



Nitrogen Uptake, Not Transfer of Carbon and Nitrogen by CMN, Explains the Effect of AMF on the Competitive Interactions Between *Flaveria bidentis* and Native Species

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Rhizophagus intraradices, one of the common arbuscular mycorrhizal fungi (AMF) grown in the roots of *Flaveria bidentis*, facilitates the invasion of this exotic plant species into China. However, it is still unknown whether nutrient transfer through the common mycorrhizal networks (CMN) between this exotic species and the native species enhances the competitive growth of *F. bidentis* over the native species. To elucidate this question and the related mechanism, an isotopic labeling technique was used to test the transfer of carbon (C) and nitrogen (N) by CMN. Native species like *Setaria viridis* and *Eclipta prostrata* were selected to compete with *F. bidentis* in a polyvinyl chloride (PVC) box. Two competitive groups (*F. bidentis*-*S. viridis* and *F. bidentis*-*E. prostrata*), three treatments (monoculture of *F. bidentis*, the mixture of *F. bidentis* and the native plant, and the monoculture of the native plant), and two levels of AMF (presence or absence) were assigned. Results showed that the corrected index of relative competition intensity (CRCI) of *F. bidentis* in the presence of AMF < 0 suggests that the competition facilitated the growth of *F. bidentis* with either *S. viridis* or *E. prostrata*. The reason was that the inoculation of *R. intra radices* significantly increased the C and N contents of *F. bidentis* in the mixtures. However, the effects of *R. intra radices* on the two native species were different: negative effect on the growth of *S. viridis* and positive effect on the growth of *E. prostrata*. The change of N content in *S. viridis* or *E. prostrata* was consistent with the variation of the biomass, suggesting that the N uptake explains the effects of *R. intraradices* on the competitive interactions between *F. bidentis* and the two native species. Moreover, the transfer of C and N via AMF hyphal links did occur between *F. bidentis* and the native species. However, the transfer of C and N by the CMN was not positively related to the competitive growth of *F. bidentis*.

Keywords: arbuscular mycorrhizal fungi, exotic species, relative competition intensity, nitrogen acquisition, carbon and nitrogen transfer

INTRODUCTION

Arbuscular mycorrhizal fungi (AMF), an ecologically and economically important fungal guild, usually establish mutualistic associations with the majority of exotic plants (Bunn et al., 2015). Increasing evidence suggested that mycorrhizal symbiosis with AMF mediates the competitiveness, diversity, and community structure of the plant species (Lin et al., 2015; Bennett et al., 2017; Teste et al., 2017), thereby contributing to the success of plant invasion (Gerz et al., 2018). For example, some studies indicated that AMF colonization of the exotic species was usually higher than that of the native species. The AMF provided more nutrients to the exotic plants and promoted the competitive ability of the exotic plants relative to the native plants (Yang et al., 2015; Zhang et al., 2017, 2018). Also, other studies showed that the symbiotic relationship between the native plants and the AMF could be changed by the invasion of the exotic species (Callaway et al., 2008; Lekberg et al., 2013; Bunn et al., 2015). The changes in the mutualistic associations might lead to an increase (i.e., positive feedback) in the relative growth rate of the exotic species and a decrease (i.e., negative feedback) in the relative growth rate of the native species (Bever, 2002; Stinson et al., 2006; Pringle et al., 2009).

Arbuscular mycorrhizal fungi usually form extensive common mycorrhizal networks (CMNs), which interconnect the neighboring root systems of the same or different plant species (Weremijewicz et al., 2018). Nutrient acquisition by AMF may come from soil *via* fungal hyphae or from plants that were connected by CMNs (Yang et al., 2014; Zhang et al., 2017). Recently, a growing body of theory and empirical evidence suggest that nutrient transfer through CMNs between the connected plants, rather than through nutrient acquisition, is relevant to plant growth (Selosse et al., 2006; Bücking et al., 2016). Bücking et al. (2007) and Selosse et al. (2016) argued that CMNs were not only passive conduits for the movement of carbon (C) (Carey and Callaway, 2004) and nutrients (He et al., 2003; Von Thun, 2013), but they might also provide sophisticated fungal–host resource exchange (Song et al., 2010; Babikova et al., 2013), including allelopathic chemicals (Barto et al., 2011) and defense signals (Lekberg et al., 2010; Weremijewicz et al., 2016). Moreover, AMF in CMNs preferentially provide mineral nutrients to those conspecific host individuals that are able to provide them with fixed C or represent the strongest sinks, thereby potentially amplifying the competition by preferentially allocating mineral nutrients to large host plants (Weremijewicz et al., 2016). Indeed, CMNs had caused size inequality between the networked plants (Fitter et al., 1999; Kiers et al., 2011; Lekberg et al., 2013; Weremijewicz and Janos, 2013). Therefore, some ecologists are of the view that the exotic species outcompeted the native ones as CMNs might have the ability to transfer more C from the native species to the invasive species (Carey and Callaway, 2004). However, others argued that CMNs had little effect on the competitive interactions among the plant species (Milkereit et al., 2018). Based on the above argument, further studies are still necessary to explore the role of CMNs on the competition between the exotic plants and the native plants.

Flaveria bidentis (L.) Kuntze (Asteraceae), an invader from South America, is one of the most problematic exotic plant species of the family Asteraceae in China (Chen et al., 2004). It typically caused changes in the composition of the plant species and in the biodiversity and community structure of the natural ecosystem (Chen et al., 2004; Ren et al., 2008). *F. bidentis* can establish symbiotic relationships with AMF (Ji et al., 2015). *Rhizophagus intraradices* was one of the dominant AMF on the roots and in the rhizosphere soil of *F. bidentis*. The relative abundance of *R. intraradices* was over 15% both in the roots and in its rhizosphere soil (Zhang et al., 2015b, 2017). Our previous study showed that *R. intraradices* facilitated the competitive growth of *F. bidentis* by promoting the nutrient levels in the leaves of *F. bidentis* (Zhang et al., 2017). However, it is still unknown whether the increased nutrient was absorbed from the soil or from the CMNs that are connected with the native species. We hypothesized that *R. intraradices* facilitated the competitive growth of *F. bidentis* by transferring C and nitrogen (N) *via* CMNs from the native plant species to the invasive species. We tested our hypothesis by studying the effects of colonization (or inoculation) of *R. intraradices* on the growth of *F. bidentis* and of two native plant species, as well as the transfer of C and N *via* CMNs.

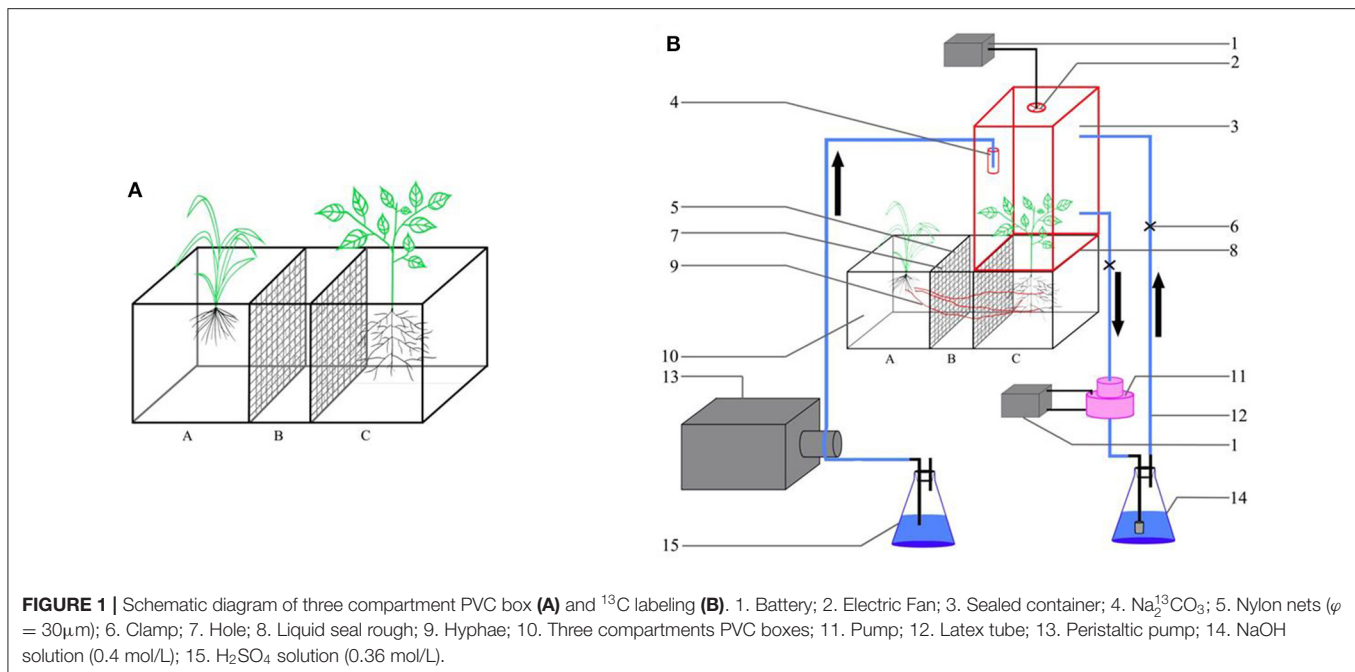
MATERIALS AND METHODS

A Study on Plant Species and *R. intraradices* Inoculum

Setaria viridis (L.) Beauv. and *Eclipta prostrata* L. were selected as the native plants. *S. viridis* and *E. prostrata* are the typical native weeds of farmlands, pasturelands, and wastelands in China. They are also the dominant plant species in the *F. bidentis*-invaded habitat in China. *S. viridis* belongs to the family Poaceae. *E. prostrata* belongs to the family Asteraceae. The seeds of *F. bidentis* and the two native species were collected from the Langfang Experimental Station of the Chinese Academy of Agricultural Science (CAAS), China. Seeds were surface-sterilized in 10% H₂O₂ and rinsed five times with sterile distilled water before sowing. The *R. intraradices* inoculum was a mixture of spores and mycelium, which was provided by Professor Liu Runjin from Qingdao Agricultural University.

The Design of the Rhizobox

Polyvinyl chloride (PVC) boxes were used to test the effect of *R. intraradices* on the competition between *F. bidentis* and the two native plants. The thickness of the PVC boxes was 0.6 cm. Each box was divided into three compartments as shown in **Figure 1A** and **Supplementary Figure 1**. Plants were grown in compartments A and C, respectively. Compartment B was set up to minimize the risk of free transfer of C and N between the compartments A and C. The size of each of the three compartments measured 20 × 20 cm (length × height), the width of compartments A and C were of 25 cm and that of compartment B was of 10 cm. Compartments A and C were separated from compartment B by a nylon mesh (pore size of 30 μm). The nylon mesh prevents the penetration of roots but allows the penetration of hyphae. The three compartments were



filled with a growth substrate (vermiculite: sand: field soil = 1:1:1). The vermiculite $[(\text{Mg,Fe,Al})_3(\text{Si,Al})_4\text{O}_{10}(\text{OH})_2 \cdot 4\text{H}_2\text{O}]$ and sand were purchased from Niuniu Plant and Flower Co., Ltd., Langfang, China. The soil was collected from a field, at the Langfang Experimental Station of CAAS, without the history of *F. bidentis* invasion. The chemical properties of the soil were measured (Olsen, 1954; Whitehead et al., 1981) as follows: organic matter, 15.4 g kg^{-1} ; available N, 56.1 g kg^{-1} ; available potassium, 214.6 g kg^{-1} ; and available phosphorus, 9.9 g kg^{-1} . The growth substrate was sterilized at 121°C for 4 h before conducting the experiment. About 2 kg of the growth substrate was added into compartments A and C, and 1 kg of the growth substrate was added in compartment B.

Design of the Competition Experiment

A controlled growth chamber experiment was set up at the Langfang Experimental Station of CAAS. There were two competitive groups, namely *F. bidentis*-*S. viridis* and *F. bidentis*-*E. prostrata*. Each group was exposed to three treatments (the monoculture of *F. bidentis*, the mixture of *F. bidentis* and the native plant, and the monoculture of the native plant). Two levels of AMF presence (AMF+) or absence (AMF-) were assigned to each treatment. Ten replicates per treatment were arranged (60 microcosms, in total, for each group). Before planting, a total of 40 g of the inoculum with about 2,400 spores mixed with 2 kg of the growth substrate was added in Compartments A and C (AMF+), respectively. The control treatment was inoculated with 40 g of the inoculum that was sterilized at 121°C for 30 min (AMF-). After germination, additional plants were removed and only one seedling per compartment was kept. Rhizoboxes were kept in a growth chamber from July to September at 25°C under a 14 h light: 10 h dark photoperiod. Treatments were arranged in a completely randomized design. The water content of the soil in

the rhizoboxes was kept at 25%, and it was adjusted frequently by weight.

^{13}C Labeling

Plants were allowed to grow for 80 days prior to $^{13}\text{CO}_2$ application. For each treatment, half of the 10 replicates were used to assess the movement of C from the plants grown in Compartment A (donor) to the plants grown in Compartment C (receiver), and the rest of the five replicates were used to assess the inverse movement of C (i.e., from Compartment C to Compartment A). Before ^{13}C labeling, the surface of the soil was covered by a tinfoil but the aboveground plants were exposed to air. The donor plant was sealed in a transparent PVC container (red box) (Figure 1), ensuring enough penetration of light. To avoid air leakage out of the PVC container, the grooves in Compartments A and C were filled with water, and the PVC container was placed in a water-sealed tank. Meanwhile, three latex tubes (blue lines) were placed into the PVC container, and the gaps between the organic glass and latex tubes were sealed by glass cement. A ^{13}C pulse labeling was conducted according to the method of Lu et al. (2003). A tube that contained 5 g of $\text{Na}_2^{13}\text{CO}_3$ was placed into the PVC container. Before $^{13}\text{CO}_2$ application, the CO_2 in the sealed container was completely absorbed by using 0.4 mol l^{-1} NaOH solution. Later, 0.36 mol l^{-1} H_2SO_4 solution was slowly pumped into the tube by the latex tubing and it was allowed to react with $\text{Na}_2^{13}\text{CO}_3$. The reaction was controlled by a peristaltic pump and the $^{13}\text{CO}_2$ concentration was maintained at 400 ppm during the process, which was measured by a carbon dioxide concentration detector. An electric fan was placed in the donor compartment to make the $^{13}\text{CO}_2$ gas diffuse evenly in the PVC container. During this process, the released $^{13}\text{CO}_2$ was fixed with photosynthesis by

synthesizing the carbohydrate inside the plants. Six hours later, the sealed container was removed after the remaining ^{13}C was absorbed by $0.4 \text{ mol l}^{-1} \text{ NaOH}$. The control was labeled using Na_2CO_3 . We labeled each plant three times, once in every 3 days (Liu et al., 2019).

^{15}N Labeling

After ^{13}C labeling, plants were labeled with ^{15}N according to the method of Cheng and Baumgartner (2004). For each plant, the leaves were inserted into three 2-ml vials which were filled with 1.2 ml 1% ^{15}N solution [99 atom% $(^{15}\text{NH}_4)_2\text{SO}_4$] for 24 h. The broad leaf of *E. prostrata* was curled tightly before it was inserted into the vials to avoid any damage. For each tested plant, three leaves were inserted into each vial. All the vials were covered with a tape to prevent the evaporation of $(^{15}\text{NH}_4)_2\text{SO}_4$.

Measurements

Colonization of AMF

The percentage of mycorrhizal root colonization was estimated by a visual observation of fungal colonization after the roots were washed in 10% KOH and stained with 0.05% Trypan blue in lactic acid (v/v) (Shi et al., 2006). The colonization of AMF on the roots of *F. bidentis*, *S. viridis*, and *E. prostrata* was determined by using the magnified intersection method of McGonigle et al. (1990). A total of 200 root segments were examined for each treatment. Ten replicates per treatment were used. The colonization of AMF in each treatment was calculated as follows:

$$\text{Colonization (\%)} = \frac{\sum(0\% \times N_0 + 10\% \times N_1 + 20\% \times N_2 + \dots + 100\% \times N_{10})}{N_{\text{Total}}} \times 100\%$$

where N_i represents the numbers of root segments of the corresponding percentage colonization and N_{Total} represents the total numbers that were examined.

Biomass and Corrected Index of Relative Competition Intensity

Plant leaves (five leaves per plant) were collected 7 days after ^{15}N labeling. The roots were washed to remove the soil particles. All shoots and roots of the exotic and the native plants were collected to measure their biomass.

The shoots and roots of *F. bidentis*, *S. viridis*, and *E. prostrata* were oven-dried at 80°C for 48 h. The dry biomass of the roots and shoots of the three species were recorded to determine the ratio of roots to shoots and the relative biomass of roots and shoots. For each treatment, the data of the weight of the total dry plant were collected to determine the biomass. The corrected index of relative competition intensity (CRCI) was calculated following the method of Oksanen et al. (2006).

$$\text{CRCI} = \arcsin[(X - Y)/\max(X, Y)],$$

where X is the average biomass of an individual plant grown intraspecific and Y is the biomass of plants grown interspecific. The CRCI value >0 indicates that the competition has a negative

effect, and the value <0 indicates that the competition has a positive effect on the target plant.

Net Transfer of ^{13}C and ^{15}N

Both the shoots and roots were ground with a Retsch Mixer Mill MM 200 (Verder Scientific Benelux NV, Aartselaar, Belgium). The concentration of C and N in the plants were measured with a CHN analyzer (LECO Corporation, St. Joseph, MI, USA). The concentrations of ^{13}C and ^{15}N were measured with a mass spectrometer [Stable Isotope Facility, Institute of Applied Ecology (IAE), Chinese Academy of Science (CAS), China]. The net transfer of ^{15}N and ^{13}C of *F. bidentis* was calculated based on the following formula:

$$\text{Net transfer (\%)} = (T_1 - T_2) \times 100,$$

where T_1 is the percentage of ^{15}N or ^{13}C transferred from *F. bidentis* to the native species, either to *S. viridis* or *E. prostrata*, and T_2 is the percentage of ^{15}N or ^{13}C transferred from the native species, either from *S. viridis* or *E. prostrata*, to *F. bidentis*.

The percent of ^{15}N and ^{13}C transferred was calculated as follows (He et al., 2003; Zhang et al., 2015a):

$$T = \frac{^{15}\text{N}_{\text{receiver}} \times 100}{(^{15}\text{N}_{\text{receiver}} + ^{15}\text{N}_{\text{donor}})}$$

or

$$T = \frac{^{13}\text{C}_{\text{receiver}} \times 100}{(^{13}\text{C}_{\text{receiver}} + ^{13}\text{C}_{\text{donor}})}$$

where, $^{15}\text{N} = \text{atom\% } ^{15}\text{N excess} \times \text{total N} / \text{atom\% } ^{15}\text{N excess}_{\text{labeled N}}$

$$^{13}\text{C} = \text{atom\% } ^{13}\text{C excess} \times \text{total C} / \text{atom\% } ^{13}\text{C excess}_{\text{labeled C}}$$

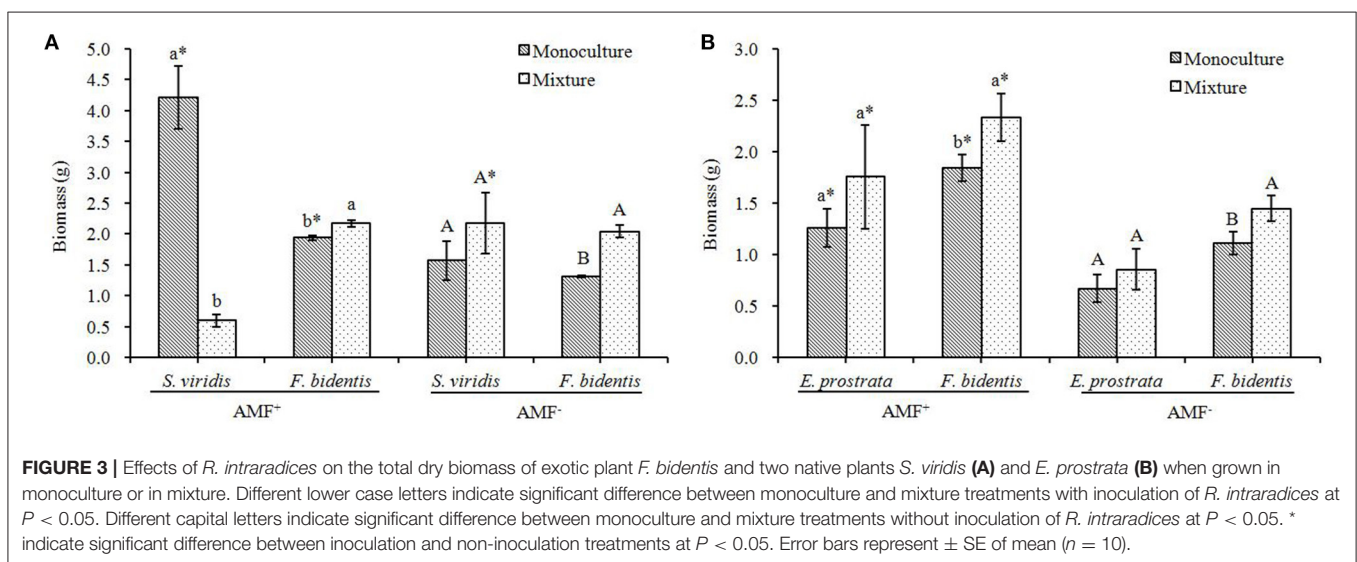
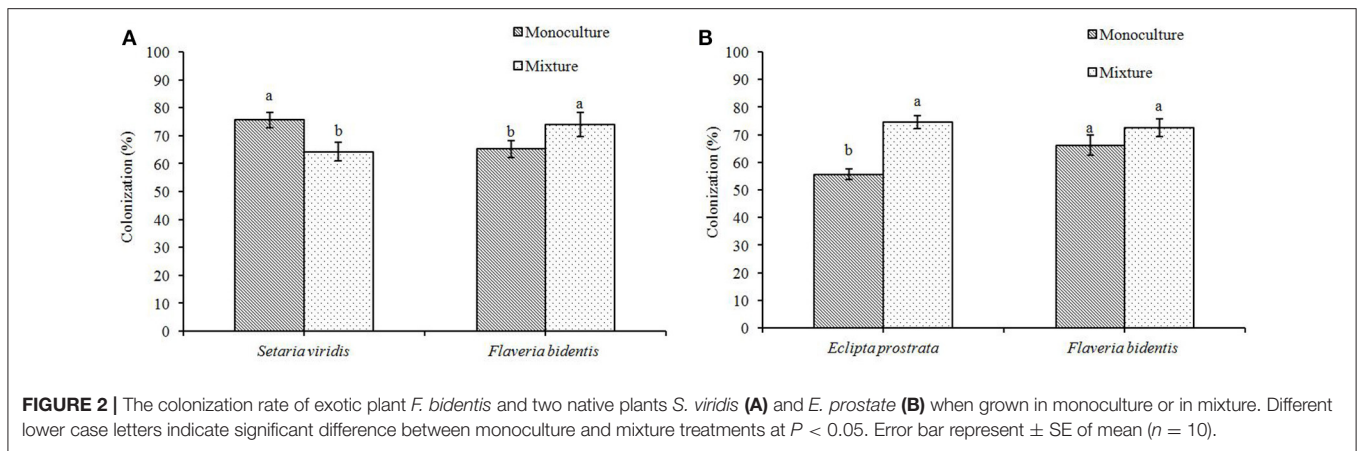
Statistical Analyses

All statistical analyses were carried out using SPSS 19.0 (IBM, Armonk, New York). Before the analyses, all data were tested for normality by the Shapiro–Wilk test. All data met the normality distribution. The effects of AMF or the competition on plant growth indicators (i.e., biomass, root to shoot ratio, total C and N uptake plant^{-1} , and C/N ratio) of each plant species were tested by a one-way ANOVA. The interactive effects of the AMF and the competition of the mycorrhizal colonization on plant growth indicators of the plant species were tested by a two-way ANOVA. The analysis of Pearson's correlation coefficient of each plant species was used to determine the correlations of the rate of root colonization on plant growth indicators (i.e., biomass and the total content of C and N).

RESULTS

Colonization Rates

In the AMF⁻ treatment, no mycorrhizal colonization of *r. intraradices* was found in the roots of each of the three plant species. In the AMF⁺ treatment, the mycorrhizal colonization of *R. intraradices* on *F. bidentis* was marginally higher in the mixture of *F. bidentis* and *S. viridis* than that in the monoculture of *F. bidentis* [$F_{(1, 18)} = 13.609$, $P = 0.006$] (Figure 2A). However, it was not significantly different in the mixture of *F. bidentis* and *E. prostrata* than that in the monoculture of *F. bidentis* [$F_{(1, 18)} = 0.031$, $P = 0.866$] (Figure 2B). The mycorrhizal colonization of *R. intraradices* on *S. viridis* was significantly lower when it competed



with *F. bidentis* than that when it was grown in the monoculture treatment [$F_{(1, 18)} = 36.470$, $P < 0.001$] (Figure 2A). However, the mycorrhizal colonization of *R. intraradices* on *E. prostrata* was significantly higher when it competed with *F. bidentis* than that when it was grown in the monoculture treatment [$F_{(1, 18)} = 204.833$, $P < 0.001$] (Figure 2B).

The Effect of *R. intraradices* on the Growth of Plant Biomass

In the AMF⁺ treatment, compared to the monoculture, the biomass of *F. bidentis* increased when it grew with *S. viridis* (Figure 3A) or *E. prostrata* (Figure 3B) [*S. viridis*: $F_{(1, 18)} = 33.547$, $P = 0.004$; *E. prostrata*: $F_{(1, 18)} = 10.034$, $P = 0.034$] while it showed different impacts on the two native species: it decreased the biomass of *S. viridis* [$F_{(1, 18)} = 144.743$, $P < 0.001$] but showed no effect on that of *E. prostrata* [$F_{(1, 18)} = 2.552$, $P = 0.185$].

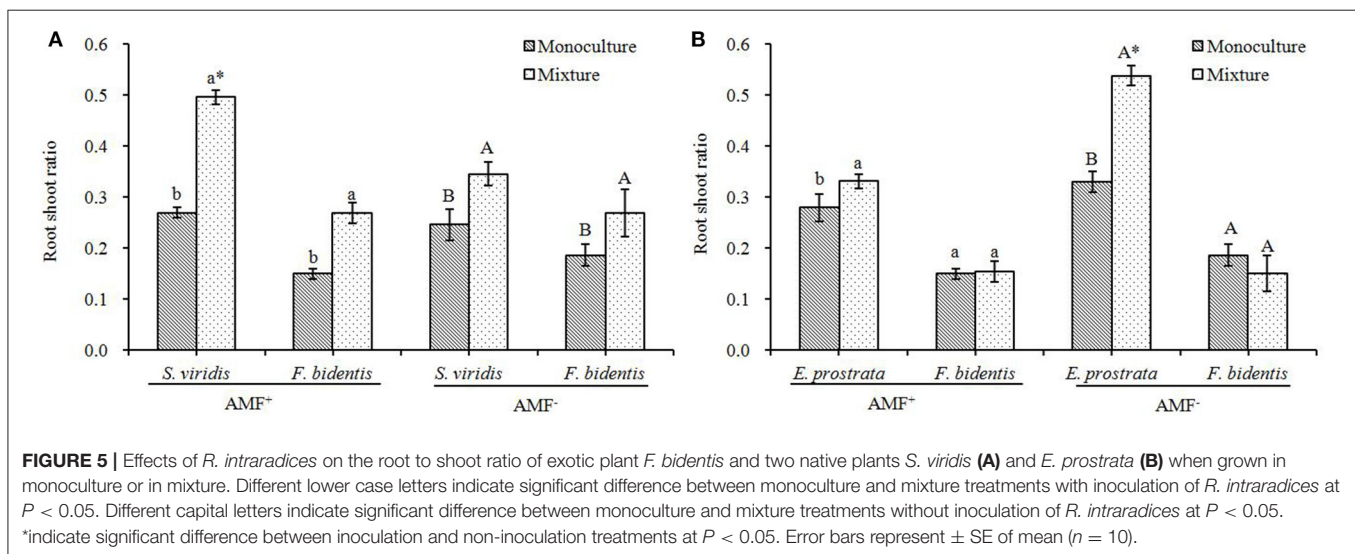
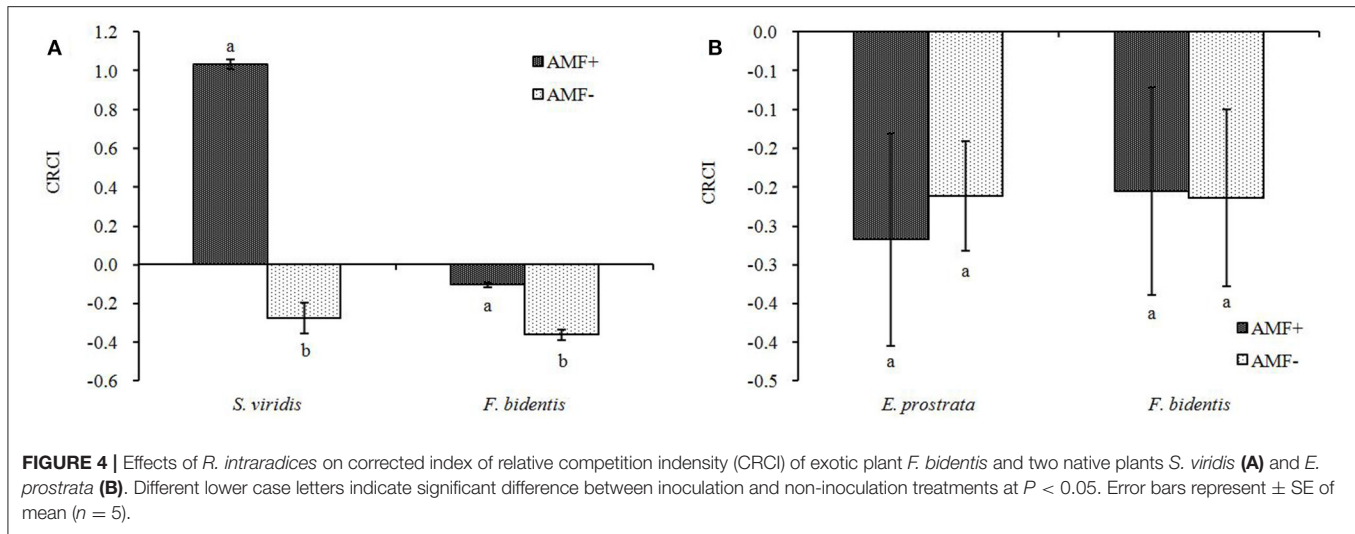
In the AMF⁻ treatment, compared to the monoculture, the biomass of *F. bidentis* increased when it grew with *S. viridis* or *E. prostrata* [*S. viridis*: $F_{(1, 18)} = 154.331$, $P < 0.001$; *E. prostrata*:

$F_{(1, 18)} = 154.331$, $P < 0.001$], but showed no effect on that of the native species [*S. viridis*: $F_{(1, 18)} = 3.271$, $P = 0.145$; *E. prostrata*: $F_{(1, 18)} = 1.804$, $P = 0.250$] (Figure 3).

Corrected Index of Relative Competition Intensity

In the AMF⁺ treatment, the CRCI of both *F. bidentis* and *E. prostrata* is < 0 , while that of *S. viridis* is > 0 , indicating that the competition had a positive effect on the growth of both *F. bidentis* and *E. prostrata*, while it showed a negative effect on the growth of *S. viridis* (Figure 4). In the AMF⁻ treatment, the CRCI of both *F. bidentis* and the two native species is < 0 , suggesting that the competition had a positive effect on their growth.

Compared to AMF⁻ treatment, the AMF⁺ treatment enhanced the positive effect of competition on *F. bidentis* when *F. bidentis* competed with *S. viridis* [$F_{(1, 18)} = 205.121$, $P < 0.001$] (Figure 4A), while it showed no effect on *F. bidentis* when *F. bidentis* competed with *E. prostrata* [$F_{(1, 18)} = 0.008$, $P = 0.932$] (Figure 4B). Meanwhile, the effect of competition on the growth of *S. viridis* shifted from positive in the AMF⁻ treatment to negative in the AMF⁺ treatment.



Ratio of Root to Shoot

The competition increased the ratio of roots to shoots in *F. bidensis* and in *S. viridis* both in the presence and absence of AMF ($F = 39.130$ or 22.704 , $P < 0.001$). Compared to the monoculture, the ratio of roots to shoots in *F. bidensis* significantly increased when *F. bidensis* grew with *S. viridis*, (Figure 5A) [AMF^- : $F_{(1, 18)} = 8.224$, $P = 0.046$; AMF^+ : $F_{(1, 18)} = 76.563$, $P = 0.001$], while there was no change when *F. bidensis* grew with *E. prostrata* (Figure 5B) [AMF^- : $F_{(1, 18)} = 2.327$, $P = 0.202$; AMF^+ : $F_{(1, 18)} = 0.062$, $P = 0.815$]. Furthermore, the ratio of roots to shoots in *E. prostrata* [AMF^- : $F_{(1, 18)} = 165.375$, $P < 0.001$; AMF^+ : $F_{(1, 18)} = 9.143$, $P = 0.039$] and *S. viridis* [AMF^- : $F_{(1, 18)} = 19.149$, $P = 0.012$; AMF^+ : $F_{(1, 18)} = 462.400$, $P < 0.001$] in the mixture treatment was significantly higher than that in the monoculture when they grew with *F. bidensis* (Figure 5).

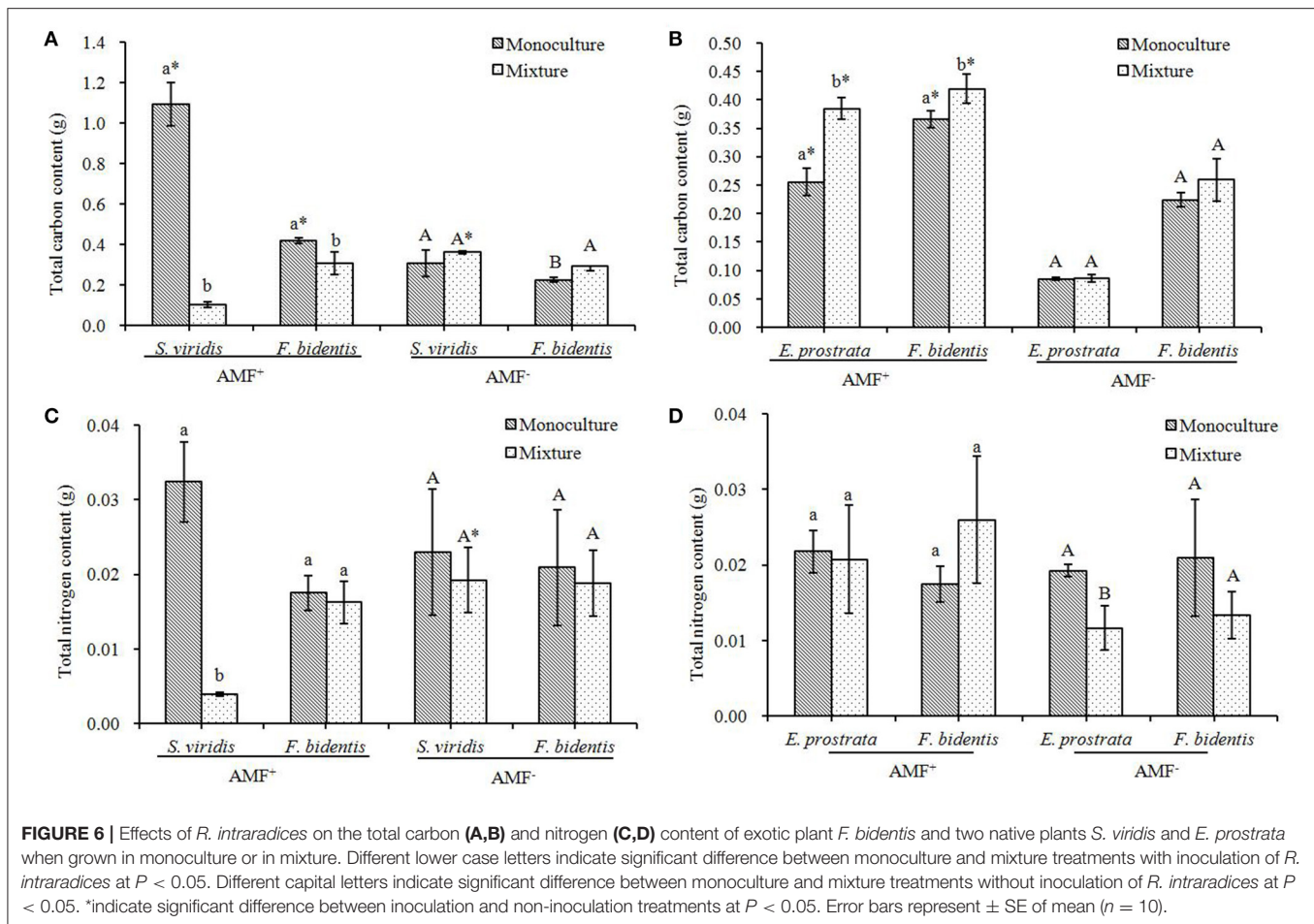
Compared to the AMF^- treatment, the ratio of roots to shoots of *S. viridis* in the mixture of the AMF^+ treatment increased (Figure 5A) [$F_{(1, 18)} = 77.885$, $P =$

0.001] while that of *E. prostrata* decreased [$F_{(1, 18)} = 202.316$, $P < 0.001$] in the mixture of the AMF^+ treatment (Figure 5B).

Carbon Content in Plant Tissue

In the AMF^+ treatment, the content of C in *S. viridis* in the mixture was lower than that in the monoculture [$F_{(1, 18)} = 255.297$, $P < 0.001$] (Figure 6A) while that of *E. prostrata* in the mixture was higher than that in the monoculture [$F_{(1, 18)} = 53.993$, $P = 0.002$] (Figure 6B). In *F. bidensis*, compared to the monoculture treatment, the content of C increased when it was grown with *E. prostrata* [$F_{(1, 18)} = 9.803$, $P = 0.035$] but decreased when it was grown with *S. viridis* [$F_{(1, 18)} = 11.616$, $P = 0.027$] (Figures 6A,B).

In the AMF^- treatment, no significant difference in the content of C of the two native species was found between the monoculture treatment and the mixture treatment (Figures 6A,B) [*S. viridis*: $F_{(1, 18)} = 1.944$, $P = 0.236$; *E. prostrata*:



$F_{(1, 18)} = 0.066$, $P = 0.810$]. The content of C in *F. bidentis* increased when it was grown with *S. viridis* compared to when it was grown in the monoculture [$F_{(1, 18)} = 20.910$, $P = 0.010$] (Figure 6A), while no significant difference was found between the monoculture and the mixture with *E. prostrata* [$F_{(1, 18)} = 2.399$, $P = 0.196$] (Figures 6A,B).

The inoculation of *R. intraradices* showed different effects on the content of C in *F. bidentis* when it was grown in the mixture treatment with the two different native species: the content of C in *F. bidentis* increased when it was grown with *E. prostrata* [$F_{(1, 18)} = 488.169$, $P < 0.001$], but no change was found when it was grown with *S. viridis* [$F_{(1, 18)} = 0.436$, $P = 0.437$] (Figures 6A,B).

Nitrogen Content in the Plant Tissue

In the AMF⁺ treatment, no significant difference was found in the content of N in *F. bidentis* [in the mixture treatment with *S. viridis*: $F_{(1, 18)} = 0.355$, $P = 0.583$; in the mixture treatment with *E. prostrata*: $F_{(1, 18)} = 2.792$, $P = 0.170$] and in *E. prostrata* [$F_{(1, 18)} = 0.065$, $P_N = 0.811$] between the monoculture treatment and the mixture treatment, while the content of N in *S. viridis* significantly decreased in the mixture treatment [$F_{(1, 18)} = 84.754$, $P_N = 0.001$] (Figures 6C,D).

In the AMF⁻ treatment, no significant difference was found in the content of N in *F. bidentis* [in the mixture treatment with *S. viridis*: $F_{(1, 18)} = 0.163$, $P = 0.707$; in the mixture treatment with *E. prostrata*: $F_{(1, 18)} = 2.474$, $P = 0.191$] and in *S. viridis* [$F_{(1, 18)} = 0.456$, $P = 0.537$] between the monoculture treatment and the mixture treatment, while the content of N in *E. prostrata* significantly decreased in the mixture treatment [$F_{(1, 18)} = 19.099$, $P = 0.012$] (Figures 6C,D).

The inoculation of *R. intraradices* showed no significant different effects on the content of N in *F. bidentis* and *E. prostrata*, regardless of the fact that they were grown in the monoculture [$F_{(1, 18)} = 0.533$ or 2.455 , $P = 0.506$ or 0.192] or in the mixture [$F_{(1, 18)} = 5.907$ or 4.117 , $P = 0.072$ or 0.112] treatments, but the content of N in *S. viridis* decreased in the inoculation treatment of *R. intraradices* when it was grown in the mixture with *F. bidentis* [$F_{(1, 18)} = 37.146$, $P = 0.004$] (Figures 6C,D).

Carbon and N Transfer Between *F. bidentis* and Native Plant Species

In the AMF⁺ treatment, the ¹³C and ¹⁵N transfer rates from *F. bidentis* to *S. viridis* were 2.67 and 2.14%, respectively, while they were 2.54 and 0.98% from *S. viridis* to *F. bidentis*, respectively

TABLE 1 | Carbon and nitrogen transfer between *F. bidentis* and two native plants (*S. viridis* and *E. prostrata*) mediated by *R. intraradices*.

Groups	With (+)/without (-) <i>R. intraradices</i>	Donor	Receivers	Transfer rate (%)		Net transfer rate (%) from <i>F. bidentis</i> to native plant	
				¹³ C	¹⁵ N	¹³ C	¹⁵ N
Group 1	AMF ⁺	<i>F. bidentis</i>	<i>S. viridis</i>	2.67 ± 0.11	2.14 ± 0.04	0.12 ± 0.01	1.05 ± 0.02
	AMF ⁺	<i>S. viridis</i>	<i>F. bidentis</i>	2.54 ± 0.06	0.98 ± 0.02		
	AMF ⁻	<i>F. bidentis</i>	<i>S. viridis</i>	0.02 ± 0.01	0.01 ± 0.002	0.01 ± 0.003	0.001 ± 0.001
	AMF ⁻	<i>S. viridis</i>	<i>F. bidentis</i>	0.01 ± 0.002	0.009 ± 0.001		
Group 2	AMF ⁺	<i>F. bidentis</i>	<i>E. prostrata</i>	3.26 ± 0.12	2.99 ± 0.21	-0.11 ± 0.01	-0.48 ± 0.02
	AMF ⁺	<i>E. prostrata</i>	<i>F. bidentis</i>	3.37 ± 0.20	4.29 ± 0.56		
	AMF ⁻	<i>F. bidentis</i>	<i>E. prostrata</i>	0.015 ± 0.001	0.013 ± 0.002	0.005 ± 0.001	-0.001 ± 0.001
	AMF ⁻	<i>E. prostrata</i>	<i>F. bidentis</i>	0.010 ± 0.001	0.014 ± 0.002		

TABLE 2 | The correlation of colonization rate with biomass and C and N content.

Groups	Plant species	Biomass	Total carbon content	Total nitrogen content
Group 1	<i>F. bidentis</i>	0.78	-0.74	0.77
	<i>S. viridis</i>	0.92*	0.96*	0.90*
Group 2	<i>F. bidentis</i>	-0.29	0.08	-0.50
	<i>E. prostrata</i>	0.65	-0.924*	0.31

*indicate the significantly correlated of colonization rate with biomass and C and N content at $P < 0.05$.

(Table 1). The net transfer rates of ¹³C and ¹⁵N from *F. bidentis* to *S. viridis* were 0.12 and 1.05%, respectively.

The transfer of ¹³C and ¹⁵N was bidirectional between *F. bidentis* and *E. prostrata*. In the AMF⁺ treatment, the transfer rates of ¹³C and ¹⁵N from *F. bidentis* to *E. prostrata* were 3.26 and 2.99%, respectively, while they were 3.37 and 4.29% from *E. prostrata* to *F. bidentis*, respectively (Table 1). The net transfer rates of ¹³C and ¹⁵N from *F. bidentis* to *E. prostrata* were -0.11 and -0.48%, respectively.

The Correlation of Colonization Rate With Biomass and the Contents of C and N

When *F. bidentis* competed with *S. viridis*, the colonization rate of *R. intraradices* on *S. viridis* was positively correlated with its biomass ($r = 0.92$, $P = 0.010$), C content ($r = 0.96$, $P = 0.003$), and N content ($r = 0.90$, $P = 0.014$) (Table 2). When *F. bidentis* competed with *E. prostrata*, the colonization rate of *R. intraradices* on *E. prostrata* was negatively correlated with its C content ($r = -0.92$, $P = 0.008$).

DISCUSSION

Arbuscular mycorrhizal fungi played a critical role in the successful invasion of certain exotic species (Klironomos, 2002). AMF could be conducive to invasiveness if exotic plants benefited more from these services than the native plants, or if the exotic plants could disrupt the mutualism between the AMF and the native plants (Reinhart et al., 2017). Our study showed that *R. intraradices* could colonize on both the exotic and the native plant species. The effects of *R. intraradices* on the competitiveness of *F. bidentis* depend on the type of native species present in the habitat. To be specific, the CRCI of both *F. bidentis* and *E.*

prostrata did not change when they were grown in the inoculated mixture with *R. intraradices*. However, when *F. bidentis* and *S. viridis* were grown in a mixture, the inoculation of *R. intraradices* amplified the positive effect on *F. bidentis* but showed a negative effect on *S. viridis*. These divergent responses caused differences in the nutrient uptake and nutrient transfer between the invasive and the native species (Reinhart and Anacker, 2014; Veresoglou and Rillig, 2014).

Resource sharing in plant communities does occur through CMNs formed by the AMF (Carey and Callaway, 2004; Høgh-Jensen et al., 2005) so that CMNs can mediate interactions among the connected plants (Chiariello et al., 1982; Wilson et al., 2006; Janos, 2007). Recently, more and more studies focus on finding whether CMNs transfer nutrients among all the interconnected plants or enhance the competition among them (Weremijewicz and Janos, 2013). Weremijewicz et al. (2018) pointed out that intact CMNs could amplify the intraspecific competition within *Andropogongerardii* population in consequence of improved mineral nutrition. Simard et al. (1997) suggested that the net transfer of C could affect the performance of plants and the magnitude of the net transfer of nutrients could regulate through the source-sink relationship. Carey and Callaway (2004) suggested that, when exotic *Centaurea maculosa* grew with their native neighbors, C was transferred from the native species to the exotic species, which may be the important mechanism through which the invasive plants outcompete their neighbors. In this study, we found that the transfer of C and N via AM hyphal links did occur between the exotic and native plants. However, the net transfer of C and N was not always from the native species to the invasive species. To be specific, ¹³C and ¹⁵N were transferred from *F. bidentis* to *S. viridis* when *F. bidentis* was grown with *S. viridis*, while ¹³C and ¹⁵N were transferred from *E. prostrata*

to *F. bidentis* when *F. bidentis* was grown with *E. prostrata*. This divergence suggested that the effects of CMN on plant interactions depend on the type of plant species involved and the interaction with *F. bidentis*, when the native species is highly species-specific. Some researchers documented that plant traits, such as photosynthetic pathways, growth forms, and competitor strategies, were associated with the community and function of AMF (Meisner et al., 2014; Davison et al., 2020). In this study, the two native plant species, *S. viridis* and *E. prostrata*, have different photosynthetic pathways and root systems; *S. viridis* is a C₄ plant and its root system is a fibrous root system, while *E. prostrata* is a C₃ plant and its root system is a tap root system. These differences between *S. viridis* and *E. prostrata* may account for the transfer rate of C and N transferred by CMNs. Importantly, compared to the AMF⁻ treatment, when *F. bidentis* and *S. viridis* were grown in an inoculated mixture of *R. intraradices*, they amplified the positive effect on *F. bidentis*, while ¹³C and ¹⁵N were transferred from *F. bidentis* to *S. viridis*. When *F. bidentis* was grown with *E. prostrata*, the inoculation of *R. intraradices* had no effect on *F. bidentis* though ¹³C and ¹⁵N were transferred from *E. prostrata* to *F. bidentis*. Our findings indicated that the C or N transferred by CMNs is not related to the competitive growth of *F. bidentis*. Our result is consistent with some previous results which stated that the C or N transferred by CMNs was not the key factors that influence the plant competition (Zabinski et al., 2002; Milkereit et al., 2018).

Increasing evidence suggested that the colonization of AMF on the roots might be a good predictor of plant growth and nutrient acquisition (Bunn et al., 2015; Zhang et al., 2017). In our study, different changes were found in the colonization rate of *R. intraradices* on the two native species in response to the competition with *F. bidentis*. Specifically, the colonization rate of *R. intraradices* on *S. viridis* was lower in the mixture treatment than in the monoculture treatment, while it was inverse in *E. prostrata*. Moreover, this difference in the colonization rate in response to the inoculation of *R. intraradices* was correlated with the differences in the nutrient uptake and growth strategies. In *S. viridis*, compared to the monoculture, the competition with *F. bidentis* decreased its C and N content in the AMF⁺ treatment. Correlation analysis showed that the colonization rate of *R. intraradices* on *S. viridis* was positively correlated with its total C content and N content. Such a decrease in the content of C in *S. viridis* may inhibit the growth of hyphae, which colonized the roots of *S. viridis* and then reduced the plant nutrient uptake (Cloos et al., 2014). In *E. prostrate*, the colonization rate of *R. intraradices* was negatively correlated with the total C content. The increase in the colonization rate of *R. intraradices* on *E. prostrate* in the mixture treatment may increase the C transfer rate from plants to the AMF, which may benefit the growth of hyphae that colonized on the roots of *E. prostrate* and then

enhance the plant nutrient uptake. Interestingly, the changed trends of N content, both in *S. viridis* and in *E. prostrata*, were consistent with the trends of their biomass in mixture treatment, respectively, in the presence of AMF. The results suggested that AMF compete with plants for N, as has been shown in the previous studies (Brooks, 2003; Janos, 2007; Smith et al., 2009; Johnson et al., 2015). Therefore, the invasion of *F. bidentis* affected the growth of the native plants by shifting its N uptake in the presence of AMF.

CONCLUSION

Carbon and N transfer *via* AM hyphal links did occur between the exotic and native plants. However, the net transfer of C and N was not always from native species to invasive species, suggesting that the C or N transferred by CMNs was not the key factor that influences the competition between the exotic *F. bidentis* and the native species. Indeed, when *F. bidentis* competed with *S. viridis* or *E. prostrata*, the *F. bidentis* affected the growth of the native plant by shifting its N uptake in the presence of *R. intraradices*.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

All authors contributed to the formulation, writing, and revision of this manuscript and made direct intellectual contributions. They all approve of its publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.625519/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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