Resource-use efficiencies of three indigenous tree species planted in resource islands created by shrubs: implications for reforestation of subtropical degraded shrublands

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Abstract Shrub resource islands are characterized by resources accumulated shrubby areas surrounded by relative barren soils. This research aims to determine resource-use efficiency of native trees species planted on shrub resource islands, and to determine how the planted trees may influence the resource islands in degraded shrublands in South China. Shrub (Rhodomyrtus tomentosa) resource islands were left unplanted or were planted with 0.5year-old indigenous tree species Schima superba, Castanopsis fissa, and Michelia macclurei. The results indicate that, after 2.5 years, the tree seedlings did not modify the physical traits (light, air temperature, and soil water) but tended to increase soil nutrients (soil organic carbon and soil nitrogen) and soil microbial biomass of the resource islands. Relative to S. superba and M. macclurei, C. fissa had greater effects on soil nutrients and microbial biomass but showed lower plant growth, survival, and resource-use efficiencies (for water, light, energy, and nitrogen). These results rejected our initial assumption that shrub resource

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islands would effectively promote the growth and resource utility of all the indigenous tree species and shorten the reforestation course in subtropical degraded shrubland. *C. fissa* performed poorly when growing on shrub resource islands, but its role in soil nutrient accumulation might have long-term impacts on the restoration of degraded shrubland. In contrast, *S. superba* and *M. macclurei* could make better use of the shrub resource islands therefore accelerating the construction of native plantations.

Keywords Nurse plant · Resource accumulation · Restoration · *Rhodomyrtus tomentosa*

Introduction

Since the 1990s, studies have shown that the autogenic development of shrub communities results in heterogeneous distribution of soil resources characterized by a mosaic of nutrient-depleted soils surrounding nutrient-rich shrubby regions known as "fertile islands" or "resource islands" (Reynolds et al. 1999; Ravi et al. 2010). Such islands developed because litter deposition and nutrient cycling occur under shrubs but not between shrubs in arid areas (Reynolds et al. 1999; Titus et al. 2002). In addition to the litter deposition beneath the shrubs, decreased light penetration through canopy, buffered fluctuation of daytime air temperatures, as well as the assembled soil microorganisms and soil microofauna contribute to the formation of such

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resource islands (Camargo-Ricalde and Shivcharn 2003; Thomas et al. 2006). Thus, resource islands are accumulations of limited biotic and abiotic resources in shrub-dominated areas that could greatly affect material cycling and energy conversion, especially in nutrient-deficient ecosystems (Camargo-Ricalde and Shivcharn 2003; Thomas et al. 2006).

Many investigations have concentrated on the formation of "resource islands" (Austin et al. 2004; Abril et al. 2009), their physical and chemical traits (Aguiar and Sala 1999; Rossi and Villagra 2003), as well as their ecological implications (Ravi et al. 2010). Related studies have also focused on the functions of microbial communities in the soils of resource islands (Reynolds et al. 1999; Perroni-Ventura et al. 2010) and on the utilization of resource islands in forest restoration (Maestre et al. 2001; Xiong and Han 2006). With respect to forest restoration, researchers have suggested shrubs as a useful tool for restoration in degraded environments and that shrub resource islands could act as preferred sites for the establishment of woody and herbaceous plants (Gasque and García-Fayos 2004; Xiong and Han 2006; Brooker et al. 2008; Blanco-García et al. 2011). To our knowledge, however, few studies have focused on the details of interactions between plant growth and soil resources on resource islands (Ridolfi et al. 2008; Perroni-Ventura et al. 2010). Moreover, the most studies of shrub resource islands have been conducted in deserts, subtropical marshes, temperate and cool temperate prairies, mountains, semi-arid woodlands, alluvial coastal plains, and in farming-pastoral areas (Camargo-Ricalde and Shivcharn 2003; Thomas et al. 2006; Xiong and Han 2006; Espinar et al. 2011), and very few studies have been carried out in areas with a subtropical, humid climate.

Our previous investigations of subtropical degraded hilly lands in Heshan, Guangdong Province, China, show that long-term deforestation can cause the formation of a grass–shrub complex with low biodiversity and ecosystem functions (Ren et al. 2008). As a pioneer shrub species, *Rhodomyrtus tomentosa* naturally covers degraded grassy slopes and transforms the grassy slopes into shrubland. These shrubs always have a cushion-shaped canopy, and the spaces between shrubs are mostly either barren or covered by grass and small shrub species, such as *Ilex asprella*, *Melastoma candidum, Clerodendrum fortunatum*, and *Dicranopteris dichotoma*. Compared with barren land or semi-barren land, the soils under the shrub canopy experience decreased sunlight radiation, increased soil surface moisture, and increased litter deposition. For this reason, the area under the shrubs represents a resource island that could be suitable for tree seedling establishment. Thus, the shrub resource islands on subtropical degraded shrubland have great potential for facilitating the recruitment of indigenous trees and for effective restoration of the degraded forests (Ren et al. 2008).

Our previous research (e.g., Yang et al. 2010) has records on microenvironmental factors and indigenous tree seedlings planted on shrub resource islands. The results indicate that subtropical resource islands differ from resource islands in arid and semi-arid areas. A major effect of shrub resource islands in the arid and semi-arid areas concerns soil nutrients, whereas the main differences on the subtropical shrub resource islands relative to surrounding areas include reduced radiation, increased soil moisture, moderation of soil temperature, altered soil texture, and reduced soil bulk density. Yang et al. (2010) also show that three native tree species (Schima superba, Castanopsis fissa, and Michelia macclurei) survive better and grow better on the shrub resource islands than in areas between the islands. In addition, differences among the tree seedlings in terms of height and basal diameter indicate that they have different resource-use efficiencies (Funk and Vitousek 2007). Moreover, the growth and development of tree seedlings may alter the characteristics of the resource islands and the suitability for forest restoration (Xiong and Han 2006). Thus, research is needed to determine how and why tree species differ in their utilization of resources and growth and in their utility to promote forest restoration on shrub resource islands.

As shrub resource islands accumulate soil resources and compose favorable microenvironment for seedling growth in degraded ecosystems, we hypothesize that such islands would effectively accelerate the growth and resource utility of all the indigenous tree species, thereby accelerate the reforestation course. Specifically, we attempt to answer the following questions: (1) is there any differences in the growth and resource-use efficiencies among the three native tree species (*S. superba*, *C. fissa*, and *M. macclurei*) on shrub resource islands? and (2) how do the tree seedlings change the shrub resource islands which are initially identical prior to seedling transplantation?

Materials and methods

Study site

This study was carried out in a typical subtropical shrubland field, located at the Heshan National Field Research Station of Forest Ecosystems (112°50'E, 22°34'N, Heshan County, Guangdong Province, China). The station is one of the national forest restoration research stations in the Chinese Ecological Research Network (CERN) and the Chinese Academy of Sciences. Due to the long-term deforestation in this area, the regional subtropical monsoon evergreen broad-leaved forests have mostly been replaced by shrubs and grasses. The laterite soil typical of this region has been severely eroded because of the lack of forest coverage. The subtropical monsoon climate is characterized by hot and humid summers, but cool and rainless winters. The annual precipitation ranges from 1,460 to 1,820 mm and mainly occurs as rain during April-August. The mean annual temperature is 21.7 °C, and the mean annual solar radiation measured at the station is $435.47 \text{ kJ cm}^{-2}$.

Plant species and shrub resource island

Rhodomyrtus tomentosa (Ait.) Hassk., which grows widely in tropical and subtropical regions of Asia, is an indicator of acid soil. Mature individuals of this regional dominant shrub have a cushion-shaped canopy and can grow as tall as 2 m (Ren et al. 2010). As shown by previous studies, shrubs with a certain canopy size can support the development of resource islands (Reynolds et al. 1999; Pugnaire et al. 2011). Similarly, compared with adjacent barren lands, R. tomentosa shrubs reduce sunlight radiation to the soil surface, accumulate litter, increase soil moisture, buffer soil temperature, and reduce soil bulk density. Meanwhile, an elevated survival, height and total biomass of the three tree species are observed in seedlings growing in the resource island than in the non-resource island spaces (Yang et al. 2010). Hence, the soil beneath an R. tomentosa individual was defined as a shrub resource island ($\sim 2-4 \text{ m}^2$) in this study.

The three tree species investigated are *Schima* superba Gardn. et Champ., *Castanopsis fissa* (Champ. ex Benth.) Rehd. et. Wils, and *Michelia macclurei* Dandy. All three are indigenous tree species that grow naturally in the subtropical forests in South China.

These species are climax evergreen broad-leaved species that could achieve a height of 20–30 m. They are common in the subtropical regions of China and are frequently planted during the reforestation of degraded land (Ren et al. 2010).

Experimental design

A natural subtropical shrubland field (2 ha) was selected and divided into three blocks according to their relative positions. The shrubland was formed by long-term deforestations and was selected as one of the typical shrubland experimental fields at the Heshan National Field Research Station of Forest Ecosystems since 2005. Within each block, four plots ($5 \times 5 \text{ m}^2$) were randomly selected and designated, and each plot contained one *R. tomentosa* shrub, i.e., one *R. tomentosa* resource island (RI). In each block, one plot was planted with *S. superba* seedlings (RI-S), or *C. fissa* seedlings (RI-C), or *M. macclurei* seedlings (RI-M), respectively, and one plot was not planted with tree seedlings (CS).

Seeds of the three tree species were collected in a village forest near the field site in 2006 and were germinated and grown in a greenhouse for 6 months to avoid chilling damage. According to Castro et al. (2002), who described the handling of tree seedlings and nurse plants for reforestation, the 6-month-old seedlings were bare-root transplanted under the *R. tomentosa* canopies. In April 2007, 50 seedlings of each species with similar size (about 5 cm in height and 1 cm in basal diameter) and vigor were transplanted to each of their designated plots. The plots were not watered or fertilized after transplanting.

By late in 2008, when Yang et al. (2010) made their last observations, tree seedling survival was quite stable. During late 2008–2009 (the end of this study), no additional seedlings died except as a consequence of destructive sampling. In late 2008, two-thirds of the tree seedlings were harvested as part of the previous study. In October 2009, 10 seedlings per plot (the seedlings were 3 years old at the time) were harvested for biomass analysis. Meanwhile, 30 leaves were collected from different trees on each plot for analysis of nutrient contents. Before the final harvest, plant growth and photosynthesis were measured on each plot. Soil physical, chemical, and biological traits of the plots were also analyzed (see details in the following sections). All sampling and measurements were conducted under the shrub canopy on each plot.

Microenvironments

On one sunny day in August 2009, air temperature and photosynthetic active radiation (PAR, μ mol m⁻² s⁻¹) were recorded on each of the plots every 2 h (8:00, 10:00, 12:00, 14:00, 16:00, and 18:00) by temperature and radiation sensors connected to a LI-6400 portable gas exchange analyzer (LI-COR, Biosciences, Lincoln, NE, USA). The mean PAR and mean air temperature were calculated for each treatment.

In September 2009, soil water content (%, g of water per 100 g of soil) was determined from nine mixed soil cores per plot. Soil organic carbon and total soil N (g of organic carbon or N per 100 g of soil) were determined from five mixed soil cores (5 cm diameter and 20 cm deep) per plot. The soil was air dried and passed through a 2-mm sieve for standard analyses (Liu 1996).

Soil microbial community

In September 2009, five mixed soil samples (from 0 to 20 cm depth) were collected from each plot and stored at -20 °C. The soil microbial community was characterized based on analysis of phospholipid fatty acids (PLFAs; see Bossio and Scow 1998). Fatty acid abundance was calculated as relative ng per kg dry soil and analyzed by standard nomenclature (Tunlid et al. 1989). Bacterial PLFAs were considered as the sum of i15:0, a15:0, 15:0, i16:0, 16:1\omega7, i17:0, a17:0, 17:0, cy17:0, and cy19:0, and fungal PLFAs were represented by the content of $18:2\omega 6$ (Bossio and Scow 1998; Wu et al. 2011). Other PLFAs ($16:1\omega$ 9c, 16:0, 17:1 ω 8c, 18:1 ω 9c, and 18:3 ω 3c) together with bacterial and fungal PLFAs were considered as total PLFAs. The ratio of fungal to bacterial PLFAs (F:B) was then calculated to estimate the ratio of fungal to bacterial biomass in soil (Bardgett et al. 1996).

Plant growth parameters

As noted above, the mean plant biomass (sum of above- and below-ground) of ten trees per plot was determined in October 2009. Before harvesting seed-lings, survivals were also recorded. The change in plant growth and biomass over time was expressed as relative growth rate (RGR), which was calculated by the following equation (Poorter 2002):

$$RGR = (\ln M_2 - \ln M_1)/(t_2 - t_1),$$

where M_1 and M_2 are the dry mass of the plants at time t_1 (April 2007) and t_2 (October 2009). The data for April 2007 were obtained from Yang et al. (2010). Thirty leaves were gathered from the tree species on each plot. Leaf areas were measured using the LI-3000 Potable Area Meter (LI-COR, Biosciences). The leaves were then oven-dried at 60 °C for 48 h to obtain the leaf dry weight. Leaf specific area (SLA) was calculated as the ratio of leaf areas and leaf dry weights for each species. Subsequently, the same leaf samples were wet digested for leaf carbon and nitrogen measurements by ICP plasma emission spectroscopy (Optima 2000, Perkin Elmer, USA).

Plant resource-use efficiencies

All measurements described in this section were performed on a sunny day in September 2009. The maximum photosynthetic rate (A) was determined with A-PPFD curves, based on the measurement of 3-5 leaves (to obtain one mean value) from different seedlings of each tree species on each plot. Only the healthy leaves were selected and the measurements were made nondestructively by a LI-6400 potable gas exchanges analyzer (LI-COR, Biosciences) (Funk and Vitousek 2007). Instantaneous light use efficiency (ILUE) was calculated as A/PPFD (Lin et al. 2007). Instantaneous water-use efficiency (IWUE) was calculated as A/T (µmol CO₂ m⁻² s⁻¹/µmol H₂O $m^{-2} s^{-1}$) (Xu and Hsiao 2004). Photosynthetic N-use efficiency (PNUE) was calculated as A \times SLA/leaf N (μ mol CO₂ g⁻¹ N s⁻¹) (Pons and Westbeek 2004). Photosynthetic energy-use efficiency (PEUE) was equal to A \times SLA/leaf C (µmol CO₂ g⁻¹ C s⁻¹) (Schoenfelder et al. 2010). The actual photochemical efficiency of PSII (Φ_{PSII}) in light was measured on 3–5 leaves (to obtain one mean value) of each tree species on each plot at 2-h intervals with a PAM-2100 portable pulse-modulated fluorometer (Walz, Germany).

Statistical analysis

We performed one-way analysis of variance (ANO-VAs) to compare microenvironment variables and soil PLFAs among the four treatments (CS, RI-S, RI-C, and RI-M), and to compare seedling biomass and resource-use efficiencies among the three kinds of plots planted with different tree species (RI-S, RI-C, and RI-M). Tukey's test was used for post hoc multiple comparisons. All statistical analyses were carried out by SPSS 13.0 (SPSS, Inc., Chicago, USA). Differences were considered significant at the 0.05 level.

Results

Microenvironmental variables

The mean daily PAR and air temperature under the shrub canopy did not significantly differ among the treatments (Table 1). Also, soil moisture did not differ between plots with tree seedlings (RI-S, RI-C, and RI-M) vs. those without tree seedlings (CS). Soil organic carbon and total soil N were much higher in RI-C than in CS (P < 0.05) but did not differ between RI-S and RI-M vs. CS (Table 1).

Soil microbial community

Total PLFAs, bacterial PLFAs, and fungal PLFAs in soil were significantly higher in RI-C than in the other treatments (P < 0.05; Table 2). PLFAs tended to be

more abundant on RI-S plots than on CS or RI-M plots, but the difference was not significant. Ratios of fungal to bacterial PLFAs did not differ among treatments.

Tree seedling survival and growth

Schima superba seedlings were much taller and had much greater basal diameters than the other two tree species, and the final dry mass per seedling was 8–12 times higher for *S. superba* than for *C. fissa* and *M. macclurei* (Fig. 1a). Data also showed that the survival of *C. fissa* seedling was much lower (P < 0.05, Fig. 1b) than that of *S. superba* and *M. macclurei* seedlings. Based on plant biomass, the calculated relative growth potential (RGR) was significantly lower for *C. fissa* seedlings than for the other two species (P < 0.05; Fig. 1c).

Plant instantaneous resource-use efficiencies

IWUE and ILUE values were lower for *C. fissa* than for *S. superba* and *M. macclurei* (P < 0.05; Fig. 1d, e) but did not differ between *S. superba* and *M. macclurei*. PNUE and PEUE values were highest for *S. superba*, intermediate for *M. macclurei*, and

Table 1 Microclimate and soil physical and chemical properties on the shrub resource island plots without tree seedlings (CS) or with *Schima superba* (RI-S), *Castanopsis fissa* (RI-C), or *Michelia macclurei* (RI-M) seedlings

Treatment	Microclimate and soil properties						
	PAR (μ mol m ⁻² s ⁻¹)	Air temperature (°C)	Soil water content (%)	Soil organic carbon (%)	Total soil N (%)		
CS	206.2 ± 69.2 a	35.8 ± 2.6 a	17.3 ± 1.1 a	$0.97\pm0.20~\mathrm{b}$	$0.070 \pm 0.018 \text{ b}$		
RI-S	367.5 ± 164.3 a	37.8 ± 3.1 a	17.9 ± 1.0 a	1.43 ± 0.21 ab	$0.132\pm0.027a$		
RI-C	275.8 ± 74.7 a	37.2 ± 2.5 a	18.8 ± 3.7 a	1.54 ± 0.49 a	0.117 ± 0.020 a		
RI-M	244.0 ± 77.2 a	$38.4 \pm 3.2 \text{ a}$	18.8 ± 2.7 a	0.98 ± 0.32 ab	$0.097\pm0.020~ab$		

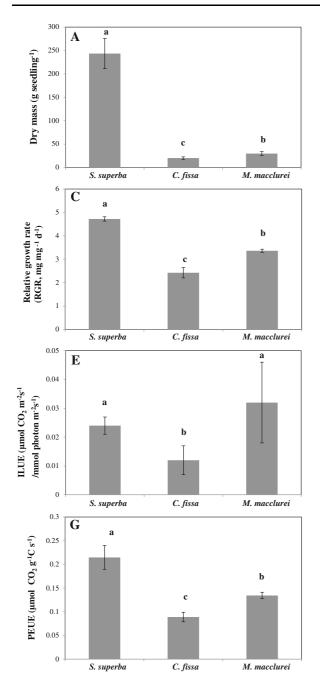
Values are mean \pm SD. Within each column, mean with different letters are significantly different at P < 0.05

Table 2 Soil phospholipid fatty acids (ng kg⁻¹ dry soil) on the shrub resource island plots without tree seedlings (CS) or with *Schima superba* (RI-S), *Castanopsis fissa* (RI-C), or *Michelia macclurei* (RI-M) seedlings

Treatment	Soil phospholipid fatty acids (PLFAs)				
	Total PLFAs	Bacterial PLFAs	Fungal PLFAs	Fungal:bacterial PLFAs	
CS	$5.92\pm1.82~\mathrm{b}$	1.32 ± 0.42 b	$0.41\pm0.12~\mathrm{b}$	0.31 ± 0.02 a	
RI-S	$7.41 \pm 3.10 \text{ b}$	$1.62\pm0.72~\mathrm{b}$	$0.54\pm0.21~\mathrm{b}$	0.34 ± 0.02 a	
RI-C	14.19 ± 0.38 a	3.08 ± 0.18 a	1.13 ± 0.10 a	0.37 ± 0.05 a	
RI-M	$5.96\pm0.57~\mathrm{b}$	1.28 ± 0.24 b	0.44 ± 0.06 b	0.35 ± 0.10 a	

Values are mean \pm SD. Within each column, mean with different letters are significantly different at P < 0.05

a



80 70 Survivorship (%) h 60 50 40 30 20 10 0 S. superba C. fissa M. macclurei 4 D a IWUE (µmol CO₂ m⁻² s⁻¹/ 3.5 3 $\mu mol \ H_2O \ m^{-2}s^{-1})$ 2.5 2 a 1.5 1 0.5 0 S. superba C. fissa M. macclurei 10 F a PNUE (µmol CO₂ g⁻¹ N s⁻¹) 8 b 6 4 с 2 0 S. superba C. fissa M. macclurei 0.7 H =S. superba -C. fissa -M. macclurei 0.6 0.5 $\Phi_{\rm PSII}$ 0.4 0.3 0.2 0.1 0 8:00 10:00 12:00 14:00 16:00 18:00 Time

90

B

a

Fig. 1 The biomass, survivorship, growth rates, and resourceuse efficiencies of S. superba, C. fissa, and M. macclurei seedlings growing on shrub resource islands. a Dry mass; b survivorship; c RGR; d IWUE; e ILUE; f PNUE; g PEUE; and

lowest for C. fissa (P < 0.05; Fig. 1f, g). Φ_{PSII} values were higher at 8:00 and 18:00 than at the other times for all three species (P < 0.05; Fig. 1h).

 \boldsymbol{h} diurnal Φ_{PSII} (actual photochemical efficiency of photosystem II). Values are mean \pm SD. Within **a**-**g**, mean with different letters are significantly different at P < 0.05

The figure also showed that Φ_{PSII} values were lower for C. fissa than for the other two species during most of the day.

Discussion

Shrub resource islands have mostly been investigated in arid and semi-arid ecosystems (Ravi et al. 2010). Our previous findings show that resource islands on subtropical degraded shrubland are more defined by reduced solar radiation beneath the canopy, reduced soil temperature extremes, increased soil moisture, and reduced soil bulk density than by increased soil nutrition (Ren et al. 2008; Yang et al. 2010). This study reveals that the 3-year-old tree seedlings do not significantly alter the physical characteristics of their growing microenvironment but could effectively accumulate soil nutrients and increase soil microbial biomass of the shrub resource islands. However, the growth status and instantaneous resource-use efficiency are different among three tested tree species performed differently when growing on shrub resource islands. Overall, our study rejected our initial assumption that all the indigenous tree species could effectively use the resource provided by resource island and hence show a similar potential to reduce restoration time course of subtropical degraded shrublands.

Responses of tree seedlings to shrub resource islands

Plant RGR refers to the rate of increase in biomass per unit plant mass already present (Poorter 2002). In a relatively stress-free habitat with a high supply of nutrients and a low intensity of competition, a plant may achieve its maximum RGR (Grime 2001). Thus, RGR is widely used to compare plant growth potential among different species under the same growing conditions. In our study, all three tree species are of comparable size when transplanted into the shrub resource islands (Yang et al. 2010), and RGR is therefore closely related to tree biomass at the end of study. After growing on shrub resource islands for 2.5 years, RGR and dry mass per seedling are highest for S. superba, intermediate for M. macclurei, and lowest for C. fissa. Because the differences in growth could not be explained by differences in microclimate (the shrub R. tomentosa provides similar microenvironment conditions for all three tree species), resource-use efficiencies are compared. Some plants (such as invasive species) outperform others by acquiring limited resources or by using resources more efficiently (Funk and Vitousek 2007; Schoenfelder et al. 2010). Our results show that C. fissa has significantly lower short-term resource-use efficiencies (IWUE, ILUE, PNUE, PEUE, and diurnal Φ_{PSII}) than the other two tree species. Photosynthetic resource-use efficiency can account for biomass accumulation in the canopy and affect population and community dynamics (Huxman et al. 2008). We suspect that the lower resource-use efficiencies of C. fissa may lead to its low growth rate and thus low biomass accumulation after growing for 2.5 years on the shrub resource islands. The lower growth rate and final biomass inhibit this species from helping the transition from shrub-grass communities to regional forest in a short term. However, this species is capable in accumulating soil nutrients on the resources island which may probably benefit to the restoration of the degraded forest at the ecosystem level over a long term. S. superba, in contrast, has much higher use efficiencies for water, light, nitrogen, and carbon, Moreover, our observations indicate that, after 2.5 years, the S. superba trees already grow as tall as the R. tomentosa shrubs and form a crown-like canopy comprised a certain canopy size. Researchers have previously proposed that a high growth rate, a crownshaped canopy, together with high resource-use efficiencies may enable a species to form mono-specific stands (Funk and Vitousek 2007). Our results therefore suggest that, among the tested tree species, S. superba is the most suitable for enhancing forest restoration (a shift from shrub-grass to regional forest communities) in subtropical degraded ecosystems.

As the native tree seedlings grow, they will undoubtedly change the resource islands. The changes will be accompanied by alternations in the soil microbial community. The increased N content of soil planted with *C. fissa* can be explained by symbiotic N fixation (this tree has symbiont), and the increased N content of soil probably explains the increased biomasses of bacteria and fungi, as indicated by increased quantities of bacterial and fungal PLFAs (Wu et al. 2011).

Implications of this research for reforestation

This study has shown that, after growing on subtropical shrub resource islands for 2.5 years, native tree seedlings have modified soil organic carbon, soil N, and soil microbial biomass. The three species all tend to enhance these variables but the degree of increase are clearly species dependent. As the trees continue to grow and mature, it is likely that they will continue to change the nature of the resource islands. This is especially evident with *S. superba*, which, after 2.5 years, has already grown taller than the shrub *R. tomentosa* and is likely to compete with the shrubs for light and other resources. Continued growth of the tree seedlings should convert the shrub resource island into a patch of native forest. Determining how the patches might be expanded and diversified, however, will require additional research in the future.

In general, shrub resource islands provide a benign microenvironment for seedling growth. However, such generally favorable condition does not support the growth of all the indigenous tree species that are being considered for reforestation of subtropical shrubland. In our study, C. fissa modified the nutrient levels of the resource islands but had less biomass accumulation and lower resource-use efficiencies. We therefore believe that C. fissa may have an indirect function in reforestation by increasing soil C and N early in restoration in a long range. It is worthwhile to point out that C. fissa might be used for the first 1-2 years to improve soil conditions before being manually replaced by other native tree species and by S. superba in particular. In contrast to C. fissa, S. superba grows rapidly and has higher PNUE and PEUE. M. macclurei is also a promising plant species in forest restoration due to higher survival, as well as higher water and light use efficiencies which is comparable to S. superba. Our findings based on the analyses of resource-use efficiency, RGR and biomass of three tree species growing on the shrub resource islands are consistent with those of Yang et al. (2010), who suggest that S. superba and M. macclurei are more suitable than C. fissa for forest restoration (via shrub resource islands) in subtropical regions in China.

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References

- Abril A, Villagra P, Noe L (2009) Spatiotemporal heterogeneity of soil fertility in Central Monte desert (Argentina). J Arid Environ 73:901–906
- Aguiar MR, Sala O (1999) Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends Ecol Evol 14:273–277
- Austin A, Yahdjian L, Stark J, Belnap J, Porporato A, Norton U, Ravetta D, Schaeffer S (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221–235
- Bardgett RD, Hobbs PJ, Frostegård Å (1996) Changes in soil fungal:bacterial biomass ratios following reductions in the intensity of management of an upland grassland. Biol Fertil Soils 22:261–264
- Blanco-García A, Sáenz-Romero C, Martorell C, Alvarado-Sosa P, Lindig-Cisneros R (2011) Nurse-plant and mulching effects on three conifer species in a Mexican temperate forest. Ecol Eng 37:994–998
- Bossio DA, Scow KM (1998) Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. Microb Ecol 35:265–278
- Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, Tielborger K, Travis JMJ, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Forey E, Kikvidze Z, Olofsson J, Pugnaire F, Quiroz CL, Saccone P, Schiffers K, Seifan M, Touzard B, Michalet R (2008) Facilitation in plant communities: the past, the present, and the future. J Ecol 96:18–34
- Camargo-Ricalde SL, Shivcharn D (2003) Endemic Mimosa species can serve as mycorrhizal "resource islands" within semiarid communities of the Tehuacán-Cuicatlán Valley, Mexico. Mycorrhiza 13:129–136
- Castro J, Zamora R, Hódar J, Gómez J (2002) Use of shrubs as nurse plant: a new technique for reforestation in Mediterranean mountains. Restor Ecol 2:297–305
- Espinar JL, Ross MS, Sah JP (2011) Pattern of nutrient availability and plant community assemblage in Everglades Tree Islands, Florida, USA. Hydrobiologia 667:89–99
- Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079–1081
- Gasque M, García-Fayos P (2004) Interaction between *Stipa tenacissima* and *Pinus halepensis*: consequences for reforestation and the dynamics of grass steppes in semiarid Mediterranean areas. For Ecol Manag 189:251–261
- Grime JP (2001) Plant strategies: vegetation processes and ecosystem properties. Wiley, Chichester
- Huxman TE, Barron-Gafford G, Gerst KL, Angert AL, Tyler AP, Venable DL (2008) Photosynthetic resource-use efficiency and demographic variability in desert winter annual plants. Ecology 89:1554–1563
- Lin ZF, Wu T, Kong GH, Lin GZ, Xie ZH, Jian SG (2007) Photosynthesis and water relations in eight urban landscape climbing plants. J Trop Subtrop Bot 15:473–481
- Liu GS (1996) Soil physical and chemical analysis and description of soil profiles. Standards Press of China, Beijing

- Maestre FT, Bautista S, Cortina J, Bellot J (2001) Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. Ecol Appl 11:1641–1655
- Perroni-Ventura Y, Montaña C, García-Oliva F (2010) Carbonnitrogen interactions in fertility island soil from a tropical semi-arid ecosystem. Funct Ecol 24:233–242
- Pons TL, Westbeek MHK (2004) Analysis of differences in photosynthetic nitrogen-use efficiency between four contrasting species. Physiol Plant 122:68–78
- Poorter H (2002) Plant growth and carbon economy. In: Encyclopedia of life sciences. Macmillan Publisher, Nature publishing group, London, pp 1–6
- Pugnaire FI, Armas C, Maestre FT (2011) Positive plant interactions in the Iberian Southeast: mechanism, environmental gradients, and ecosystem function. J Arid Environ 75:1310–1320
- Ravi S, D'Odorico P, Huxman TE, Collins SL (2010) Interactions between soil erosion processes and fires: implications for the dynamics of fertility islands. Rangel Ecol Manag 63:267–274
- Ren H, Yang L, Liu N (2008) Nurse plant theory and its application in ecological restoration in lower subtropics of China. Prog Nat Sci 18:137–142
- Ren H, Cai XA, Li CH, Ye YS (2010) Atlas on tool species of vegetation recovery in South China. Huazhong University of Science & Technology Press, Wuhan
- Reynolds JF, Virginia RA, Kemp PR, de Soyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecol Monogr 69:69–106
- Ridolfi L, Laio F, D'Odorico P (2008) Fertility island formation and evolution in dryland ecosystems. Ecol Soc 13:5

- Rossi BE, Villagra PE (2003) Effects of *Prosopis flexuosa* on soil properties and the spatial pattern of understory species in arid Argentina. J Veg Sci 14:543–550
- Schoenfelder AC, Bishop JG, Martinson HM, Fagan WF (2010) Resource use efficiency and community effects of invasive *Hypochaeris radicata* (Asteraceae) during primary succession. Am J Bot 97:1772–1779
- Thomas LT, Eli Z, Pang HC, Thomas BW, Dean AM (2006) Soil C and N pools in patchy shrublands of the Negev and Chihuahuan deserts. Soil Biol Biochem 38:1943–1955
- Titus JH, Nowak RS, Smith SD (2002) Soil resource heterogeneity in the Mojave Desert. J Arid Environ 52:269–292
- Tunlid A, Hoitink HAJ, Low C, White DC (1989) Characterization of bacteria that suppress rhizoctonia damping-off in bark compost media by analysis of fatty-acid biomarkers. Appl Environ Microbiol 55:1368–1374
- Wu JP, Liu ZF, Wang XL, Sun YX, Zhou LX, Lin YB, Fu SL (2011) Effects of understory removal and tree girdling on soil microbial community composition and litter decomposition in two Eucalyptus plantations in South China. Funct Ecol 25:921–931
- Xiong XG, Han XG (2006) Resource islands and its roles in the thicketization of grasslands and thicketization-grasslands. Acta Pratacul Sin 15:9–14
- Xu LK, Hsiao TC (2004) Predicted versus measured photosynthetic water-use efficiency of crop stands under dynamically changing field environments. J Exp Bot 55:2395–2411
- Yang L, Ren H, Liu N, Wang J (2010) The shrub *Rhodomyrtus tomentosa* acts as a nurse plant for seedlings differing in shade tolerance in degraded land of South China. J Veg Sci 21:262–272