mg/ plant) were 200 %-300 % as much as those in the Eucalyptus species and 400 %-500 % of the native species (Fig. 4b). The greatest amount of P was found in A. mangium (150 mg/plant). Exotic species accumulated more than 100 mg P in each plant, and these amounts were 200 %-500 % more than in the native plants (Fig. 4c).

The relationships among growth rate, plant N and P concentrations and soil variables

Plant growth rate was correlated negatively with P concentration in leaves and stems (r=-0.573, P<0.01 and r=-0.484, P<0.01, respectively, Table 4). Plant tissues N concentrations had no significant relationships with plant growth rate. However, the leaf N/P ratio was correlated positively with the growth rate (r=0.417, P<0.05). Furthermore, significantly negative correlations were found between plant growth rate and soil available N variables (DON: r=-0.657, P<0.01; soil solution NO₃-N: r=-0.754, P<0.01; soil NO₃-N: r=-0.416, P<0.05; and soil NH₄-N: r=-0.362, P<0.05), while a positive relationship between soil available P and plant growth rate was found (r=0.442, P<0.05). Using partial correlation analysis with plant growth rate as a controlling factor, soil available P was associated positively with root, stem and leaf N concentration (r= 0.464, r=0.451 and r=0.443, respectively, P<0.01 for root N concentration and P<0.05 for stem and leaf N, Table 4). In addition, no relationship was found between soil extracted N (soil NO₃–N and NH₄–N) and plant N and P traits (Table 4).

Discussion

Plant species effects on soil nutrient availability

Many studies have shown that dissolved organic matters (DOM) play a critical role in a large number of soil processes (McDowell 2003). Recent findings emphasized the turnover of DOC in soil as a major pathway of elements cycling (James and Lungo 2005). In this present study, plant growth enhanced the level of DOC in soil solution. This result was in agreement with many previous studies which have found that plant growth could increase soil DOC (Khalid et al. 2007; Lu et al. 2000; Yano et al. 2005). Plant root exudates, which induced decomposition of soil organic matter and stimulated soil microbial activity, could be responsible for the increased DOC levels in planted soils (Farrar et al. 2003; Grayston et al. 1997; Nardi et al. 2000; Nardi et al. 2002; Toal et al. 2000). Khalid et al. (2007) found that the content of phenolic substances increased in soil solution in the presence of plants. Cheng et al. (2003) found that presence of roots could stimulate microbial activity in the mineralization of soil organic matter, and that further enhance the release of soluble products from soils. In this study, DOC increased even in control pots, likely due to the breakdown of SOC during the study (1.63 % at the beginning to 1.53 % at the end).

In this study, as what we had hypothesized, exotic species always had lower NO₃–N concentration than the native species, which was in accordance with their high growth rates. Because the availability of NO₃–N in soil could be reflected easily in its solution content (Khalid et al. 2007; Yanai et al. 1995), much lower soil NO₃–N level under fast growing exotic species indicates that these species have greater demand of soil N, even among N-fixing *Acacia*. The correlation analysis also showed that soil solution NO₃–N and soil extractable NO₃–N was both associated negatively with plant

Fig. 4 The plant biomass and total N and P amount in different parts of plants. (Data are illustrated as means; Error bars represent 1 SE, n=4). Tree genera are abbreviated as *Eucalyptus* (*E.*), *Acacia (A.)*, *Castanopsis (C.) Michelia (M.)*, *Schima (S.)*



growth. Moreover, although root nodules have been observed in N-fixing species (data not shown), there were no differences in soil NH₄–N or NO₃–N between these N-fixing species and *Eucalyptus* species. This result was consistent with our findings in an early field experiment (Wang et al. 2010a). In that study, we compared soil N availability among several young plantations, and found that the N-fixing *A. crassicarpa* monoculture had low soil N availability as *E. urophylla* monocultures, and were all less than native species plantation. Thus, in the case of exotic *Acacia*

plants, both 'newly' fixed N and 'old' mineralized N have been used to support fast plant growth, while in exotic *Eucalyptus* plants, fast plant growth greatly reduced soil N, both in extractable pools and in soil solution.

Soil solution DON is also regarded as a major mode of N export in terrestrial ecosystems, and plays an important role in determining the balance and accumulation of N (Qualls 2000). Previous studies have shown that compared to NO₃–N, DON also represents a significant "leak" of N in various ecosystems

	Growth Rate	DOC	DON	NH ₄ -N	NO ₃ -N	Available P	Soil NO ₃ –N	Soil NH ₄ –N
Growth Rate	1	0.21	-0.657^{a}	0.03	-0.754^{a}	0.442 ^b	-0.416 ^b	-0.362 ^b
Leaf [N]	-0.23	-0.221	0.086	-0.172	-0.032	0.443 ^b	-0.048	-0.013
Stem [N]	-0.29	-0.112	-0.025	0.085	-0.018	0.451 ^b	-0.001	-0.052
Root [N]	0.06	-0.170	-0.235	0.209	-0.287	0.464 ^a	-0.263	-0.224
Leaf [P]	-0.573^{a}	-0.086	0.273	-0.431	-0.027	0.097	-0.096	0.136
Stem [P]	-0.484^{a}	0.128	0.564	-0.517	0.191	-0.027	-0.052	0.039
Root [P]	-0.19	0.371 ^b	-0.082	0.037	-0.289	0.092	-0.144	0.032
Leaf N/P	0.417 ^b	-0.142	-0.149	0.191	0.025	0.409 ^b	0.057	-0.155
Stem N/P	0.33	-0.225	-0.374^{b}	0.269	-0.178	0.308	0.018	-0.054
Root N/P	0.15	-0.420^{b}	-0.278	0.211	-0.114	0.366 ^b	-0.074	-0.133

Table 4 Pearson correlation and partial correlation coefficients among growth rate, plant N and P concentrations and soil variables

^a Correlation is significant at the 0.01 level (2-tailed). ^b Correlation is significant at the 0.05 level (2-tailed). Growth rate was regarded as a controlling variable in the analysis of relationships between soil variables and plant N and P variables

(Dittman et al. 2007; Finzi and Berthrong 2005; Jones et al. 2004). In the current study, the soil solution DON and NO₃-N were negligible in the fastgrowing exotic species. The results, thus, indicated that the exotic fast growing species could retain N in plant biomass and leach less during heavy rainfall (as typical during the rainy growing season in southern China). Our field observations in young plantations also found that exotic species could increase N retention in biomass and had much lower N leaching loss than native species (Wang et al. 2010a). Nutrient retention is important for afforestation in southern China, where most of plantations were established on degraded land, and the eluviations by heavy rainfall lead to soil depletion (Ren et al. 2007). The results in this study, combined with the results in our field studies (Wang et al. 2010a), manifested that, in afforestation of poor soils with high leaching potential, exotic fast-growing species were better than native species at reducing nutrient loss.

Contrast to our hypothesis, the fast-growing *A. auriculaeformis* had the most soil available P among all treatments. The result was the same as our observation in older plantations in the area (Wang et al. 2010b). In a 23 year old plantation, we found that *A. auriculaeformis* maintained higher soil available P than *A. mangium, Eucalyptus* species, *S. superba* and other native tree species (Wang et al. 2010b). Some plants have been shown to produce low-molecular weight organic acids, which could release phosphate through chelating Fe or Al in soils (Ae et al. 1990). Although the mechanisms through which *A*. *auriculaeformis* improve soil P availability warrant further study, the results of this pot experiment, combined with field observations in older plantations (Wang et al. 2010b), suggested that *A. auriculaeformis* could improve soil P availability in comparison with other species tested. We thus hypothesize that the root of *A. auriculaeformis* could secrete more lowmolecular weight organic acids to improve the soil P availability.

Nutrient Accumulation in Plants

The exotic Eucalyptus always had the least concentration of N in leaves, stems and roots, while the two Nfixing exotics had the greatest values. As a result, the two N-fixing species had more than two times N content in its biomass than non-N-fixing species. However, contrast to our hypothesis, no difference on soil N availability was found between N-fixing species and non-fixing species. This result was in contrast to the observations in 13 year and 23 year old Acacia plantations in this region (Li et al. 2001; Wang et al. 2010b), where the researchers found that N-fixing Acacia plantation contained higher soil N availability than non-N-fixing species. In the old Acacia plantations, the higher litter mass and higher litter N concentrations should be responsible for the higher soil N availability (Li et al. 2001). However, in this one year pot experiment, the litter fall was limited. As aboveground and belowground litter inputs was a major pathway of plant-soil interactions, in a longer time frame, N-fixing Acacia species could contribute positively to soil N availability by their higher N content in aboveground litters and roots (Khanna 1997; Wang et al. 2010a; Wang et al. 2010b).

Phosphorus is often deficient in this region, and is regarded as a key nutrient that constrains productivity in plantations (Liu et al. 2012; Wang et al. 2010a; Xu et al. 2002; Xu et al. 2005). In this study, soil available P was lower than 1.5 mg/kg, and was correlated positively with plant growth rate (r=0.442, P<0.05). We also found that exotic fast-growing species have accumulated two times more P in biomass than native species. Contrary to our hypothesis, fast-growing exotic plants may not cause immediate P depletion. Conversely, the result suggests that faster growth rate may combine with higher soil P supply. Binkley et al. (2000) have found that soil P supply under fastgrowing Eucalyptus saligna was double that under Albizia falcataria, an N-fixing species but with slower growth rate. Furthermore, in our study the plant growth rates were associated negatively with P concentrations in plant leaf and stem; the faster the growth rates, the lower the leaf and stem P concentrations. These results, thus, indicated that fast-growing species had higher soil P supply and P use efficiency to meet their high growth rate. Consequently, fast-growing plants, here the exotics, may have a better capacity to transfer P from soil to plant, and in the long term, through litter decomposition and nutrient mineralization, contribute positively to soil nutrient availability.

Recommendations for management

Selection of plant species plays an important role in afforestation (Eviner and Hawkes 2008; Wang et al. 2010a). The use of exotic species in afforestation, was in great dispute (D'Antonio and Meyerson 2002; Lamb 1998). Thus, evaluation of the pros and cons of exotic species versus native species and selecting some native species to replace exotics is critical to advance plant-soil interactions and to provide better recommendations for management (Wang et al. 2010a).

Our study found that: 1) Exotics, with their fastgrowth rates, could retain more N in plant biomass and minimize leaching loss from the soil; 2) N fixing *Acacia* performed better than *Eucalyptus* in N acquisition, but did not improve soil N availability in the short term; 3) The fast-growing exotics took up more P than natives, but did not lead to P depletion in soils. 4) Planting of *A. auriculaeformis* could improve soil P availability. 5) native species C. fissa had the growth rate comparable to exotic plants. Based on these findings, we recommend that: 1) The use of exotic species versus native species in afforestation should be site dependent, in degraded land with poor soils, exotics are better than natives in nutrient retention. 2) Acacia is better than *Eucalyptus* in improving ecosystem N budget, but in their early stage, N-fixing Acacias are actually good N miners rather than N providers. 3) Planting of A. auriculaeformis is a better choice than other species tested in improving soil P availability. 4) C. fissa is a fast-growing native species, and may potentially replace or supplement fast-growing exotic species in afforestation of southern China. 5) In the future study, the comparison of exotic vs. native species should include taxa with more comparable growth rates (fast-growth vs. slow-growth) or symbiotic associations (N-fixing vs. non-N-fixing), which will not only test more appropriately the original idea but also will encourage the diversification of potential species for afforestation, especially for degraded area with conservation proposes.

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