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Soil microbes enhance competition ability of the exotic *Ageratina adenophora* Sprengel against native plant species

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Abstract: 【Background】The soil microbial community plays an important role in plant establishment, growth and nutrition. Invasion success may be linked to plant-microbe interactions. 【Method】Under glasshouse conditions, we compared the effect of soil microbial communities to the growth and interactions between the exotic weed *Ageratina adenophora* and native plants. The microbial communities were from soil invaded by *A. adenophora* (IS) vs. that dominated by native weeds (NS). 【Result】*A. adenophora* which received inoculum from IS had higher arbuscular mycorrhizal colonization rate than that from NS, especially when *Medicago falcata* or *Setaria viridis* grew near *A. adenophora*. Microbial inoculum from IS accelerated the growth of *A. adenophora*, when planted in polyculture with the native plant *S. viridis*, but the native species growth was not affected. *A. adenophora*, receiving an inoculum from IS, inhibited the growth of its two neighboring native species, while no such effect was observed when using inoculum from NS. *A. adenophora* responded positively to the inoculum taken from IS in all planting combinations, but responded negatively to inoculum from NS both in monoculture and in polyculture with *M. falcata*. 【Conclusion and significance】Soil microbes, including arbuscular mycorrhizal fungi present in soil in the rhizosphere of *A. adenophora* enhanced the competiveness of this invasive weed against native species, which may be an important invasion mechanism of exotic plants.

Key words: *Ageratina adenophora* Sprengel; soil microbe; microbial feedback to plant; exotic plant; invasion mechanism; rhizosphere; competition

土壤微生物增强了外来植物紫茎泽兰对本地植物种的竞争力

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摘要: 【背景】土壤微生物群落对植物种群建立、生长及其营养都起着至关重要的作用,植物入侵进程也可能与植物—土壤微生物互作相关。【方法】在温室条件下,研究了从紫茎泽兰入侵的土壤(IS)和本地植物生长的土壤(NS)中获得的微生物群落对外来杂草紫茎泽兰与本地植物生长及其互作的影响。【结果】接种来自 IS 接种剂的紫茎泽兰,特别是与黄花苜蓿或狗尾草共同种植时,较接种 NS 接种剂具有更高的丛枝菌根侵染率。来自 IS 的接种剂促进了与本地植物狗尾草共同栽培

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的紫茎泽兰的生长,但这一本地植物种的生长却未受影响。接种 IS 接种剂的紫茎泽兰抑制了与其临近种植的 2 种本地植物的生长,而接种 NS 接种剂时,未受此影响。接种 IS 接种剂时,所有种植组合中的紫茎泽兰对接种剂均呈正响应;而接种 NS 接种剂时,单独种植或与黄花苜蓿共同种植的紫茎泽兰对接种剂呈负响应。【结论与意义】存在于紫茎泽兰根周包括丛枝菌根真菌在内的土壤微生物,增强了这一入侵杂草与本地植物种的竞争力,这可能是外来植物入侵的一个重要机理。

关键词: 紫茎泽兰; 土壤微生物; 微生物对植物的反馈; 外来植物; 入侵机理; 根周; 竞争

INTRODUCTION

Some special soil microbes alter the interaction between exotic and native plants (Batten *et al.*, 2008; Callaway *et al.*, 2004a, 2008), whilst some exotic plants also alter soil microbial communities and their functioning (Kao-Kniffin & Balser, 2008; Kourtev *et al.*, 2002; Stinson *et al.*, 2006; Walling & Zabinski, 2004). The soil microbe-plant interaction affects the co-existence of exotic and native plants (Klironomos, 2002), and the invasion-induced soil microbial community changes can enhance the spread of exotic plants (Carey *et al.*, 2004; Reinhart & Callaway, 2006; Stinson *et al.*, 2006; Wardle *et al.*, 2004). On the other hand, arbuscular mycorrhizal fungi (AMF), an important component of soil microbes, affects plant succession and ecological domination by altering plant-plant interactions and nutrient availability (Karasawa & Takebe, 2001; Marler *et al.*, 1999; van der Heijden & Horton, 2009). AMF also enhances plant tolerance to unfavorable conditions (Beltrano & Ronco, 2008; Cartmill *et al.*, 2008), maintains plant diversity and plant resource distribution (Dhillion & Gardsjord, 2004), which promotes ecosystem stability and resilience (van der Heijden *et al.*, 1998). Approximately ~80% of higher plants including almost all invasive species are able to form AMF, resulting in the transfer of nutrients and water from the fungi to the host plant (Brundrett, 2009; Wang & Qui, 2006). Therefore, AMF may regulate resource competition between native and exotic plants and mediate the successful invasion of exotic plants. For instance, AMF from soils dominated by exotic plants can counterbalance the negative influence of the exotic species (Kisa *et al.*, 2007) or facilitate the competition of invasive plants in invaded areas (Callaway *et al.*, 2004b; Fumanal *et al.*, 2006). Several mechanisms of AMF affecting plant invasion have been suggested: (1) Resistance Hypothesis; (2) Enhanced Mutualisms Hypothesis; (3) Mutualisms Hypothesis; and (4) Degraded Mutualisms Hypothesis (Shah *et al.*, 2009). However, limited literature exists on how the growth of native and exotic plant species could be influenced by soils from invaded or non-invaded areas which hold different AMF communities.

Ageratina adenophora Sprengel (or *Eupatorium adenophorum* Sprengel), an exotic plant native to Mexico, has rapidly spread, since 1930′s, to southeastern Asia, eastern Australia, New Zealand, and southwestern Africa (Cronk & Fuller, 1995; Wang, 2005). *A. adenophora* was firstly found in China in 1935 in Yunnan Province, from where it has rapidly spread to southwestern China. Presently, it has invaded 80% of Yunnan, and has become one of the worst invasive exotic species in Guizhou, Sichuan, Guangxi, Xizang, Chongqing and Hubei Provinces (Lu & Ma, 2006; Xie *et al.*, 2001). *A. adenophora* is expanding northwards at an annual rate of 20 km in those regions, leading to serious loss of native plants (Wang & Wang, 2006). *A. adenophora* invasion affects both soil bacterial (Niu *et al.*, 2007; Yu *et al.*, 2005) and AMF communities (Yu *et al.*, 2012). However, information on how a changed microbial community could affect the competition between *A. adenophora* and native plants is limited. The present research, therefore, aimed to study in greenhouse pot experiments the effect of distinct microbial communities, from freshly-invaded and not invaded forest soils, on *A. adenophora* and native plants, as well as their interactions in greenhouse pot experiments.

MATERIALS AND METHODS

Soil collection

Collections of rhizosphere soils and roots were

made according to Sigüenza *et al.* (2006). In the middle of July 2009, soils at 0 ~ 20 cm depth were collected under two vegetation types (500 ~ 2000 m away from each other) in a coniferous and broad-leaved mixed forest, located in Kunming, Yunnan, China (25°03′N and 102°52′E, ~ 1980 m above sea level). The area has been severely invaded by *A. adenophora* for at least 15 years. Kunming has a sub-tropical monsoon climate, with an annual mean temperature of 15 ℃ and precipitation of 1100 mm. The vegetation type Ⅰ was dominated by native plants (*Setaria viridis*, *Medicago falcata*, *Stellaria chinensis*) without the invasion of *A. adenophora*, so that the collected soil was referred to as non-invaded soil (NS). The vegetation type Ⅱ was dominated by *A. adenophora* with a ten-year invasive history so that the collected soil was referred to as invaded soil (IS). The soil type was typical red soil in southern China (Hapludult, US system). The soil at 0 ~ 20 cm has pH 7.7, 39.3 g · kg^{-1} DW organic carbon, 1.9 g · kg^{-1} N, 25.0 mg · kg^{-1} available P and 132.8 mg · kg^{-1} available K.

The soil samples were randomly collected under each vegetation type within an area of 100 m × 300 m from 10 plots. Each plot had a size of 9 ~ 25 m^2 and were 15 ~ 20 m away from each other. Soil samples about 3 kg · $plot^{-1}$ from each vegetation type was collected and stored in plastic bags with dry ice plates and immediately transported to the glasshouse for the pot experiments.

Plant species and experimental design

To test the effects of soil inocula on the growth of native and exotic plants, three species were selected: the invasive *A. adenophora*, and the native plants *S. viridis* and *M. falcata*. Seeds of the three species were collected from the different vegetation types and planted as monocultures: *A. adenophora* (A), *S. viridis* (S) or *M. falcata* (M) as well as in combination: *A. adenophora* with *S. viridis* (A + S) or with *M. falcata* (A + M).

Each of these seed combinations were planted into four different soils: NS and IS, with or without autoclave sterilization (105 ℃, 1.5 h), giving a total, of 20 treatments. Each treatment was replicated 12 times. We used 2 L tubby pots (6 cm bottom diameter, 9 cm top diameter, 11 cm high), containing 1.8 kg growth substrate (1∶4 perlite/sterile sand mix, *v*/*v*), and 10 g sterilized or non-sterilized fresh soil that was buried 0.5 cm beneath the substrate surface (Klironomos, 2002). Seeds were sown in the soil inoculation. Plants were grown between 21 September 2009 and 20 November 2009 under natural light conditions and controlled temperature of 32/18 ℃ (day/night), which was similar to the summer weather in the soil collecting area, in a glasshouse on the campus of Chinese Academy of Agricultural Sciences, Beijing, China. The pots were randomly arranged and their position changed weekly or biweekly, watered every other day with tap water, and fertilized biweekly with 100 mL Hoagland's solution. Four (two for each species in the two combinations) seedlings in each pot were maintained after two weeks of sowing.

The plants were harvested after 2 months (including shoots and roots) and were oven-dried at 70 ℃ for 60 h. To measure AMF root colonization, fresh fibrous 1 cm root segments of *A. adenophora* were cleared with 10% KOH for 25 min, rinsed with 2% hydrochloric acid for 5 min, and stained with 0.01% acid fuchsin-lactic acid-glycerin dye at 90 ℃ for 25 min (acid fuchsin 0.1 g, lactic acid 875 mL, glycerin 63 mL, distilled water 300 mL), followed by immersion in 10 ~ 20 mL 99% lactic acid until AMF root colonization had been scored. AMF root colonization was scored by light microscope (http://invam.caf.wvu.edu/; Biermann & Linderman, 1981). Microbial responsiveness, the relative response of plant growth to soil microbes was calculated with the following formula: $RD = (B - B_0)/B \times 100\%$, in which B and B_0 were dry biomass of plant with un-sterilized and sterilized soil inocula, respectively (Harner *et al.*, 2010).

Data analysis

Effects of soil inoculum source on root AM colonization, plant biomass production and microbial responsiveness were subjected to ANOVA and significant differences of data (means ± *SE*) between treatments

were compared with LSD under $P < 0.05$ with General Linear Model. Data were analyzed using the software SPSS version 13.0 (SPSS Inc., Chicago, USA).

RESULTS

Effects of soil inocula on the root colonization rates of *A. adenophora*

At harvest, no obvious AMF structures were observed in any plant roots grown in sterilized soil inoculum, whereas all plants grown in the non-sterilized inoculum were colonized by AMF. The rates of AMF root colonization of *A. adenophora* ranged from 81.7% to 97.7%. The mycorrhizal colonization rate of *A. adenophora* was not affected by inoculum sources ($P = 0.163$). However, *A. adenophora* in A + S (A/A + S) and *A. adenophora* in A + M (A/A + M) inoculated with soil inculum from IS had a higher AMF colonization rate than that from NS ($P_1 = 0.020$, $P_2 < 0.0001$) (fig. 1), indicating that AMF in invaded soil preferred to colonize *A. adenophora* while AMF in native soil did not.

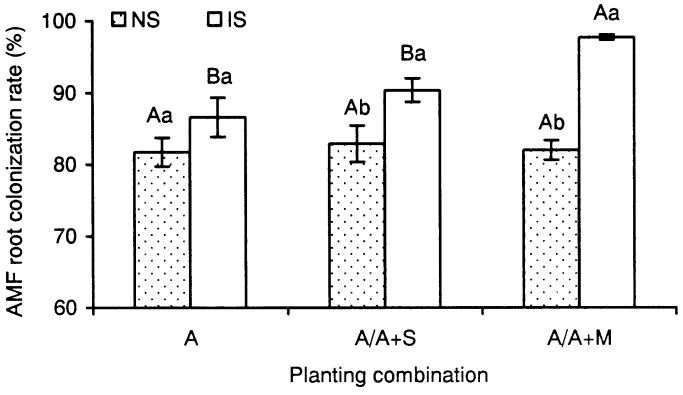

Fig. 1 AMF root colonization rate (means ± *SE*) of *A. adenophora*

NS and IS represents AMF inoculum of native plants dominated and exotic plants invaded soil respectively. On the x-axis: A = *A. adenophora* in monoculture; A/A + S = *A. adenophora* in mixed stands of *A. adenophora* and *S. viridis*; A/A + M = *A. adenophora* in mixed stands of *A. adenophora* and *M. falcata*. Different capital letters above the columns in the same soil inoculum source treatment indicate significant differences among planting combinations; Different small letters above the columns in the same planting combination indicate significant differences between soil inoculum sources.

Effect of microbial inoculum source, sterilization and neighboring plant on plant growth

Soil inocula from different sources had variable effects on the growth of *A. adenophora* and native plants. The total biomass of *A. adenophora* sown with non-sterilized inoculum from IS was 17.4% higher than that inoculated with NS, but inoculum source had no effect on growth of the two native plant species. Sterilization retarded the growth of both *A. adenophora* and native plants. The neighboring plants accelerated the growth of *A. adenophora*, but it retarded the growth of the two native species. The interaction of inoculum source and sterilization on the growth of all plants was non-significant. The interaction of inoculum source and neighbor plant was significant for the native plants, but it was non significant for *A. adenophora*. The interaction of sterilization and neighbor plants was significant for *A. adenophora*, but non significant for native plants. The interaction of soil source, sterilization and neighbor plants was significant for native plants, but non significant for *A. adenophora* (table 1 ~ 2).

Microbial inoculum source

Sterilization had no effect on plant biomass when inoculated NS and IS in all planting combinations except for *S. viridis* planted alone. But in the non-sterilized treatment, the plant biomass was higher for IS than NS except *M. falcata* planted with *A. adenophora* (table 1).

Effect of sterilization

In NS, sterilization accelerated the growth of all plants except *A. adenophora* planted with *S. viridis*; While sterilized IS retarded the growth of *A. adenophora* when planted with *S. viridis*, but facilitated the growth of the native plants (table 1).

Table 1 Dry biomass (g) per plant with different inoculum sources and planting combination

Inoculum	Planting combination	Sterilized inoculum	Non-sterilized inoculum
Native soil	A	0.44 ± 0.02Aa	0.47 ± 0.06Ba
	A/A + S	0.51 ± 0.05Aa	0.65 ± 0.06Ab
	A/A + M	0.54 ± 0.04Aa	0.48 ± 0.04Bb
	S	0.14 ± 0.01Ab *	0.04 ± 0.003Ab
	S/A + S	0.10 ± 0.01Ba *	0.04 ± 0.003Ab
	M	0.17 ± 0.01Aa *	0.12 ± 0.005Ab
	M/A + M	0.14 ± 0.02Aa	0.12 ± 0.01Aa
Invaded soil	A	0.46 ± 0.03Ba	0.56 ± 0.05Ba
	A/A + S	0.62 ± 0.03Aa *	0.85 ± 0.05Aa
	A/A + M	0.54 ± 0.03ABa	0.62 ± 0.05Ba
	S	0.20 ± 0.01Aa *	0.10 ± 0.01Aa
	S/A + S	0.09 ± 0.01Ba	0.07 ± 0.004Ba
	M	0.18 ± 0.01Aa	0.18 ± 0.01Aa
	M/A + M	0.14 ± 0.01Aa *	0.09 ± 0.01Bb

A = *A. adenophora* in monoculture; A/A + S = *A. adenophora* in polyculture of *A. adenophora* and *S. viridis*; A/A + M = *A. adenophora* in polyculture of *A. adenophora* and *M. falcata*; S = *S. viridis* in monoculture; M = *M. falcata* in monoculture. Different capital letters in the same row (in a given inoculum source) indicate significant differences among/between planting combinations within the same soil inoculum source; Different small letters in the same row (in a given planting combination) indicate significant differences between soil inoculum sources within the same planting combination. * indicates significant differences in means in the same row (sterilized inocula vs. non-sterilized inocula).

Table 2 Summary of ANOVA of the effects on plant biomass of soil source (invaded, non-invaded), sterilization (sterilized or nonsterilized), and their interactions

Plant	Inoculum source (1)	Sterilization treatment (2)	Neighbor plant (3)	1 * 2	1 * 3	2 * 3	1 * 2 * 3
A. adenophora	0.000	0.001	0.000	0.051	0.205	0.018	0.855
S. viridis	0.203	0.005	0.000	0.758	0.005	0.465	0.022
M. sativa	0.206	0.005	0.000	0.765	0.002	0.672	0.010

Number in the table means *P* value.

Effect of neighbouring plants

S. viridis facilitated the growth of *A. adenophora* especially with non-sterilized IS inoculum, but *M. falcata* did not have such an effect. *A. adenophora* retarded the growth of the two native plants, especially in the IS (table 1).

Soil inocula from *A. adenophora* invaded area (IS) facilitated the growth of *A. adenophora* when planted with the two native plant species as neighbors. The growth of the native plants was retarded by the neighbor *A. adenophora* when soil inoculum from IS was used. The results were opposite when NS soil inoculum was used.

Effect of inoculum source and sterilization on plant biomass

Plant biomass per pot of the five planting combinations was A > A + S ($P < 0.0001$) > A + M ($P = 0.028$) > M ($P < 0.0001$) > S ($P = 0.004$). The inoculum source and sterilization had no effect on plant biomass in A and A + M. The inoculum from IS resulted in higher biomass than NS in the A + S treatment, but sterilization decreased the biomass. The inoculum from IS yielded lower biomass than NS for S, and sterilization decreased this biomass. The inoculum of IS resulted in higher biomass of *M. falcata* than of NS, it was not affected by sterilization, but significant interaction was found between them (fig. 2).

Response of *A. adenophora* and native plant species to microbial inoculum

A. adenophora exhibited varied response to soil inocula from different sources. When sown with inoculum from NS, *A. adenophora* showed a negative response in monoculture and when grown with *M. falcata*, but a positive response with *S. viridis*. *A. adeno-*

phora showed strong positive response for IS (in monoculture: $P < 0.0001$; in mixture of A + S: $P = 0.05$; in mixture of A + M: $P < 0.0001$). The response of *S. viridis* (in monoculture: $P < 0.0001$; in mixture of A + S: $P < 0.0001$) and *M. falcata* (in monoculture: $P < 0.0001$; in mixture of A + M: $P < 0.0001$) to microbes was also different. The native *S. viridis* yielded a stronger negative response to the inoculum from NS than that from IS, and *M. falcata* showed negative response to the inoculum from NS but positive response to the inoculum from IS in monoculture, while it yielded a strong negative response when planted with *A. adenophora* (fig. 3).

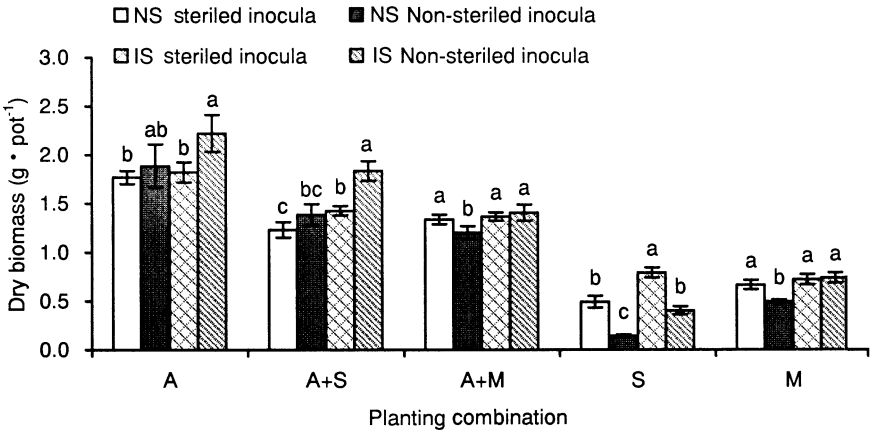

Fig. 2 Effects of sterilization on biomass (means ± *SE*) of plants

NS and IS represents soil inocula of native plants dominated and exotic plants invaded soil respectively. On the x-axis: A = *A. adenophora* in monoculture; A + S = mixed stands of *A. adenophora* and *S. viridis*; A + M = mixed stands of *A. adenophora* and *M. falcata*; S = *S. viridis* in monoculture; M = *M. falcata* in monoculture. Different letters above the columns in the same planting combination indicate significant differences among treatments.

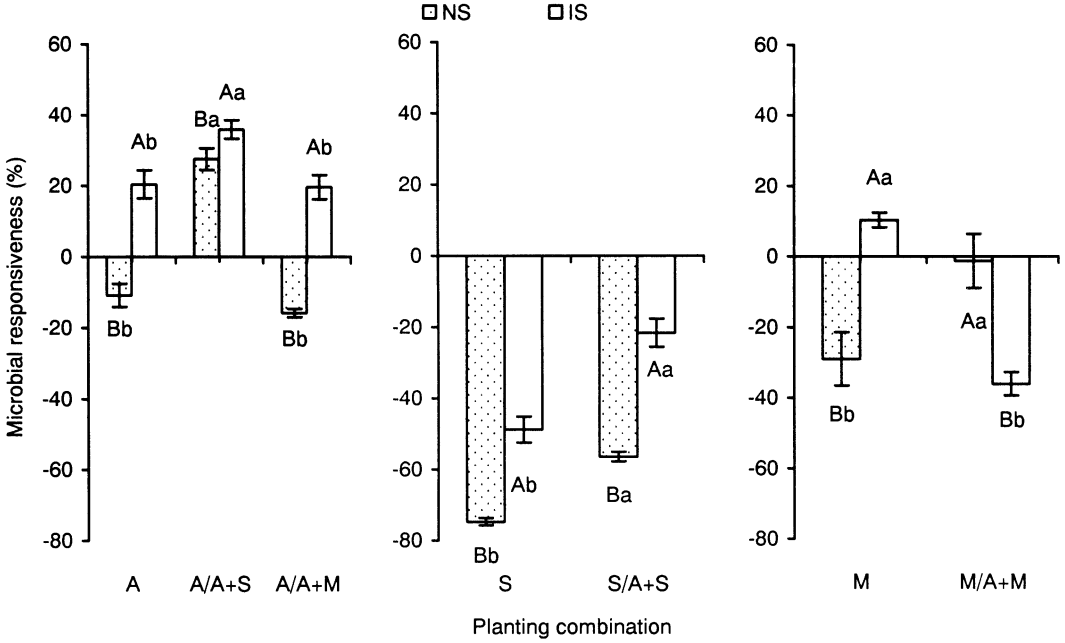

Fig. 3 Microbial responsiveness (means ± *SE*) of plant growth

NS and IS represents soil inocula of native plants dominated and exotic plants invaded soil respectively. On the x-axis: A = *A. adenophora* in monoculture; S = *S. viridis* in monoculture; M = *M. falcata* in monoculture; A/A + S = *A. adenophora* in mixed stands of *A. adenophora* and *S. viridis*; S/A + S = *S. viridis* in mixed stands of *A. adenophora* and *S. viridis*; A/A + M = *A. adenophora* in mixed stands of *A. adenophora* and *M. falcata*; M/A + M = *M. falcata* in mixed stands of *A. adenophora* and *M. falcata*. Different capital letters above the columns in the same planting combination indicate significant differences between soil inoculum sources; Different small letters above the columns in the same soil inoculum source treatment indicate significant differences among planting combinations.

DISCUSSION

Invaded soil microbial community changes the competitive interactions between exotic and native plants

During invasion, *A. adenophora* releases allelochemicals that strongly affect the composition of the soil microbial community (Niu *et al.*, 2007; Yang *et al.*, 2006, 2008), and altering the AMF community is an important invasive mechanism for *A. adenophora* (Yu *et al.*, 2012). In the present study, *A. adenophora* responded positively to the changed soil microbial community that became more favorable to *A. adenophora* than to the native species inoculum from native soil had no effect on the root colonization rates of *A. adenophora* in different planting combinations but adding invaded soil resulted in higher AMF colonization rate of *A. adenophora* in polyculture with *S. viridis* or *M. falcata*, even when compared to monoculture plantings. And inocula from native and invaded soils had different effects on the growth of *A. adenophora* and the native plants suggesting that microbes in invaded soil including AMF, changes the competitive interactions between these plants (Dhillion & Gardsjord, 2004).

M. falcata showed stronger resistance to *A. adenophora* invasion. Its growth was not retarded by *A. adenophora* when inoculum from native soil was used. *S. viridis* showed no ability of resisting the invasion, but it grew better with inoculum from invaded soil than native plant dominated soil, so this native plant can be considered as the substitute plant in the restoration of *A. adenophora* invaded ecosystem.

Exotic plants exploit the resources of native plants via AMF

The growth of *A. adenophora* was also accelerated by inoculum from invaded soil when grown in polyculture with *S. viridis*, which resulted in a positive feedback loop and further spreading of *A. adenophora*. However, this positive feedback loop only happens when exotic plants are grown with neighboring native plants, a situation where the exotic plants exploit the resources of native plants (Callaway *et al.*, 2004a; Marler *et al.*, 1999; Zabinski *et al.*, 2002). After the AMF community had been altered, the AMF colonization rate increased in *A. adenophora* grown in polyculture with *S. viridis* or *M. falcata*.

Non-sterilized soil inocula enhanced AMF colonization rates and growth of *A. adenophora*. The effects of AMF on plant growth are stronger if nutrition is not enough (Harner *et al.*, 2010). In our experiment we had to fertilise the plants. Each plant species in different planting combinations had the same biomass when they were inoculated with sterilized inoculum (both NS and IS) or inoculated with non-sterilized inoculum from soil dominated by native plants, which served as a negative control, showing that regular soil fungi do not change the invasive weed's growth. The non-sterilized inoculum from *A. adenophora* invaded soil, however, significantly contributed to the vigorous growth of *A. adenophora* and its further spread. The mutualistic enhancement of invasive plants by AMF most likely causes changes to the outcome of competitive interactions between exotic and native species. These changes may come from the impacts of AMF on the uptake and exchange of nutrients (Shah *et al.*, 2009). Future studies could focus on the effect of environmental factors on the interactions among exotic plants, soil microbes and native plants, to better understand the interactions between non-native vegetation and soil microbial communities, along with their feedbacks to the native plants in highly invaded areas. The synergistic effects of the plant growth promoting rhizobacteria (PGPR) and the AMF on exotic plants and native plants should also be investigated (Khan & Zaidi, 2007).

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