

Effects of Arbuscular mycorrhizal fungi and soil substrate on invasive plant *Alternanthera philoxeroides*

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Abstract

Arbuscular mycorrhizal (AM) fungi in soil form a symbiotic relationship with plants, using their hyphae to help plants growth. And *Alternanthera philoxeroides* pose a serious threat to China's agriculture, forestry, and urban ecosystems. There is lack of studies on how AM fungi affect invasive plants in different environment. Therefore, *A. philoxeroides* and AM fungi were used study to study the different growth substrate and effects of AM fungi on invasive plants. In this study, the result showed that mycorrhizal dependency ranged 6.09% and 37.00%. Both AM fungi type and growth substrate significantly altered photosynthetic pigment (chlorophyll a, chlorophyll b, and carotenoid content of invasive *A. philoxeroides*). Similarly, the interaction between AM fungi and the type of growth substrate affected the content of photosynthetic pigment. The type of growth substrate, and the interaction between growth substrate type and AM fungi affected the height of *A. philoxeroides*. This study suggested that soil substrate, AM fungi type, and their interactions affect their invasion and spread. AM fungi lead to high aboveground biomass of *A. philoxeroides* promoting invasion. Therefore, in the future, invasive plants *A. philoxeroides* should be divided into corresponding control zones based on the gradient of different soil nutrients, especially in critical areas as key monitoring and prevention zones.

Introduction

Biological invasion not only causes losses to agriculture, forestry, and animal husbandry production, but also has long-term ecological effects. The direct and indirect losses caused by invasive alien species each year reach 119.876 billion yuan, accounting for 1.36% of the gross domestic product in China^[1]. After the invasion of alien species, the structure and function of the ecosystem are destroyed. *A. philoxeroides*, originally from South America, has now invaded North America, Oceania, Southeast Asia, and China^[2]. It mainly grows in the vast areas of China south of 44°N and east of 97°E with low altitude and relatively warm and humid climate. In 2003, it is included in the "List of the First Batch of Invasive Alien Species in China" published by the State Environmental Protection Administration of China. The success of plant invasion into a new environment is crucially dependent on the relationship between the invasive plant and the local arbuscular mycorrhizal fungi^[3].

Mycorrhiza is a very common and important symbiotic phenomenon in nature, and arbuscular mycorrhizal fungi form symbiotic relationships with 80% of terrestrial plants^[4]. During the growth process, extra-root hyphae can infect other plants again, forming a hypha network connecting plant roots between plants. Mycorrhiza can scavenge nutrients, water, and other substances from neighbor regions to supply host plants^[5-6], improving the drought resistance of host plants and enhancing their resistance to various diseases^[7-9]. Similarly, some study found that the invasion of *Solidago canadensis* promotes the growth of *Glomus mosseae*, while it inhibited the growth of *Glomus geosporu*^[10]. And some research hold that exotic plant (*Bromus tectorum* and *Euphorbia esula*) had improved AMF growth^[11]. *Solidago canadensis* promoted the growth of the AMF (*Glomus geosporum*)^[10]. The invasion of *Eupatorium*

adenophorum had reduced the abundance of species such as *Glomus geosporum*, while stimulated growth of *Glomus claroideum*^[12].

And some studies suggested that AM fungi didn't help invasive plants growth^[13]. This indicated that AM fungi did not form a symbiotic relationship with alien plant. Some studies hold that there was negative relationship between AM fungi and exotic plants^[14–15]. For example, the biomass of two weed of species was obviously reduce by 59% and 66% under AM fungi condition, and the biomass of other four weed species was reduced between 20% and 37%^[14]. Some researchers hold that AM fungi antagonistic effect on *Luzula campestris* (reduced plant biomass)^[16]. Even some researchers considered that there was no interaction between AM fungi and exotic species^[17]. Similarly, some studies demonstrated that there wasn't interaction between *Luzula campestris* and AM fungi^[18]. Even a meta-analysis showed that AM fungi did not change colonization between invasive species^[19]. These confused results showed that the interactions between invasive plants and local AM fungi may lead to positive feedback^[20], negative feedback^[10].

Mycorrhizal fungi play an important role in helping host plants acquire nutrients. And some studies suggest that soil nutrition is an important factor affecting plant invasion^[21–22]. Studies found that successfully invasive alien plants typically responded more strongly to nutrient increases^[23]. On the contrary, there were reports that increased nutrient availability is not conducive to the establishment of a favorable symbiotic relationship between invasive plants and AM fungi^[24]. Studies on how invasive plants respond to nutrients in the environment showed that increasing available resources can promote the invasive plants adapting to the local environment^[23, 25].

Despite a substantial amount of research on the relationship between invasive plants and AM fungi^[8, 20, 23, 25], there is a lack of studies focusing on the relationship between AM fungi and *A. philoxeroides*. And the allocation of plant biomass between aboveground and belowground parts reflects the growth strategies and resource utilization patterns of plants under different growth substrates. Plants may tip the balance towards resource limited such as, acquisition of light energy (aboveground parts), and absorption of water and nutrients (belowground parts). This trade-off determines the growth strategies and adaptive capabilities of plants^[26–27]. Therefore, this study tests three hypotheses: (1) There is a positive feedback relationship between the invasive plant *A. philoxeroide* and AM fungi; (2) *A. philoxeroide* exhibits different mycorrhizal dependencies on two different types of mycorrhizal fungi; (3) The invasive plant *A. philoxeroide* allocates more root biomass.

Results

2.1 Infection rate of AM fungi

Compared with the control group (Fig. 1), the infection rates of AM fungi on *A. philoxeroides* were higher than that of AM fungi b. Infections were at the marginal significant ($F = 3.87$, $p = 0.05$) between A.

philoxeroide and AM fungi (a and b). Similarly, four types of growth substrates (soil treatment, cow manure, vermicompost, and mix manure) had obviously affected infection rate of AM fungi on *A. philoxeroide* ($F = 15.44$, $p < 0.01$). Four types of growth substrates didn't change mycorrhizal dependency ($F = 1.71$, $p = 0.17$) in *A. philoxeroide*. And two types AM fungi (a and b) didn't shift mycorrhizal dependency ($F = 1.40$, $p = 0.24$).

2.2 AM fungi and substrates on chlorophyll

For the chlorophyll content of *A. philoxeroides*, different nutrient substrates had no significant effect on its Chl a and Chl b content (Fig. 2, $p > 0.05$) with Chl a content fluctuating between 0.89 mg/g and 0.98 mg/g, and Chl b fluctuating between 0.33 mg/g and 0.34 mg/g.

The content of Chl a in *A. philoxeroides* treated with cow manure, vermicompost, and mix manure were the highest by AM fungi, and there was a significant difference between the soil treatment and the other treatment groups. The content of Chl a and Chl b in *A. philoxeroides* treated with AM fungi was higher than that of the corresponding AM fungi b treatment group (Fig. 2).

2.3 AM fungi on growth of *A. philoxeroides*

From Fig. 3, it showed that treatment with AM fungi a had an increasing effect on the invasive height in *A. philoxeroides*, however, two type of AM fungi had not affects invasive height of *A. philoxeroides* ($F = 0.91$, $p = 0.41$). On the contrast, different nutrient substrates (soil treatment, cow manure treatment, vermicompost treatment, and mix treatment) had obviously affected height of *A. philoxeroides* ($F = 6.81$, $p < 0.01$).

To the root length of *A. philoxeroides*, four different substrates had remarkably change it (Fig. 4, $F = 3.06$, $p < 0.05$). And AM fungi type didn't alter the root length of *A. philoxeroides*. And there was a significant difference ($p < 0.05$) compared to other treatment groups (cow manure treatment, vermicompost treatment, and mixture treatment).

Conversely, AM fungi type obviously changed root biomass of *A. philoxeroides* ($F = 5.88$, $p < 0.01$). And growth substrate didn't change the root biomass ($F = 0.59$, $p > 0.05$, Fig. 3). The root biomass of *A. philoxeroides* also increased with the increase of nutrient content in the growth substrates ($p > 0.05$). However, in the nutrient poor soil treatment, the root biomass of *A. philoxeroides* was the highest in the two groups treated with AM fungi. The types of AM fungi (a and b) had a significant impacted on the root biomass of *A. philoxeroides*. Although different types of nutrient substrates had an impact on the root biomass of *A. philoxeroides*, there was no interaction between the type of AM fungi and the nutrient substrate ($p > 0.05$, Fig. 4).

2.4 AM fungi effect on growth of *A. philoxeroides*

Growth substrates had affected numbers of invasive plant *A. philoxeroides* ($F = 3.06$, $p < 0.05$) rather than AM fungi type between a and b ($F = 0.50$, $p > 0.05$, Fig. 5). This indicated that the nutrients content took critical role in regulating leaf numbers of *A. philoxeroides*. AM fungi types had obviously altered the leaf

area of *A. philoxeroides* ($F = 4.07$, $p < 0.05$). And growth substrates didn't significantly change leaf area of invasive plant *A. philoxeroides* ($F = 0.48$, $p > 0.05$). That is to say, leaf number and leaf area showed different respond to growth substrates and AM fungi.

AM fungi types had significantly affected above ground biomass accumulation of *A. philoxeroides* ($F = 4.68$, $p < 0.01$, Fig. 6). And different growth substrates didn't obviously change above ground biomass accumulation of *A. philoxeroides* ($F = 1.76$, $p > 0.05$). To without AM fungi group, the above-ground biomass of *A. philoxeroides* showed an increasing trend with the increase of growth substrates treatment. The above ground biomass of *A. philoxeroides* treatment group by AM fungi (a and b) enhanced with the increase of nutrients in the treatment group. To the biomass, there was no significant interaction between the four growth substrates and AM fungi on the growth of *A. philoxeroides* ($F = 0.43$, $p > 0.05$).

Similarly, AM fungi types had obviously affected total biomass of each plant *A. philoxeroides* ($F = 5.17$, $p < 0.01$). And growth substrates didn't change total biomass accumulation of each plant *A. philoxeroides* ($F = 1.37$, $p > 0.05$, Fig. 6). To without AM fungi, the total biomass of *A. philoxeroides* showed an increasing trend with the increase of nutrient content in the growth substrates.

Discussion

3.1.1 AM fungi colonization and mycorrhizal dependency

The AM fungi b, which originates from a natural environment, has a stronger mycorrhizal dependency on its host *A. philoxeroides* than does the arbuscular mycorrhizal fungi a from an agricultural field. Judgment of symbiosis is mainly based on the comprehensive consideration of mycorrhizal fungi and hosts. The infection rate of AM fungi is an important indicator of the degree of symbiosis between fungi and plants, and can also be used to evaluate their ecological adaptability. Plants that form symbiotic relationships with AM fungi exhibit better growth conditions (biomass), which can also be used as an indicator to judge symbiotic relationships. In this study, the infection rate of AM fungi a on *A. philoxeroides* fluctuated between 18.61% and 31.31% in four different growth substrates. And the infection rate of AM fungi b on *A. philoxeroides* was slightly lower than that of AM fungi a, fluctuating between 5.89% and 13.44%. This supports previous studies that showed 11 exotic invasive species had infected by AM fungi^[13, 28]. Similarly, previous study showed good symbiotic relationship between *Flaveria bidentis* and AM fungi with high colonization under monoculture or mixed with native species^[29]. This may be invasive forb *Solidago canadensis* can exuded some carbohydrate material helping AM fungi colorization^[30]. Once AM fungi successfully infected the host plant, they obtained more nutrients for the plant and promoted its growth. In turn, the plant provided more carbohydrates to promote the growth of mycorrhizae^[31]. To the AM fungi a, total biomass of *A. philoxeroides* increased from 6.16–22.04%, compared to control group. Similarly, the total biomass of *A. philoxeroides* increased between 6.10% and 24.65% in the group treated with AMF b, compared to the control group.

Mycorrhizal dependency of *A. philoxeroides* ranged from 8.96–21.95% in four different growth substrates by AM fungi a. Likewise, the mycorrhizal dependency of *A. philoxeroides* in the four growth substrates fluctuated between 6.09% and 37.21% by AM fungi b. The mycorrhizal dependence in this study was significantly lower than the average mycorrhizal dependence of 260 plants in previous studies by 56%^[32]. This may be the sample belong to indigenous plants for 250 species, which has been formed a symbiotic relationship by long-term evolution. In this study, *A. philoxeroides* belong to grass plant, this in line with previous study grass have a low mycorrhizal dependency in adverse condition^[33]. And in nutrient-poor growing substrates and stress environment, the mycorrhizal dependency of the host plant on mycorrhizae is enhanced^[34]. In this study, AM fungi (a, b) in the soil treatment group of this study exhibited the highest mycorrhizal dependency, which are corroborated previous opinion.

Although the relationship between AM fungi and plants has shifted from parasitism to neutrality (no effect) and obligate symbiosis^[18, 35–36], and this coexistence phenomenon gradually exists for a long time, especially under extreme conditions such as nutrient deficiency and drought.

The physiological state of plants and the characteristics of fungal mycorrhizal partners in the soil environment are key factors affecting the formation of symbiotic relationships^[37]. Mycorrhizal fungi can secrete vitamins and protective effects on plants through interactions with soil microorganisms (pathogens and mycorrhizal symbionts). It is this mycorrhizal symbiosis that affects the nutrient uptake by the plant's underground root system and the plant's phytochemical signal^[38]. Therefore, different types of AM fungi influence plant growth by forming specific functional groups through their plant partners. Our study used alien species *A. philoxeroides* and two type AM fungi (a and b), there are experience 45 days growth, which is very short time and may form a weak symbiotic relationship. The comprehensive infection rate of AM fungi, biomass increase, and mycorrhizal dependence in this study confirmed hypothesis 1 and 2.

3.1.2 Biomass allocation

High resource can facilitate invasive plant. In the treatment group without inoculation with AM fungi, the biomass of *A. philoxeroides* was higher in the substrate with higher nitrogen content (Fig. 3). This are corroborated to previous research showed that high nitrogen fertilizer helped to improve competitive abilities of exotic *Flaveria bidentis*^[29]. Under the mediation of AM fungi, the above biomass of *A. philoxeroides* showed an increasing trend, fluctuating between 4.35% and 33.48%. In the nutrient poor soil treatment, above biomass of *A. philoxeroides* was increased by 18.90% and 33.48% in AM fungi (a and b), respectively, compared to the control group. That may be AM fungi have obviously promoted biomass accumulation of invasive plant.

This may be that AM fungi obtain mineral nutrients from other regions through hyphae to supply their host plants growth. Even some authors hold that there are formed novel symbioses cosmopolitan AM fungi^[19, 39–40], which can protect plant from pathogens and environmental stressors^[13, 41]. Thus, plant

growth is beneficial to AM fungi biomass accumulation, compared to control group. And it alters plant height, leaf number, leaf area, and root length in different growth substrate.

Similarly, in the four growth substrates, the root biomass of nutrient poor soil treated with AM fungi a increased by a maximum of 37.93% compared to non-inoculated AM fungi. After treatment with AM fungi b in nutrient poor soil, the root biomass increased by up to 83.30% compared to non-inoculated AM fungi, while the increase in growth substrates in the other three was much lower than this value. This study strongly supports the previous research's "optimal resource allocation hypothesis" which indicates that plants allocate their biomass to structures that help them obtain more constrained resources^[42–45]. And some researchers confirmed that higher resource supply significantly promotes the accumulation of above-ground biomass in invasive plants, compared to low resource conditions^[43–44]. This is supported our hypothesis that nutrient poor substrates are beneficial for plants to invest more root biomass under the intervention of AM fungi.

A high investment in belowground biomass promotes the acquisition of more water and soil nutrients, which in turn facilitates the construction of aboveground photosynthetic leaves, promoting the accumulation of aboveground biomass. The photosynthetic capacity per unit area is major related to specific leaf area with high growth rate^[28, 45].

In this study, the increase in leaf area of *A. philoxeroide* across four growth substrates treated with AM fungi a ranged from 3.93–31.11% compared to those without inoculated group. The nutrient poor soil treatment group showed the largest increase of 31.11% leaf area of under AM fungi a. Similarly, the leaf area of the four growth substrates treated with AM fungi b increased by 6.61–50.30%, compared to those not inoculated with AM fungi. And nutrient poor soil treatment group showed the largest increase of 50.30% leaf area of under AM fungi b (Fig. 5). Under different growth substrates, the beneficial effects of AM fungi providing nutrients to the host outweigh the cost of providing carbohydrate. And AM fungi form a mutually beneficial symbiotic relationship with host plants^[35, 46]. Under different growth substrates conditions, the beneficial effect of AM fungi providing nutrients to the host is less than the cost of the host providing carbon sources for AM fungi. And there are form parasitic relationships between host plants and AM fungi^[47]. Plants tend to absorb nutrient through their roots rather than AM fungi^[48]. And previous study should that AM fungi and growth substrate regulate plant growth^[49]. This study is in line with those research that different substrate composition can influence plant growth by changing the belowground root activity for foraging nutrient^[50–51].

Due to the fact that stems and roots are important reproductive organs of *A. philoxeroide*, the intervention of AM fungi (a and b) promoted an increase in the total biomass of *A. philoxeroide* in all four growth substrates studied. However, the increase is greater in the nutrient-poor soil substrates, implying that AM fungi can more effectively facilitate the invasion of *A. philoxeroide* in nutrient-depleted environments.

Conclusion

The growth substrate affects the leaf physiology (Chl a and Chl b content), leaf number, and resource acquisition organs (plant height and root length) of the invasive plant *A. philoxeroides*, ultimately achieving higher aboveground, underground, and total mass, thereby promote the spread and invasion of *A. philoxeroides* in China.

Different types of AM fungi (a and b) affect the light absorption capacity (Chl a and Chl b content), above ground nutrient acquisition ability, plant height, and underground acquisition ability of invasive plant *A. philoxeroides*, ultimately affecting its above-ground biomass, underground biomass, and total biomass.

These results indicate that the increase in nutrients during growth period affects the leaf area of invasive plant light harvesting organs and the chlorophyll content of light energy adsorbents, thereby promoting their growth. At the same time, it affects the root length of the invasive plant *A. philoxeroides* in order to obtain more nutrients. This means that growth substrates and AM fungi type affect their ability to capture resources, thereby promoting their successful invasion.

Implications

In this study, our result confirmed that mycorrhizal dependency value is lower some previous study. Some research hold that plant function group and soil environment take critical role in plant growth by AM fungi^[18]. And some considered that AM fungi type have promoted biomass increase. In contrast, some ancient AM fungi have less effect plant accumulation biomass than that of recent evolution AM fungi taxa^[6], which indicated that we should strengthen interaction between different AM fungi strain and plants.

On the other hand, we can see that soil nutrient pronounced affect the total biomass of *A. philoxeroides*. To some extent, this may be reflected invasion plant scavenge more source. For example, previous study showed that invasive plant increase height for sunlight, soil microbe, nitrogen, light and water and so on^[3, 56]. That is to say, environmental factors are key factors affecting the success of plant invasion. Furthermore, invasive plants adapt to different environments through organ plasticity because of the plasticity of plant organs. In this study, *A. philoxeroides* take measures by changing the number and area of leaves, root length, and root mass in different growth mechanisms and environments with AM fungi consisting with the environment. Previous studies have shown that invasive plant species *Erigeron canadensis* L can alter their reproductive strategies by changing their individual size, roots, leaves, and flowers in different habitats^[27]. In the further, it is necessary to strengthen the above ground and underground resources of plant growth resources in the habit, the plasticity of plant organs, and comprehensively explain the invasion mechanism of invasive plants by considering their reproductive strategies.

Materials and Methods

4.1 Materials

In this experiment, we studied *Alternanthera philoxeroides* were used as experimental material from abandoned farmland invaded by the species in Zunyi (Longitude: 107.05, Latitude: 27.71). Stems with similar growth conditions were selected from the middle part of the plants, with each stem segment measuring approximately 6 cm in length and containing one node. Soak the plant and stem nodes in 70% alcohol for 5 seconds before quickly removing, and insert them into the corresponding growth matrix. During this time, keep the water retaining tissue moist and use deionized water to replenish the water. The conditions are a daily temperature ranged from 23°C to 27°C. AM fungi a is *Rhizophorus intramadices* (BGCBJ09) isolated from the roots of host tomatoes. AM fungi b, also known as *Funneliformes mosseae* (BGC XZ02A), was isolated from its host (*Incarvillea younghusbandii*). The two AM fungi strain was provided by plant nutrition and resources institute of Beijing academy of agriculture and forestry (<http://www.baafs.net.cn/index.aspx>).

In this experiment, we used four types of growth substrates as described in detail below. The soil treatment is mainly composed of river sand, vermiculite, perlite, and loess, with a ratio of 1:1:1:1, including organic matter of 0.74%, and total nitrogen of 0.39‰. Cow manure treatment is mainly composed of river sand, vermiculite perlite, and cow manure, with a ratio of 1:1:1:1, including organic matter of 6.41%, and total nitrogen of 0.24%. Vermicompost treatment is mainly composed of river sand, vermiculite perlite, and vermicompost, with a ratio of 1:1:1:1, including organic matter of 4.87%, and total nitrogen of 1.13%. Mix treatment is mainly composed of river sand, vermiculite perlite, cow manure, and vermicompost, with a ratio of 1:1:1:1, including organic matter of 11.27%, and total nitrogen of 0.52%.

4.2 Experimental design

The experiment was conducted using a pot cultivation method, with each pot containing 2kg of sterilized substrate. The size of the plastic pot used is 20.5cm×14.5cm×18.5cm. The experiment is conducted in outdoors, with a daytime temperature of ranged from 23°C to 27°C. The substrate humidity is maintained at approximately 80%. The experiment considered two types of AM fungi (AM fungi a, b) and four types of growth substrates. The experimental treatments included: control group without arbuscular mycorrhizal inoculation. The inoculation treatment group consisted of soil group, cow manual, vermicompost, and mix manual, each inoculated with 15g of soil containing spores of AM fungi a (with an average of 3.2 spores per gram of soil). Similar to the previous treatment, the four types of growth substrates were inoculated with 15g of soil containing spores of AM fungi b (with an average of 3 spores per gram of soil). Three plants of *A. philoxeroide* were planted in each pot. Each treatment had three replicate pots, for a total of 36 pots.

4.3 Data measurement and analysis

4.3.1 Experiment

During the growth period, the plant height was measured using a tape measure. After 45 days of cultivation, the number and area of leaves were measured before harvesting. After harvesting, the above- and under-ground biomass of the plant, root length, and chlorophyll content were measured.

Fresh *A. philoxeroides* roots were collected, cleaned with potassium hydroxide, and then stained with Trypan Blue according to the previous reported method^[53]. The grid line intersection method was used for mycorrhizal root colonization^[54].

Calculation the infection rate of 100 root segments for each sample, and take the average as the AM fungi infection index for that sample.

$$\text{Colonization Rate (\%)} = \left(\frac{\text{Number of Colonized Root Segments}}{\text{Total Number of Root Segments Examined}} \right) \times 100$$

(1)

Number of Colonized Root Segments: the number of root segments (out of the total segments) that show visible signs of AMF colonization (e.g., presence of hyphae, arbuscules, or vesicles).

Total Number of Root Segments Examined: the total 100 number of root segments into which the roots were divided.

4.3.2 Determination of chlorophyll

Collect fresh *A. philoxeroides* leaves of treat groups, remove coarse leaf veins, and cut them into pieces. Weigh about 0.5 g of fresh leaves, add them to quartz sand and calcium carbonate, grind them in a mortar, extract them with a solvent, and finally measure the absorbance values at wavelengths of 663nm, 645nm, and 470nm using a UV spectrophotometer, calculating the photosynthetic pigment content according to the following formula1, 2, 3 and 4^[55–56].

$$\text{Chl a} = 12.7A_{663} - 2.69A_{645} (\text{mg/L}) \quad (2)$$

$$\text{Chl b} = 22.9A_{645} - 4.68A_{663} (\text{mg/L}) \quad (3)$$

$$\text{Car} = (1000A_{470} - 3.27C_a - 104C_b) / 229 \quad (4)$$

Chl a:Chlorophyll a concentration;Chl b:Chlorophyll b concentration□Car: Carotenoid concentration.

4.3.3 Data analysis

Preliminary data processing using Excel, perform statistical analysis on experimental data using SPSS 18 software generalized linear model (GLM, mixed-effects model), and perform multiple comparison tests on different processed data ($P < 0.05$).

Declarations

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Author contributions

Baocheng Zhang and Gang Zeng conceived and designed the experiments. Linlin Shen performed the experiments. Ziping Pan and Changbin Pan analyzed the data . All authors have reviewed and agreed with the paper.

Data availability

Data is provided within the supplementary information files

Competing Interest

The authors declare no competing interests.

References

1. Wang, R. and Feng, Y., 2009. The effects of leaf phenology, construction cost and payback time on carbon accumulation in invasive plants. *Acta Ecologica Sinica*, 2009(5): 2568-2577.
2. Julien, M.H., Skarratt, B. and Maywald, G.F., 1995. Potential geographical distribution of alligator weed and its biological control by *Agasicles hygrophila*. *Journal of Aquatic Plant Management*, 33(4): 55-60.
3. Zhang, B., Wang, P. and Jin, X., 2018. Ornamental Plants and Biological Invasion. *Northern Horticulture*(5): 178-183.
4. Brundrett, M., and Tedersoo, L., 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytol.*, 220(4): 1108-1115
5. Bender, S., Wagg, C. and Van der Heijden, M., 2016. An Underground Revolution: Biodiversity and Soil Ecological Engineering for Agricultural Sustainability. *Trends Ecol. Evol.*, 31(6): 440-452.
6. Säle, V., Azcon-Aguilar, C., Sánchez-Castro, I., Silva, G., Seitz, B., Sieverding, E., Van der Heijden, M., Oehl, F., 2021. Ancient lineages of arbuscular mycorrhizal fungi provide little plant benefit. *Mycorrhiza*, 31(5):559-576.
7. Jia, Y., Van der Heijden, M., Wagg, C., Feng, G. and Walder, F., 2020. Symbiotic soil fungi enhance resistance and resilience of an experimental grassland to drought and nitrogen deposition. *Journal of Ecology.*, 109:1365-1390.

8. Zhou, L., Zhou, L., Zhou, X., He, Y., Fu, Y., Du, Z., Lu, M., Sun. X., Li, C., Lu, C., Liu, R., Zhou, G., Bai, S., Thakur, M., 2022. Global systematic review with meta-analysis shows that warming effects on terrestrial plant biomass allocation are influenced by precipitation and mycorrhizal association. *Nature Communications* 13: 4914.
9. Van der Heijden, M., Martin, F., Selosse, M. and Sanders, I., 2015. Mycorrhizal Ecology and Evolution: The past, the present and the future. *New phytologist.*, 205: 1406–1423.
10. Zhang, Q., Yang, R., Tang, J., Haishui, Y., Hu, S., Chen X, Marcel, V., 2010. Positive Feedback between Mycorrhizal Fungi and Plants Influences Plant Invasion Success and Resistance to Invasion. *PLOS ONE*, 5(8): e12380.
11. Lekberg, Y., Gibbons, S., Rosendahl, S., and Ramsey, P., 2013. Severe plant invasions can increase mycorrhizal fungal abundance and diversity. *The ISME Journal*, 7(7): 1424-1433.
12. Yu, W., Liu, W. and Gui, F., 2012. Invasion of exotic *Ageratina adenophora* Sprengel. alters soil physical and chemical characteristics and arbuscular mycorrhizal fungus community. *Acta Ecologica Sinica*, 32(22): 7027-7035.
13. Chęcinska Sielaff, A., Polley, H., Fuentes-Ramirez, A., Hofmockel, K. and Wilsey, B., 2019. Mycorrhizal colonization and its relationship with plant performance differs between exotic and native grassland plant species. *Biological Invasions*, 21(6): 1981-1989.
14. Rinaudo, V., Bàrberi, P., Giovannetti, M. and Van der Heijden, M., 2010. Mycorrhizal fungi suppress aggressive agricultural weeds. *Plant and Soil*, 333: 7-20.
15. Urcelay, C., Vaieretti, M., Pérez, M. and Diaz, S., 2011. Effects of arbuscular mycorrhizal colonisation on shoot and root decomposition of different plant species and species mixtures. *Soil Biology & Biochemistry*, 43: 466-468.
16. Veiga, R., Faccio, A., Genre, A., Pieterse, C., Bonfante, P., Van der Heijden, M., 2013. Arbuscular mycorrhizal fungi reduce growth and infect roots of the non-host plant *Arabidopsis thaliana*. *Plant, cell & environment*. 223: 867-881.
17. Shah, M., Reshi, Z. and Khalsa, D., 2009. Arbuscular Mycorrhizas: Drivers or Passengers of Alien Plant Invasion. *Botanical Review*, 75: 397-417.
18. Romero, F., Argüello, A., de Bruin, S. and van der Heijden, M.G.A., 2023. The plant–mycorrhizal fungi collaboration gradient depends on plant functional group. *Functional Ecology*, 37(9): 2386-2398.
19. Bunn, R., Ramsey, P. and Lekberg, Y., 2015. Do native and invasive plants differ in their interactions with, arbuscular mycorrhizal fungi? A meta-analysis. *Journal of Ecology.*, 103: 1547–1556.
20. Han, X., Su, J., Yao, N. and Chen, B., 2020. Advances in root foraging behavior of exotic invasive plants. *Biodiversity Science*, 28(6): 727-733.
21. Bradley, B., Blumenthal, D., Wilcove, D. and Ziska, L., 2010. Predicting plant invasions in an era of global change. *Trends Ecol. Evol.*, 25: 310-8.
22. Enders, M., Havemann, F., Ruland, F., Bernard-Verdier, M., Catford, J., Gómez-Aparicio, L., Haider, S., Heger, T., Kueffer, C., Kühn, I., Meyerson, L., Musseau, C., Novoa, A., Ricciardi, A., Sagouis, A., Schittko, C., Strayer, D., Vilà, M., Essl, F., H, Philip E., van Kleunen, M., Kumschick, S., Lockwood, J.,

- Mabey, A., McGeoch, M., Palma, E., Pyšek, P., Saul, W., Yannelli, F., Jeschke, J., 2020. A conceptual map of invasion biology: Integrating hypotheses into a consensus network. *Global Ecology and Biogeography*, 29(6): 978-991.
23. Liu, Y., Oduor, A., Zhang, Z., Manea, A., Tooth, I., Leishman, M., Xu, X., van Kleunen, M., 2017. Do invasive alien plants benefit more from global environmental change than native plants? *Glob. Change Biol.*, 23(8): 3363-3370.
 24. Hoeksema, J., Chaudhary, V., Bala G., Karst, J., Koide, R., Pringle, A., Zabinski, C., Bever, James D., Moore, J., 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecol. Lett.*, 13(3): 394-407.
 25. Dawson, W., Fischer, M. and van Kleunen, M., 2012. Common and rare plant species respond differently to fertilisation and competition, whether they are alien or native. *Ecol. Lett.*, 15: 873-80.
 26. Zhou, L., Zhou, X., He, Y., Fu, Y., Du, Z., Lu, M., Li, C., Lu, C., Liu, R., Zhou, G., Bai, S., Thakur, M., 2022. Global systematic review with meta-analysis shows that warming effects on terrestrial plant biomass allocation are influenced by precipitation and mycorrhizal association. *Nat. Commun.*, 13.4914
 27. Zhang, B., Sun, Q., Huang, X. and Zeng, G., 2022. Resource allocation characteristics of invasive small flying pods of different sizes. *Jiangsu Agricultural Sciences*, 50(5): 107-113.
 28. Kleunen, M., Weber, E., and Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. 13(2): 235-245.
 29. Zhang, F., Li, Q., Chen, F., Xu, H., Inderjit, Wan., Fang H., 2017. Arbuscular mycorrhizal fungi facilitate growth and competitive ability of an exotic species *Flaveria bidentis*. *Soil Biology & Biochemistry*, 115(115): 275-284.
 30. Yuan, Y., Tang, J., Leng, D., Hu, S., Yong, J., Chen, X., 2014. An Invasive Plant Promotes Its Arbuscular Mycorrhizal Symbioses and Competitiveness through Its Secondary Metabolites: Indirect Evidence from Activated Carbon. *PLOS ONE*, 9(5): e9716
 31. Chen, E., Liao, H., Chen, B.-M. and Peng, S., 2020. Arbuscular mycorrhizal fungi are a double-edged sword in plant invasion controlled by phosphorus concentration. *New Phytologist.*, 226:295-300.
 32. Tawarayama and Keitaro, 2003. Arbuscular mycorrhizal dependency of different plant species and cultivars. *Soil Science & Plant Nutrition*, 49(5): 655-668.
 33. Brundrett, M., 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytologist.*, 154(2): 275-304.
 34. Camuy-Velez, L., Chakraborty, D., Young, A., Paudel, S., Elvers, R., Vanderhyde, M., Walter, K., Herzog, Chantal Banerjee, S., 2025. Context-dependent contributions of arbuscular mycorrhizal fungi to host performance under global change factors. *Soil Biology and Biochemistry*, 204: 109707.
 35. Johnson, N., 2009. Resource Stoichiometry Elucidates the Structure and Function of Arbuscular Mycorrhizas across Scales. *The New phytologist*, 185: 631-47.
 36. Johnson, N., 2013. The continuum concept remains a useful framework for studying mycorrhizal functioning. *Plant and Soil*, 363.

37. Willing, C., Wan, J., Yeaman, J., Cessna, A., Peay, Kabir G., 2024. Arbuscular mycorrhizal fungi equalize differences in plant fitness and facilitate plant species coexistence through niche differentiation. *Nature Ecology & Evolution* 8(12): 2337-2337.
38. Tedersoo, L., Bahram, M., Zobel, and M., 2020. How mycorrhizal associations drive plant population and community biology. *Science* 367(6480): eaba1223.
39. Moora, M., Berger, S., Davison, J., Opik, M., Bommarco, R., Bruelheide, H., Kühn, I., Kunin, W., Metsis, M., Rortais, A., Vanatoa, A., Vanatoa, E., Stout, J., Truusa, M., Westphal, C., Zobel, M., Walther, G., 2011. Alien plants associate with widespread generalist arbuscular mycorrhizal fungal taxa: Evidence from a continental-scale study using massively parallel 454 sequencing. *J. Biogeogr.*, 38: 1305-1317.
40. Nuñez, M. and Dickie, I., 2014. Invasive belowground mutualists of woody plants. *Biological Invasions*, 16(3): 645-661.
41. Smith, S. and Read, D., 2008. *Mycorrhizal symbiosis* (3rd edn.). Academic, Berlin.
42. Bloom, A., Chapin Iii, F.S. and Mooney, H.A., 1985. Resource Limitation in Plants– an Economic Analogy. *Annual Review of Ecology and Systematics*, 16: 363-392.
43. Ren, Z., Sun, Y. and Huang, W., 2023. Responses of invasive alien plant *Erigeron canadensis* L. to nutrient availability and fluctuations. *Plant Science Journal*, 41(5): 626-635.
44. Huang, Q. Fan, Z., Li, X., Wang, Y., Liu, Y., Shen, Y., 2018. Effects of nutrient addition and clipping on biomass production of invasive and native annual Asteraceae plants. *Weed Res.*, 58(4): 318-326.
45. Grotkopp, E., Rejmanek, M. and Rost, T., 2002. Toward a Causal Explanation of Plant Invasiveness: Seedling Growth and Life-History Strategies of 29 Pine (*Pinus*) Species. *The American naturalist*, 159: 396-419.
46. Bever, J., Dickie, I., Facelli, E., Facelli, J., Klironomos, J., Moora, M., Rillig, M., Stock, W., Tibbett, M., 2010. Rooting Theories of Plant Community Ecology in Microbial Interactions. *Trends Ecol. Evol.*, 25: 468-78.
47. Schulz, B. and Boyle, C., 2005. The endophytic continuum. *Mycological research*, 109: 661-86.
48. Eissenstat, D.M., Kucharski, J.M., Zadworny, M., Adams, T.S. and Koide, R.T., 2015. Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New phytologist.*, 208(1): 114-124.
49. Shen, K. et al., 2022. Effects of AMF on plant nutrition and growth depend on substrate gravel content and patchiness in the karst species *Bidens pilosa* L. *Front. Plant Sci.*, 13: 968719.
50. Facelli, E. and Facelli, J., 2002. Soil phosphorus heterogeneity and mycorrhizal symbiosis regulate plant intra-specific competition and size distribution. *Oecologia*, 133: 54-61.
51. Maestre, F., Bradford, M. and Reynolds, J., 2006. Soil nutrient heterogeneity interacts with elevated CO₂ and nutrient availability to determine species and assemblage responses in a model grassland community. *New phytologist*, 168: 637-50.
52. Funk, J. and Vitousek, P., 2007. Resource-Use Efficiency and Plant Invasion in Low-Resource Systems. *Nature*, 446: 1079-81.

53. Phillips, J.M. and Hayman, D.S., 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Transactions of the British Mycological Society, 55(1): 158-161.

54. Giovannetti, M. and MOSSE, B., 1980. An evaluation of techniques for measuring vesicular arbuscular infection in roots. New Phytol., 84(3): 489-500.

55. Wang, X. and Huang, J., 2015. Principles and Techniques of Plant Physiology and Biochemistry Experiments. [M]: Beijing. Higher Education Press.

56. Zhang, B., Peng, Y., Zang, L. and Qin, K., 2017. Plasticity of *Alerantlhera philoxeroites* in response to three kast habitats Guithaia, 37(6): 702-706.

Figures

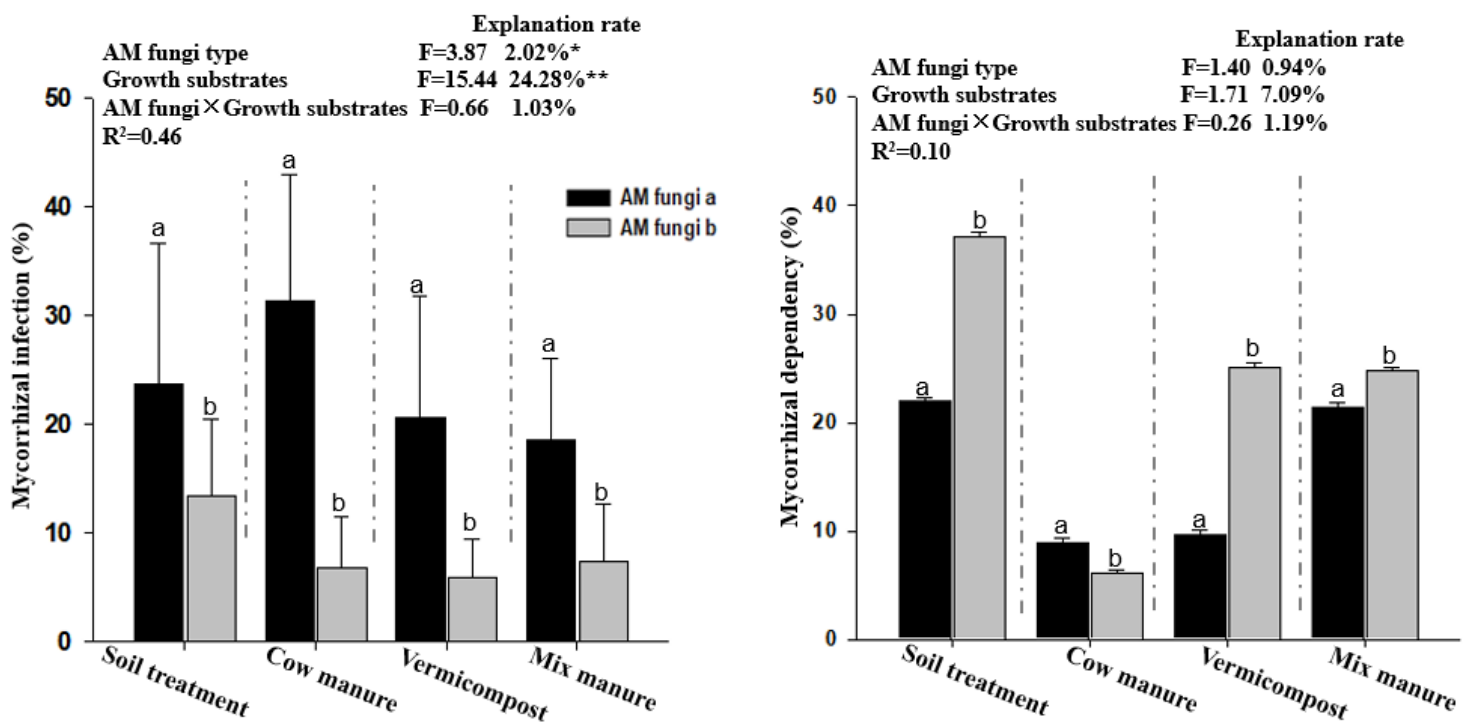


Figure 1

Effects of AM fungi (a and b) on the infection of *A. philoxeroides*

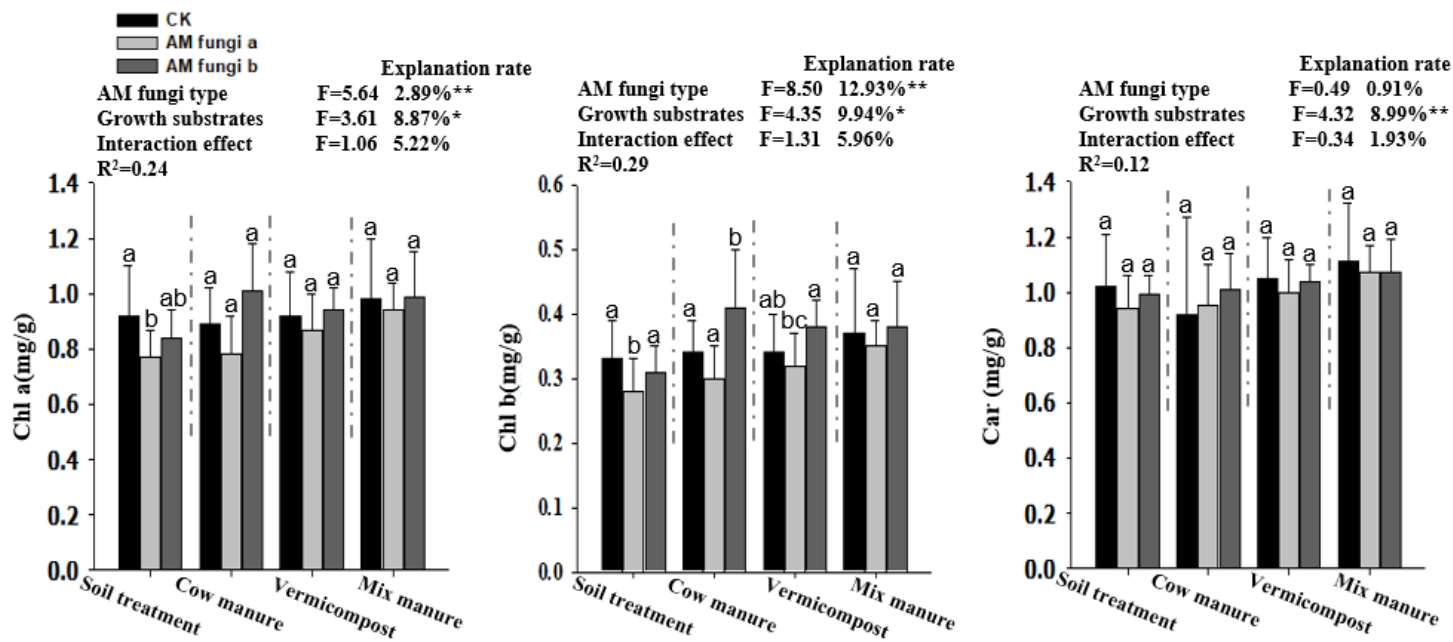


Figure 2

The effect of different growth substrates and treatment with AM fungi (strain a and b) on chlorophyll content in *A. philoxeroides* [abbreviation: Chl a:chlorophyll a; Chl b:chlorophyll b; Car: carotene]

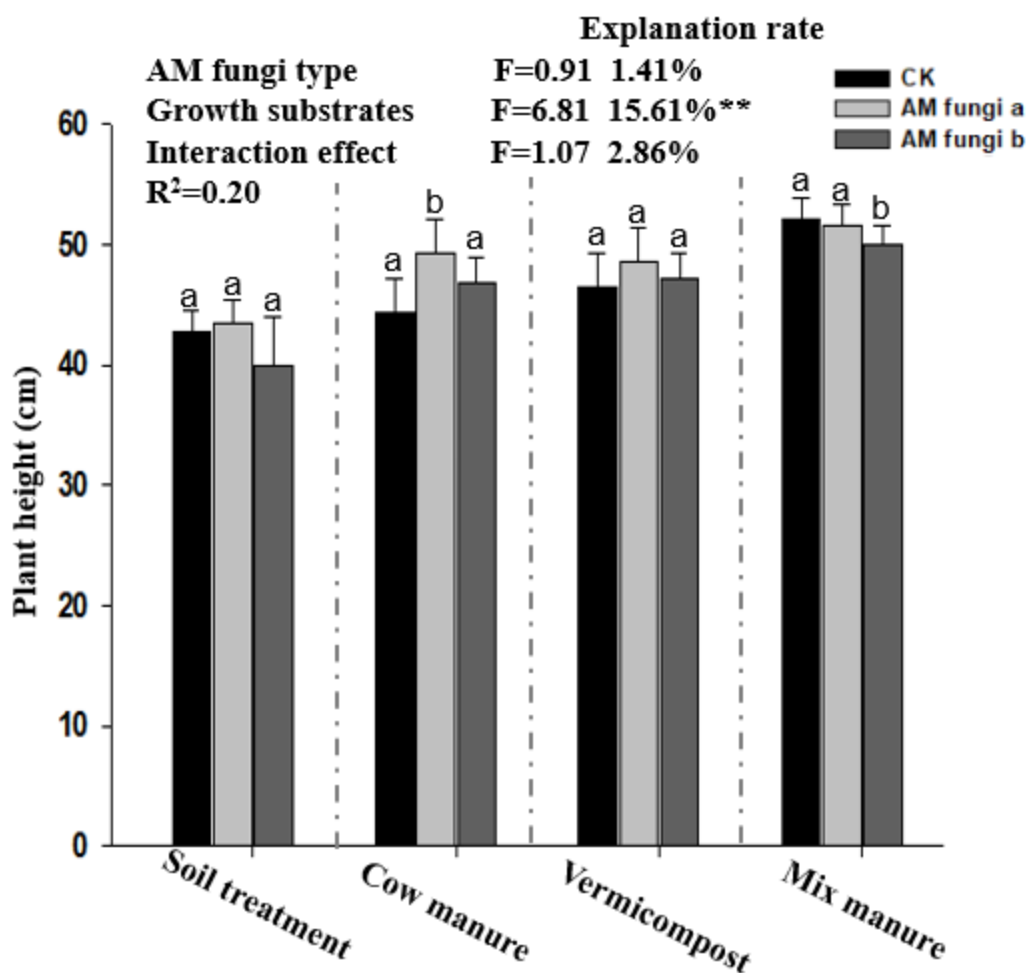


Figure 3

Height of *A. philoxeroides* treated with AM fungi(a and b) under different substrates treatment

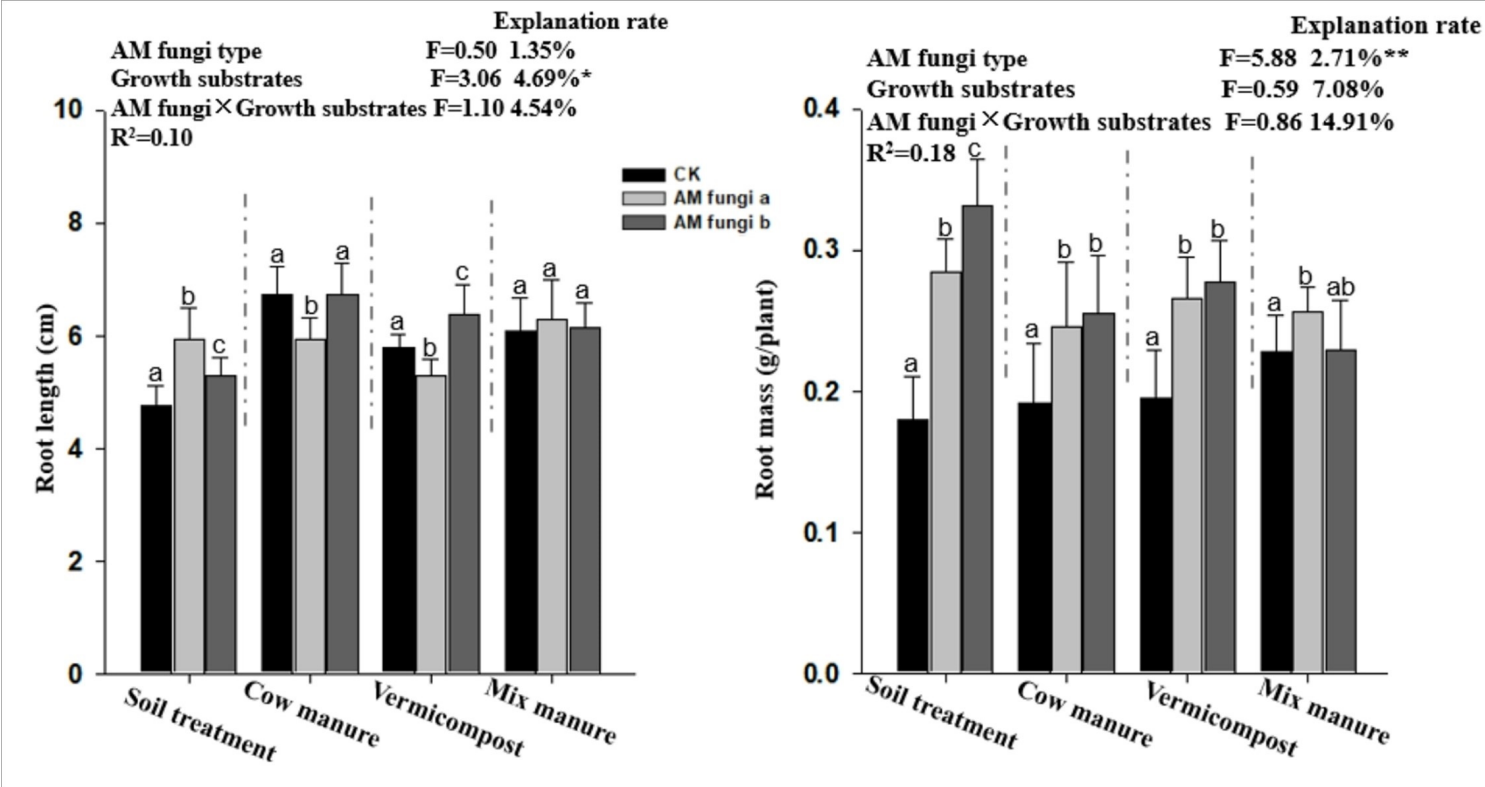


Figure 4

Effects of AM fungi and different substrates on root character of *A. philoxeroides*

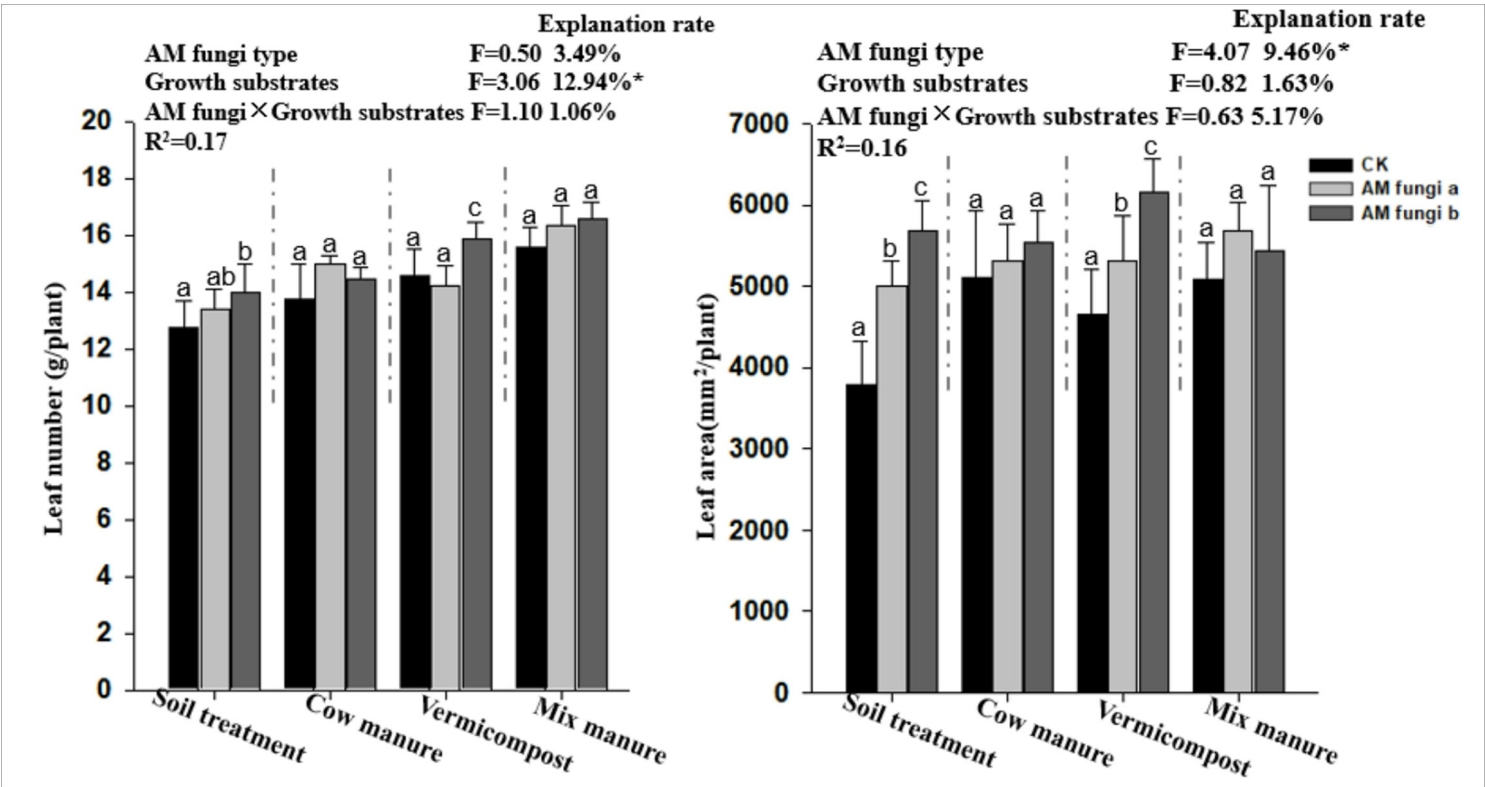


Figure 5

AM fungi (strain a and strain b) on the leaves of number and area of *A. philoxeroides* under different substrates

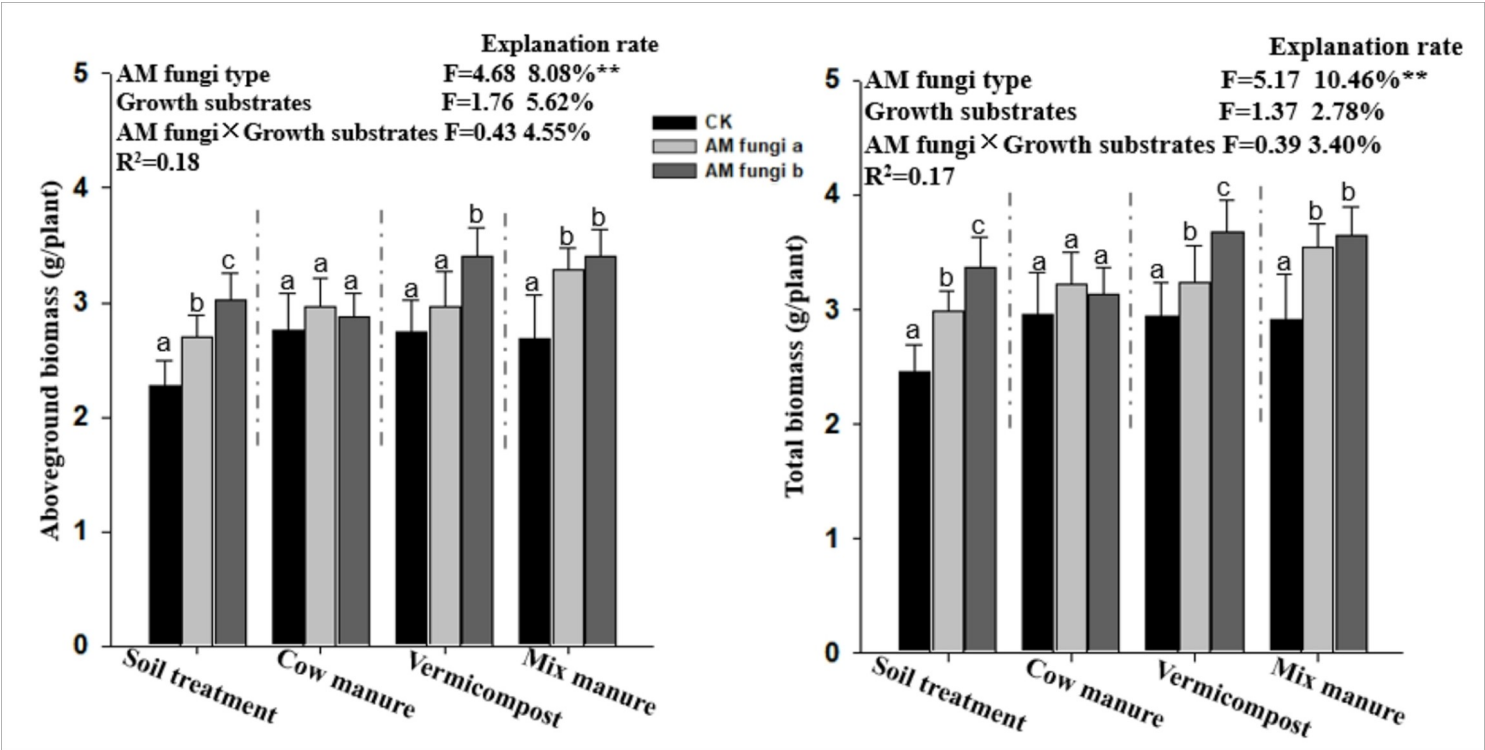


Figure 6

AM fungi (strain a and strain b) on the biomass of *A. philoxeroides* under different substrates

Supplementary Files

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