

RESEARCH ARTICLE

Testing the Stress-Gradient Hypothesis During the Restoration of Tropical Degraded Land Using the Shrub *Rhodomirtus tomentosa* as a Nurse Plant

Nan Liu,¹ Hai Ren,^{1,2} Sufen Yuan,¹ Qinfeng Guo,³ and Long Yang⁴

Abstract

The relative importance of facilitation and competition between pairwise plants across abiotic stress gradients as predicted by the stress-gradient hypothesis has been confirmed in arid and temperate ecosystems, but the hypothesis has rarely been tested in tropical systems, particularly across nutrient gradients. The current research examines the interactions between a pioneer shrub *Rhodomirtus tomentosa* (the nurse plant) and seedlings of a transplanted native woody *Schima superba* (the target species) in a tropical system in which position on a slope corresponds with a nutrient gradient; high soil nutrients at the slope bottom and relatively low soil nutrients at the slope top. In contrast, soil physical traits were more favorable for seedling growth under the shrub than in open spaces. The effect of

R. tomentosa on *S. superba* survival was positive (facilitation) at the top of the slope, as indicated by the relative interaction index (RII), but negative in the bottom (competition). RII indicated a positive effect on seedling height at the top of the slope but was not at the bottom. Seedling survival was positively related to soil nutrient level and negatively related to soil acidity, but seedling growth of *S. superba* seemed to be enhanced by the shrub canopy. Thus, the results seem to support stress-gradient hypothesis in terms of target species survival but not growth. We suggest using the shrub as a nurse plant in forest restoration in tropical degraded land with caution because not all of its effects on target species are positive.

Key words: abiotic stress, facilitation, plant–plant interaction, reforestation, woody plants.

Introduction

Plant community structure and dynamics are greatly affected by the biotic interplay among neighboring plants, interactions that can be negative if competitive in nature or more positive if facilitative (Maltez-Mouro et al. 2010). The relative strength of these two opposing processes is determined by multiple factors including the degree of abiotic stress (Maestre & Cortina 2004), the ontogenesis of the plants (Forrester et al. 2011), and the ecological characteristics of the interacting species (Maltez-Mouro et al. 2010). In the past two decades, the interactive effects of facilitation and competition among plants and the relationship to abiotic stresses has become a major topic in community ecology (Brooker et al. 2008). One of the most influential models of plant interactions is the “stress-gradient hypothesis” (Bertness & Callaway 1994), which predicts that facilitation is more common under conditions of

high abiotic stress while competition is more common under benign environmental conditions.

Although, the stress-gradient hypothesis has received substantial support in arid environments (Maestre et al. 2005, 2009), its strength may vary with stage of community development (Tielbörger & Kadmon 2000; Holzapfel et al. 2006). For example, facilitation may decrease with extreme stress (Michalet et al. 2006), and the relative dominance of either competition or facilitation may depend on the traits of tested species (Choler et al. 2001), the nature of the stress gradient (Kawai & Tokeshi 2007), and how the plant performance is measured (Maestre et al. 2005). Thus, to effectively apply this hypothesis to specific restoration situations, more research is needed to refine the stress-gradient hypothesis so that it provides more accurate predictions of plant interactions along stress gradients (Maestre et al. 2009). Additionally, most previous studies on the stress-gradient hypothesis have been conducted in deserts (López et al. 2007; Pugnaire et al. 2011), Mediterranean mountains (Maestre et al. 2003), alpine ecotone (Cavieres et al. 2006), subtropical forests (Li et al. 2010), coastal wetland (Egerova et al. 2003) and temperate forest (Blanco-García et al. 2011), but rarely in tropical systems (Bonanomi et al. 2011; Lin et al. 2012). As a result, it is not clear whether findings from different ecosystem types will be useful for understanding and predicting the outcomes of

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

²Address correspondence to H. Ren, email renhai@scbg.ac.cn

³USDA FS – Eastern Forest Environmental Threat Assessment Center, 200 WT Weaver Boulevard, Asheville, NC 28804, U.S.A.

⁴Guangzhou Institute of Geography, Guangzhou, 510070, China

plant interactions along stress gradients in tropical ecosystems including those with degraded land.

Because their crown-shaped canopies and deep roots moderate the environment and increase soil resources (Goergen & Chambers 2012), forb and shrub species have been considered nurse plants with the potential of facilitating other species (Abella et al. 2011; Pugnaire et al. 2011). In an initial effort to evaluate the restoration potential of shrub species (Yang et al. 2010), we found in a relatively mild region in the subtropical region of China that the evergreen shrub, *Rhodomyrtus tomentosa*, acts as a pioneer woody species that can facilitate the establishment of *Schima superba*, which is a desired tree. The seedlings of *S. superba*, grew more rapidly under the canopy of *R. tomentosa* than they did when in the open. When the *S. superba* seedlings reached the height of *R. tomentosa*, the growth of the shrub species was negatively affected, suggesting that this interaction might promote forest succession and restoration in subtropical degraded ecosystems. However, it is unclear whether shrub *R. tomentosa* can facilitate *S. superba* under more extreme environmental conditions than those in the initial study.

In this study, our general goal was to increase our understanding of how *R. tomentosa* can be used as a nurse plant for the target plant *S. superba* in the context of restoration in a tropical degraded land. Moreover, we examine how the interactions between the *R. tomentosa* and *S. superba* are affected by nutritional gradient. Natural differences in soil nutrition were used to create this gradient; low soil nutrients were found at the top of a natural slope and high soil nutrients at the bottom of the same slope. The specific objective was to determine whether the interactions between *R. tomentosa* and *S. superba* are consistent with the stress-gradient hypothesis. Specifically, we attempt to answer the following questions: (1) How do *R. tomentosa* and soil nutrient conditions affect the growing conditions of the target species *S. superba* in tropical degraded ecosystem? (2) Are these interactions consistent with the stress-gradient hypothesis?

Methods

Research Area and Plant Species

We conducted this study at the Xiaoliang Tropical Forest Long-Term Ecosystem Research Station (Xiaoliang station) in Dianbai County, Guangdong, China (110°54'18", 21°27'49"). The regional climate is tropical monsoon with an average annual temperature of 23°C and an average annual precipitation between 1,400 and 1,700 mm. The region has distinct wet (April–October) and dry seasons (November–March) (Yu & Pi 1985). The original regional climax vegetation is tropical monsoon rain forest but this community was eliminated by complete deforestation. Derived from granite, the laterite soil is typically acidic, and has low water-holding and nutrient-holding capacities. The environmental condition of the degraded land is generally too harsh for woody plant establishment.

Rhodomyrtus tomentosa (Ait.) Hassk. (Myrtaceae) is an evergreen shrub that grows naturally on acidic soil as a pioneer species in most tropical and subtropical regions in Asia (Ren et al. 2010). Our observations indicate that the mature shrubs intercept sunlight radiation and improve soil moisture. As a consequence, the species could be considered a nurse plant. *Schima superba* Gardn. et Champ (Theaceae) is an evergreen broadleaved tree species commonly used for reforestation in tropical and subtropical regions of China.

Experimental Design

The experiment was set up in the bare land catchment of Xiaoliang Station. The area is barren—soil has been eroding for more than 100 years, total plant cover was greater than 5%, with no sign of natural vegetation recovery (Ren et al. 2007). When this experiment was initiated, scattered individuals of the xeric shrub (*R. tomentosa*) and a few small grasses species (e.g. *Eriachne pallescens* and *Dicranopteris dichotoma*) provided the only vegetation. *R. tomentosa* is a dominant pioneer plant species in these tropical degraded settings. Observations prior to the experiment suggest that the redistribution of soil nutrient along slopes by water creates a stress gradient, which was subsequently verified by soil chemical analysis. The physical effects of this gradient, based on the productivity serving as a good proxy for abiotic stress (Ren et al. 2007; Soliveres et al. 2010), supported the presence of a nutrient gradient as low vegetation coverage dominated at the top of the slope and relatively high coverage at the bottom.

The 3.7-ha experimental catchment was divided into a top block and a bottom block according to their positions on the slope. Six plots (5 × 5 m) were randomly assigned to each block, and within each plot three randomly selected 2 × 2 m subplots were assigned the “canopy” treatment and three were assigned the “open” treatment. Canopy subplots were located under the circular edges of the *R. tomentosa* canopies (from 1.0 m to 1.8 m in height) and open subplots were located without woody plant coverage. *S. superba* seedlings of similar size and vigor (about 6 months old, 17–22 cm tall) were purchased from the Guangdong Academy of Forestry. On 4 April 2010, 15–20 *S. superba* seedlings were transplanted into all subplots in both the top and bottom blocks, with 30–50 cm between individual seedlings. On 20 April 2010, we counted the number of live seedlings in each subplot. Those that died during this period were assumed to have failed to survive transplanting and were excluded from the experiment.

Soil Physical and Chemical Properties

Before the experiment, samples for soil chemical analyses were obtained from five soil cores (5 cm diameter and 20 cm deep) collected at random within each subplot and combined to form one sample. Air-dried soil samples were passed through a 2-mm sieve and analyzed for pH, total soil nitrogen (N), total soil phosphorus (P), soil organic carbon (C), and soil exchangeable potassium (K). Soil physical characteristics were assessed from soil samples gathered using ring knives from

five intact soil cores at random locations within each subplot. Soil bulk density and soil moisture content were determined by weighing the intact soil cores before and after oven-drying at 105°C. Soil chemical and physical analyses followed standard methods (Liu 1996).

Survival, Growth, and Photosynthesis of Target Species

The survivorship, height, and basal diameter of all *S. superba* seedlings were measured ten times over one year (20 April, 24 May, 18 June, 23 July, 11 August, 25 September, 20 October, and 20 November of 2010, and on 18 January and 22 April of 2011). The relative interaction index (RII) was used as a measure of interaction intensity because it indicates the effect of one plant (the nurse plant *R. tomentosa* in this case) on another (*S. superba* in this case) without consideration of the abiotic environment (Schiffers & Tielbörger 2006). RII was calculated on the basis of *S. superba* survivorship, basal diameter, and shoot height at the end of the 1-year experiment; RII > 0 indicates a positive effect (facilitation) on the target species, and RII < 0 indicates a negative effect (competition) on the target species (Armas et al. 2004). RII was calculated as:

$$RII = \frac{(X_{+N} - X_{-N})}{(X_{+N} + X_{-N})};$$

where X_{+N} is the survivorship, basal diameter or shoot height of *S. superba* in canopy subplots (growing with a neighboring plant), and X_{-N} is the survivorship, basal diameter or shoot height of *S. superba* in open subplots (growing without a neighboring plant). RII was calculated for *S. superba* growing in both top and bottom block separately.

A gas exchange analyzer LI-6400 (LI-COR, Biosciences, Lincoln, NE, U.S.A.) was used to measure leaf photosynthesis of four to five representative *S. superba* seedlings in each subplot. Only healthy and fully developed leaves were selected and the measurements were conducted at ambient light and temperature conditions using a transparent leaf chamber. The orientation of each leaf in the chamber was consistent with its original orientation to maintain its natural growing position. The diurnal changes in photosynthetic rate and stomatal

conductance were measured at 2-h intervals from 8:00 to 18:00 on a sunny day in September 2010.

Data Analysis

Two-way analysis of variances (ANOVAs) were used to test the relationship of position on the slope (top or bottom block), shrub canopy (canopy or open subplots), and their interactions to: soil physical and chemical characteristics before the experiment started; mean diurnal photosynthetic rate and stomatal conductance during the experiment; and target plant seedling survival and allometric growth at the end of the experiment. All statistical analyses were performed with SPSS 13.0 (SPSS, Inc., Chicago, IL, U.S.A.). Although position on slope was not replicated, as there was only one block in each location, the two blocks are representative of conditions at the two extremes of a gradient; as a result, we have used the plots as statistical replicates of the top and bottom blocks.

Results

Most soil chemical characteristics were significantly affected ($p < 0.05$) by position on slope (top vs. bottom block), and most soil physical characteristics were significantly affected by shrub canopy (canopy subplots vs. open subplots). However, the interactions between slope position and canopy were not significant ($p > 0.1$) for either soil physical or chemical variables. Soil N, P, and organic C were higher at the bottom of the slope than at the top (Table 1). Soil moisture content was much higher in subplots under the canopy of *Rhodomyrtus tomentosa* than in open subplots, whereas soil bulk density and pH were lower under the canopy than in the open. Soil exchangeable K was not affected by position on slope or shrub canopy (Table 1).

In all treatments, survival of *Schima superba* declined at the beginning of the growing season and then remained relatively constant at more than 30% (Fig. 1a). The presence of *R. tomentosa* canopy increased the survival and vigor of *S. superba* seedlings at the top of the slope, where the soil nutrient levels were lower (height 1.3 times higher in canopy

Table 1. Soil physical and chemical characteristics (mean \pm SD) in the open subplots (OS, without woody plant coverage) and canopy subplots (CS, beneath the canopy of the shrub *Rhodomyrtus tomentosa*) in the top block and bottom block on a slope.

Variables	Top block		Bottom block		p values	
	OS	CS	OS	CS	Slope	Canopy
Soil pH	3.92 \pm 0.06	3.80 \pm 0.14	3.95 \pm 0.08	3.79 \pm 0.07	0.620	0.044
SMC	3.88 \pm 0.98	6.58 \pm 2.12	5.40 \pm 1.46	11.14 \pm 4.90	0.080	0.019
SBD	1.28 \pm 0.02	1.10 \pm 0.21	1.42 \pm 0.08	1.09 \pm 0.15	0.344	0.002
SOC	0.30 \pm 0.14	0.40 \pm 0.17	0.68 \pm 0.19	1.13 \pm 0.32	0.011	0.120
TN	0.024 \pm 0.006	0.028 \pm 0.013	0.049 \pm 0.018	0.080 \pm 0.021	0.013	0.169
TP	5.66 \pm 0.74	7.59 \pm 2.19	9.02 \pm 1.82	10.14 \pm 1.28	0.026	0.377
TK	0.077 \pm 0.017	0.077 \pm 0.030	0.086 \pm 0.028	0.096 \pm 0.025	0.186	0.699

SMC, soil moisture content (%); SBD, soil bulk density (g cm^{-3}); SOC, soil organic carbon (%); TN, total soil nitrogen (%); TP, total soil phosphorus (mg kg^{-1}); TK, total exchangeable potassium (%).

The p values were based on the two-way ANOVAs that examined the effects of slope (top vs. bottom block) and canopy (OS vs. CS). Bold-face values indicated significant effects ($p < 0.05$).

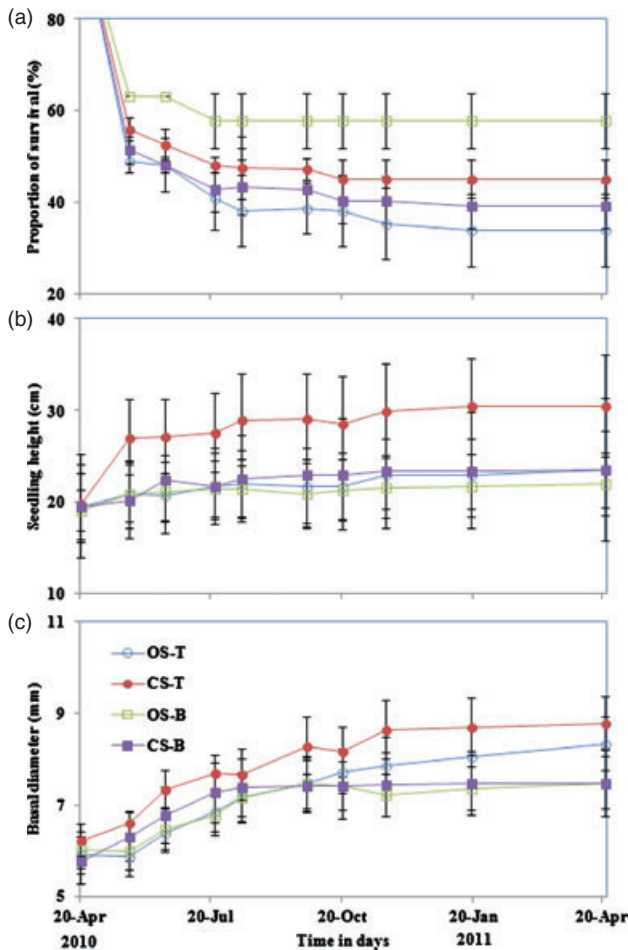


Figure 1. Survivorship (a), height (b), and basal diameter (c) of *Schima superba* seedlings in open subplots (OS, without woody plant coverage) and canopy subplots (CS, beneath the canopy of the shrub *Rhodomyrtus tomentosa*) in the top block (T) and bottom block (B) on a slope. Values (means \pm SD) are from the first growing season (April 2010 to April 2011). This figure appears in color in the online version of the article (doi: 10.1111/j.1526-100X.2012.00937.x).

than open subplots, Fig. 1b); at the bottom of the slope, where nutrients were more abundant, the canopy reduced seedling survival ($57.8 \pm 5.9\%$ for open subplots; $39.2 \pm 5.1\%$ for canopy subplots; $p < 0.05$) but had no effect on the size of the remaining seedlings (Fig. 1b). Seedling basal diameter was not significantly affected by either position on slope or shrub canopy (Fig. 1c).

These findings were confirmed by the RII analysis in which RII values indicated that the *R. tomentosa* canopy increased *S. superba* survival in the top block ($\text{RII} > 0$, $p < 0.05$) but decreased survival in the bottom block ($\text{RII} < 0$, $p < 0.05$) (Fig. 2) and that the *R. tomentosa* canopy significantly increased *S. superba* height at the top of the slope. Interestingly, the RII values indicated the canopy also increased seedling height at the bottom of the slope but the effect was

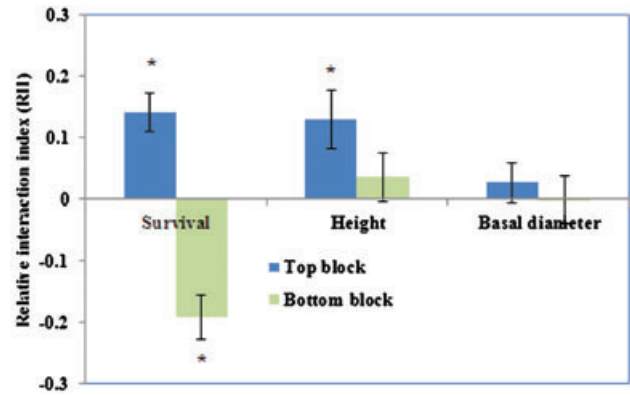


Figure 2. Effects of the nurse plant *Rhodomyrtus tomentosa* on survival, height, and basal diameter of seedlings of the target species *Schima superba* as indicated by the relative interaction index (mean \pm SD). * Indicates that the mean is significantly different from zero. Significant positive and negative values indicate facilitation and competition, respectively. This figure appears in color in the online version of the article (doi: 10.1111/j.1526-100X.2012.00937.x).

not significant (Fig. 2). In support of the ANOVA, RII values also indicated no significant effect on *S. superba* basal diameter from slope position (Fig. 2).

All *S. superba* photosynthetic rates peaked in the late morning (10:00) and again in the afternoon (14:00–16:00) (Fig. 3a), regardless of canopy condition or position on the slope. At the top of the slope, the daily average photosynthetic rates of *S. superba* were significantly higher in canopy subplots than in open subplots, while at the bottom of the slope, no difference was observed between canopy and open subplots. In both slope positions, the stomatal conductance of *S. superba* leaves was lower in open subplots than in canopy subplots ($p < 0.05$) (Fig. 3b).

Discussion

Studies in arid and semi-arid ecosystems show that soils beneath the canopy of perennial species are often richer in nutrients than soils in surrounding open areas (Carrillo-Garcia et al. 2000; Pugnaire et al. 2011). However, in our study in a tropical degraded land, we found no significant difference in soil nutrients between the areas underneath nurse plant canopy and areas in the open. We suspect that the high frequency of rains in this region redistributes soil nutrients, removing this canopy effect. Redistribution of litter and nutrients by rain would also explain why nutrient levels are greater at the bottom of the slope than at the top.

Our results also suggest that soil moisture is higher under shrub canopies than in open spaces, which is consistent with findings from arid or semiarid systems (Maestre et al. 2003; Pugnaire et al. 2011) and is consistent with our earlier work in the subtropical degraded ecosystems (Yang et al. 2010). Although shade is clearly the main factor causing the increase in soil moisture under plant canopies, deep-rooted plants may be engaged in hydraulic lift, the passive movement of water

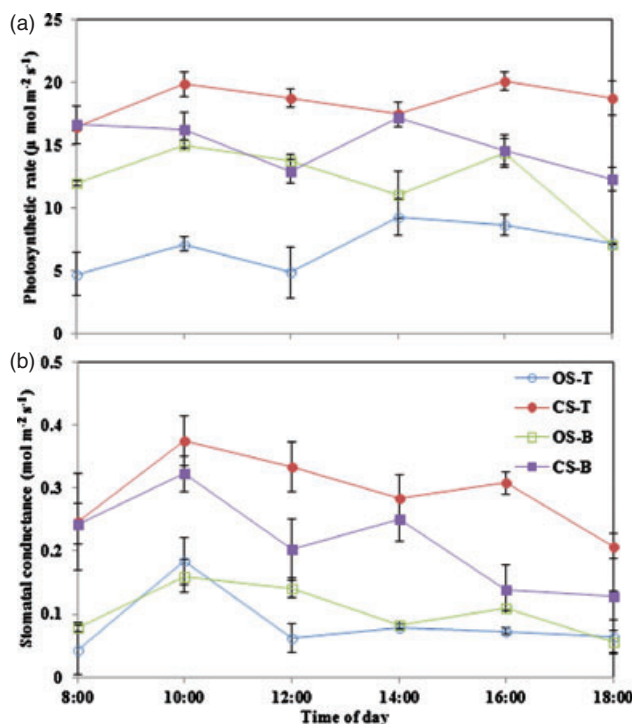


Figure 3. Diurnal changes in photosynthetic rate (a) and leaf stomatal conductance (b) of *Schima superba* in open subplots (OS, without woody plant coverage) and canopy subplots (CS, beneath the canopy of the shrub *Rhodomyrtus tomentosa*) in the top block (T) and bottom block (B) on a slope. Values (means \pm SD) are from the first growing season (April 2010 to April 2011). This figure appears in color in the online version of the article (doi: 10.1111/j.1526-100X.2012.00937.x).

through plant roots from deep and wet soils to drier soil near the surface (Pugnaire et al. 2011). Soil bulk density is also lower beneath the shrub canopy than in the open spaces, which again is consistent with our earlier work in this ecosystem type (Yang et al. 2010).

In addition to reducing bulk density and increasing soil moisture content, both of which should favor the growth of tree seedlings, *Rhodomyrtus tomentosa* decreases soil pH creating a relative acidic microenvironment in this tropical degraded land. The drop in pH could result from litter decomposition (Wang et al. 2004) and also from selective absorption and secretion of ions from roots (Xu et al. 2003). Previous findings (e.g. Goldberg 1985; Xu et al. 2003; Wang et al. 2004) have indicated that pH is often lower in the rhizosphere environment of mature plants (trees or perennial shrubs) than in the surrounding soil and that low pH can restrict the establishment and distribution of other plants. The better survival and growth of *Schima superba* seedlings under *R. tomentosa* canopies at the top of the slope suggests that any harmful effects of reduced pH could be balanced with other conditions (e.g. higher soil moisture content, lower soil bulk density) associated with *R. tomentosa*.

Shrubs have been considered common nurse plants in water-limited ecosystems (Carrillo-García et al. 2000; López et al. 2007), and researchers have argued that the nurse

plant syndrome mainly occurs in dry habitats or temperate ecosystems (Niering et al. 1963; Pugnaire et al. 2011). According to our recent studies, however, shrubs can also act as nurse plants in tropical and subtropical degraded ecosystems (Ren et al. 2008; Yang et al. 2010). These studies demonstrate that the shrub *R. tomentosa* greatly affects light penetration and soil physical characteristics and thus influences the performance of *S. superba* seedlings. Other work (Moro et al. 1997) found higher survival of plants under shrub canopies because of the more moderate microclimate, higher water availability, or higher soil nutrient levels. In this study, we found that the importance of canopy cover on seedling survival depends on position on the slope and the associated availability of nutrients. At the bottom of the slope we found lower *S. superba* survival under shrub canopies than in the open space. Because soil nutrient and physical characteristics affect seedling establishment (Goldberg 1985), we believe that the negative effect of higher soil acidity may overwhelm the positive effects of the shrub at the bottom of the slope. At the top of the slope, in contrast, soil nutrients are limiting and survival of *S. superba* seedlings benefits from growing under the *R. tomentosa* canopy. Additionally the higher soil porosity under the shrub canopy than in the open space may increase the availability of water and oxygen, promoting the establishment of target plant seedlings (Yang et al. 2010). Thus, variability of survival of *S. superba* seedlings on a natural slope in a tropical degraded land is consistent with the stress-gradient hypothesis.

Once established, the growth and physiological performances of *S. superba* seedlings were found related. *S. superba* seedlings grow taller under the shrub canopies than in the open spaces at the top of the slope. This is consistent with photosynthetic rates, which are higher in canopy subplots than in open subplots in this part of the slope. The height of *S. superba* seedlings is similar in both kinds of subplots at the bottom of the slope, which is consistent with the lack of difference in photosynthetic rates in this area. As for water release, diurnal stomatal open degree (stomatal conductance) of *S. superba* seedlings is higher when growing under shrub *R. tomentosa* than in the open. Shading under the shrub canopy may protect seedlings from radiation stress and thermal stress (Moro et al. 1997; Pugnaire et al. 2011) and these facilitative effects seem to be stronger than competitive effects at the bottom of the slope.

Facilitation and competition between species can occur simultaneously, and the net outcome relies on the strength of the two opposing processes (Maestre et al. 2003; Maestre & Cortina 2004; Goergen & Chambers 2012). The relative intensity of facilitation and competition can shift along the gradients of resource availability causing the outcome of species interactions to vary with abiotic conditions (Bertness & Callaway 1994; Pugnaire et al. 2011). In the present study, the shrub *R. tomentosa* has both positive effects (e.g. increased shade, increased soil moisture, reduced bulk density) and negative effects (e.g. reduced pH) on *S. superba* seedlings, and the responses of *S. superba* seedlings to shrub nurse effects change along the soil nutrient gradient. At the top of the slope, where soil nutrient contents is low (higher abiotic

stress), the shrub effect is mainly positive as indicated by increased seedling survival, growth, photosynthetic rate, and stomatal conductance in the summer. However, at the bottom of the slope, where soil nutrient content is high (lower abiotic stress), the shrub effect is negative for seedling survival and weakly positive for seedling growth. Nursed by the canopy of *R. tomentosa*, even with elevated photosynthetic performances and growth, the survival of *S. superba* is largely restricted (perhaps from low soil pH). Therefore, our results support the stress-gradient hypothesis in terms of seedling survival but not growth along a soil nutrient gradient in a tropical ecosystem. For forest restoration practices, nurse shrubs are especially encouraged in facilitating tree seedling survival and growth in places with low soil nutrient level but not with relatively better soil nutrient condition.

Implications for Practice

- Although shrubs can serve as nurse plants, they should be integrated into the reforestation of degraded ecosystems selectively. Soil fertility, shrub canopy density, intrinsic traits of target plants (e.g. shade tolerance), as well as their stress tolerances (e.g. sensitivity to low pH), should be considered.
- The use of nurse shrubs to enhance the establishment of target tree species in forest restoration projects should carefully consider the balance between facilitation and competition. The negative effects may overwhelm positive effects from shrub nurse plant in places with relatively higher soil nutrient level.
- The traditional approach to reforestation of *Rhodomyrtus tomentosa*-dominated shrublands, which involves clear cutting and burning before the outplanting of tree species, reduces competitive effects and may improve survival of planted tree seedlings without adversely affecting growth rates.

Acknowledgments

This research was financially supported by the National Natural Science Foundation of China (No. 31270013). The authors are grateful to their colleagues in Heshan National Field Research Station of Forest Ecosystems and Xiaoliang Tropical Forest Long-Term Ecosystem Research Station, especially to Z. F. Lin, Z. A. Li and X. Gou for experimental design guidance, to H. L. Zhang for soil chemical analyses and to K. M. Liang, L. L. Guan, B. Zou, G. Wang, Y. B. Ma and Z. Li for field assistance. The authors are also thankful for the comments from S. Yates, J. Parrotta, B. Jaffee and three anonymous reviewers on the early version of this manuscript. Also, thanks are extended to J. Brown for assistance with language editing.

LITERATURE CITED

- Abella, S. R., D. J. Craig, S. D. Smith, and A. C. Newton. 2011. Identifying native vegetation for reducing exotic species during the restoration of desert ecosystems. *Restoration Ecology*, DOI: 10.1111/j.1526-100X.2011.00848.x
- Armas, C., R. Ordiales, and F. I. Pugnaire. 2004. Measuring plant interactions: a new comparative index. *Ecology* **85**:2682–2686.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* **9**:191–193.
- Blanco-garcía, A., C. Sáenz-romero, C. Martorell, P. Alvarado-Sosa, and R. Lindg-Cisneros. 2011. Nurse-plant and mulching effects on three conifer species in a Mexican temperate forest. *Ecological Engineering* **37**:994–998.
- Bonanomi, G., G. Incerti, and M. Stefano. 2011. Assessing occurrence, specificity, and mechanisms of plant facilitation in terrestrial ecosystems. *Plant Ecology* **212**:1777–1790.
- Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, et al. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* **96**:18–34.
- Carrillo-García, A., Y. Bashan, E. D. Rivera, and G. J. Bethlenfalvay. 2000. Effects of resource-island soils, competition, and inoculation with *Azospirillum* on survival and growth of *Pachycereus pringlei*, the Giant Cactus of the Sonoran Desert. *Restoration Ecology* **8**:65–73.
- Cavieres, L. A., E. I. Badano, A. Sierra-Almeida, S. Gómez-González, and M. A. Molina-Montenegro. 2006. Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologist* **169**:59–69.
- Choler, P., R. Michalet, and R. M. Callaway. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* **82**:3295–3308.
- Egerova, J., E. Proffitt, and S. E. Travis. 2003. Facilitation of survival and growth of *Baccharis halimifolia* L. by *Spartina alterniflora* Loisel in a created Louisiana salt marsh. *Wetlands* **23**:250–256.
- Forrester, D. I., J. K. Vanclay, and R. I. Forrester. 2011. The balance between facilitation and competition in mixtures of *Eucalyptus* and *Acacia* changes as stands develop. *Oecologia* **166**:265–272.
- Goergen, E., and J. C. Chambers. 2012. Facilitation and interference of seedling establishment by a native legume before and after wildfire. *Oecologia* **168**:199–211.
- Goldberg, D. 1985. Effects of soil pH, competition, and seed predation on the distributions of two tree species. *Ecology* **66**:503–511.
- Holzapfel, C., K. Tielbörger, H. A. Pavag, J. Nigél, and H. Sternbeug. 2006. Annual plant–shrub interactions along an aridity gradient. *Basic and Applied Ecology* **7**:268–279.
- Kawai, T., and M. Tokeshi. 2007. Testing the facilitation-competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proceedings of the Royal Society B: Biological Sciences* **274**:2503–2508.
- Li, Q., Y. Liang, B. Tong, X. Du, and K. Ma. 2010. Compensatory effects between *Pinus massoniana* and broadleaved tree species. *Journal of Plant Ecology* **3**:183–189.
- Lin, L., L. S. Comita, Z. Zheng, and M. Cao. 2012. Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. *Journal of Ecology* **100**:905–914.
- Liu, G. S. 1996. Soil physical and chemical analysis and description of soil profiles. Standards Press of China, Beijing, China.
- López, R. P., S. Valdivia, N. Sanjines, and D. Quintana. 2007. The role of nurse plants in the establishment of shrub seedlings in the semi-arid subtropical Andes. *Oecologia* **152**:779–790.
- Maestre, F. T., and J. Cortina. 2004. Insights into ecosystem composition and function in a sequence of degraded semiarid steppes. *Restoration Ecology* **12**:494–502.
- Maestre, F. T., S. Bautista, and J. Cortina. 2003. Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology* **84**:3186–3197.
- Maestre, F. T., F. Valladares, and J. F. Reynolds. 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology* **93**:748–757.
- Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* **97**:199–205.

- Maltez-Mouro, S., F. T. Maestre, and H. Freitas. 2010. Co-occurrence patterns and abiotic stress in sand-dune communities: their relationship varies with spatial scale and the stress estimator. *Acta Oecologia* **36**:80–84.
- Michalet, R., R. W. Brooker, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, F. I. Pugnaire, A. Valiente-Banuet, and R. M. Callaway. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* **9**:767–773.
- Moro, M. J., F. I. Pugnaire, P. Haase, and J. Puigdefabregas. 1997. Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment. *Functional Ecology* **11**:425–431.
- Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The saguaro: a population in relation to environment. *Science* **142**:15–23.
- Pugnaire, F. I., C. Armas, and F. T. Maestre. 2011. Positive plant interactions in the Iberian Southeast: mechanisms, environmental gradients, and ecosystem function. *Journal of Arid Environments* **75**:1310–1320.
- Ren, H., Z. A. Li, W. J. Shen, Z. Y. Yu, S. L. Peng, C. H. Liao, M. M. Ding, and J. G. Wu. 2007. Changes in biodiversity and ecosystem function during the restoration of a tropical forest in south China. *Science in China Series C* **50**:277–284.
- Ren, H., L. Yang, and N. Liu. 2008. Nurse plant theory and its application in ecological restoration in lower subtropics of China. *Progress in Natural Science* **18**:137–142.
- Ren, H., X. A. Cai, C. H. Li, and Y. S. Ye. 2010. Atlas on tool species of vegetation recovery in South China. Huazhong University of Science & Technology Press, Wuhan.
- Schiffers, K., and K. Tielbörger. 2006. Ontogenetic shifts in interactions among annual plants. *Journal of Ecology* **94**:336–341.
- Soliveres, S., L. Desoto, F. T. Maestre, and J. M. Olano. 2010. Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. *Perspectives in Plant Ecology, Evolution and Systematics* **12**:227–234.
- Tielbörger, K., and R. Kadmon. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* **81**:1544–1553.
- Wang, X. X., Q. M. Li, H. Cao, Y. Q. He, and T. L. Zhang. 2004. Preliminary discussion on red soil acidification induced by plant and its mechanism. *Chinese Journal of Soil Science* **35**:73–77.
- Xu, R. K., A. Z. Zhao, Q. M. Li, X. L. Kong, and G. L. Ji. 2003. Acid regime of the red soils in a subtropical region of southern China under field conditions. *Geoderma* **115**:75–84.
- Yang, L., H. Ren, N. Liu, and J. Wang. 2010. The shrub *Rhodomyrtus tomentosa* acts as a nurse plant for seedlings differing in shade tolerance in degraded land of South China. *Journal of Vegetation Science* **21**:262–272.
- Yu, Z. Y., and Y. F. Pi. 1985. Ecological studies on vegetation rehabilitation of tropical and subtropical degraded ecosystems. *Tropical and Subtropical Forest Ecosystem* **3**:97–108.