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RESEARCH ARTICLE

Arbuscular mycorrhizal symbioses improved biomass allocation and reproductive investment of cherry tomato after root-knot nematodes infection

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Abstract

Aims and methods This study aimed to evaluate the effects of four AMF inoculation treatments (*Funneliformis mosseae*, *Rhizophagus intraradices*, *Glomus versiforme* and a mixture of these three AMF strains) and *Meloidogyne incognita* inoculation on the growth and reproductive performance of cherry tomato (*Solanum lycopersicum* var. *cerasiforme*), and the effect of AMF on *M. incognita* density in soil under greenhouse conditions.

Results The results showed that AMF colonization could alleviate the biomass decline of cherry tomato caused by *M. incognita* and could reduce the density of *M. incognita* in soil. Moreover, AMF colonization promoted the biomass allocation of aboveground parts to alleviate the consumption of photosynthetic products by belowground parts of cherry tomato. Different AMF inoculation treatments had different effects on the uptake of nitrogen and phosphorus in the aboveground and belowground parts after *M. incognita* infection and they had interactive effects, indicating that AMF played an important role in regulating nutrient uptake of cherry tomato after *M. incognita* infection, and there were functional differences among different species. Furthermore, AMF colonization increased flower and fruit weight, and the resource investment to seeds under the stress of *M. incognita* infection.

Conclusion Our results clearly indicated that AMF significantly increased the growth and nitrogen uptake of cherry tomato inoculated by *M. incognita*. *F. mosseae* was the most effective treatment enhancing resistance to RKN and improving reproductive capacity of cherry tomato, indicating its application potential.

Keywords *Meloidogyne incognita* · Mycorrhizal symbioses · *Solanum lycopersicum* · Nutrient uptake · Reproductive traits

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Introduction

Plant root-knot nematodes (*Meloidogyne*) (RKN) are a category of nematodes that is extremely harmful to plants, which mainly endangers the normal growth of plants and limits plant productivity (Jones et al. 2013; Mukhtar et al. 2013). RKN are usually parasitic in the plant roots on which they feed to obtain nutrients needed for growth and reproduction, and they complete a part or all of their life cycle in the plant roots (Detrey et al. 2022). Typical galls are formed on

roots when RKN infect them. Galls are composed of giant cells, which are enlarged multi-nucleated cells usually derived from the vascular tissues of plants. Giant cells provide nutrients to RKN by reallocating plant metabolites (Philbrick et al. 2020). A large number of galls formed on the root system can reduce the ability of the root system to absorb and transport nutrients, inhibit the function of the root system, and affect the biomass allocation and nutrient supply of the plant (Khalid et al. 2021). The galls usually make the plant to show symptoms of wilting, yellowing, growth retardation, hinder the growth and development of the plant, and finally reduce the number and size of fruits (Bardgett et al. 1999; Schöning and Wurst 2016; Nacar and Özarslandan 2021). It should be noted that most plants, especially crops, are vulnerable to RKN. The biological stress caused by RKN has become a challenging problem to maintain sustainable development of plant productivity worldwide (Ismael and Mahmood 2020; Ralmi et al. 2021).

Arbuscular mycorrhiza formed between a variety of soil fungi (Glomeromycota) and plant roots is a typical mutualistic symbiosis. Most plants can form symbiosis with mycorrhizal fungi which are widely distributed in diverse ecosystems worldwide (Oehl et al. 2011; Berruti et al. 2016). Colonization by arbuscular mycorrhizal fungi (AMF) in the root systems of host plants is conducive to the growth and development of the host plants by promoting plant nutrient uptake (nitrogen and phosphorus) from soil, and also improves the resistance of host plants to stress from RKN infection (Lax et al. 2011; Jajoo and Mathur 2021). In particular, arbuscular mycorrhizal symbiosis can help host plants effectively resist infection by various plant pathogens and damage by herbivorous animals (Hol and Cook 2005; Rodriguez-Heredia et al. 2020). Studies have confirmed that AMF can promote and induce the production of defense-related metabolites (such as H_2O_2, jasmonic acid, peroxidase (POD) and polyphenol oxidase (PPO), etc.) in host plants to prevent diseases and pest attacks (Li et al. 2013; Vos et al. 2013; Wang et al. 2019; Ralmi et al. 2021). In addition, AMF can improve the resistance of host plants to disease to some extent by promoting plant growth and nutrient absorption and competing with other microorganisms for photosynthate and infection sites (Vos et al. 2013; Schouteden et al. 2015). In the AMF-plant symbiotic system, AMF mycelia can obtain carbon compounds from the host plant root and reserve it in the intraradical mycelium which acts as a carbon sink (Pfeffer et al. 2004). As the key position of pathogen propagation, the root system also is the first position of soil pathogen invasion. The availability of photosynthates in the plant root system is extremely important to pathogenic organisms because they infect plants mainly to obtain it (Wheatley and Poole 2018). A high demand of carbohydrate (sugar and lipid) for AMF may have a negative impact on infection by pathogenic organisms when AMF colonize plant roots. Therefore, the ability of AMF to absorb and collect photosynthates from the root system can affect the ability of plants to resist pathogenic organisms (Poveda et al. 2020; Dowarah et al. 2021).

At present, numerous studies have focused on the response of plant growth performance and reproductive traits to AMF or RKN inoculation (Campos et al. 2017; Detrey et al. 2022). However, people are interested in the interaction between AMF and RKN when they both infect plant roots, mainly because AMF may enhance the resistance of host plants to RKN which has potential application in pest control (Hol and Cook 2005; Lax et al. 2011). The interaction between AMF and plant RKN depends on a variety of factors, including host plant, AMF species and RKN species (Hol and Cook 2005). AMF may induce or increase host plant resistance, especially to RKN. The presence of AMF also could inhibit reproduction of RKN and help to alleviate the damage to plants caused by RKN (Lax et al. 2011; Banuelos et al. 2014). Moreover, some studies have confirmed that the symbiosis of AMF with plant roots can improve the growth and reproduction performance, and regulate the flowering and fruiting processes of host plants to some extent (Jimenez-Leyva et al. 2017; Bennett and Meek 2020; Gonźalez-Gonźalez et al. 2020). Unfortunately, these aspects have been neglected in most previous studies, especially how the reproductive traits of plants under RKN stress were regulated by AMF colonization.

Dwarf cherry tomato (*Solanum lycopersicum* var. *cerasiforme*) is an important crop and has the advantages of short shoot, short growth period and small space demand for cultivation. Moreover, we found that cherry tomato can be colonized by AMF and it was also easily infected by *Meloidogyne incognita* without AMF colonization recorded in our previously unpublished study. In this study, the effects of AMF

and RKN inoculation treatments alone or in combination on the growth, reproductive performance and mineral nutrient uptake of cherry tomato were investigated.

Materials and methods

Experiment materials

The seeds of dwarf cherry tomato (*Solanum lycopersicum* var. *cerasiforme*, Beijing Dongsheng Seed Industry Co., Ltd) were soaked with 0.5% potassium permanganate for 5 min and 5% $NaClO_3$ for 1 min for surface disinfection and rinsed thrice with sterile distilled water, and then were germinated on wet filter paper at 25 °C (constant temperature and 60% humidity) to obtain seedlings with two cotyledons.

Three species of AMF (*Funneliformis mosseae*, *Rhizophagus intraradices* and *Glomus versiforme*, Table S1) were used for fungal inoculation in this study. After extensive propagation of the three single AMF species as monosporal cultures in sand with *Trifolium repens* L. for 4 months, spores were isolated by wet sieving and the density of spores was examined under stereomicroscope (model B302, Chongqing Optec Instrument Co., Ltd, China) at × 100 magnification. Then, after subsequent dilution with sterilized sand, AMF strains containing an average of 25 spores/ g sand were obtained. In order to better reveal the joint interaction mechanisms of multiple AMF species, the three AMF strains were mixed equally by weight to get a mixture which was used for an AMF mixture inoculation treatment. The spore density of the mixed inoculum also was 25 mixed spores/ g sand.

Meloidogyne incognita which is a common RKN and is known to have strong ability to infect and reproduce on tomato roots was used in this study. Second-stage juveniles (J2) of a pure population of *M. incognita* were provided by the Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences. The pure population of *M. incognita* was inoculated into cherry tomatoes grown in sterile soil substrate. J2 of *M. incognita* were extracted by the modified extraction-tray method after two months of incubation in a 25 °C greenhouse and then were made into a suspension for subsequent inoculation (Ismael and Mahmood 2020).

A mixture of peat soil and sand was used as substrate for cherry tomato cultivation. Peat soil and sand were mixed in a volume ratio of 1:2. The mixed soil substrate was high-temperature sterilized twice (interval of 3 days) at 121 °C for 120 min each time. After natural cooling, the soil substrate was put into sterilized pots (inner diameter 16.5 cm, height 12.5 cm) with 2 L of mixed substrate in each pot. The nutrient contents of the substrate after sterilization were as follows: Organic matter content (OM): 2.17%, Total nitrogen (TN): 710.89 mg/kg, Available nitrogen (AN; alkali hydrolysis diffusion): 46.65 mg/kg, Total phosphorus (TP): 923.67 mg/kg, Available phosphorus (AP; 0.5 mol/L sodium bicarbonate extraction): 27.60 mg/kg, Available potassium (AK; ammonium acetate extraction): 617.95 mg/kg.

Experiment design

The AMF (Five levels: Without AMF inoculated (CK), *F. mosseae* (Fm), *R. intraradices* (Ri), *G. versiforme* (Gv) and mixed agent (Ma)) and RKN (Two levels: Inoculated (Y) and Non-inoculated (N)) inoculation were combined in a fully crossed manner as the two main factors. So, there were 10 treatment combinations, and each treatment combination was replicated 6 times, with one cherry tomato seedling per pot. Thus, the total sample size of cherry tomato seedlings was 60.

AMF and RKN inoculation

According to the experiment design, we dug a hole in the substrate in the middle of the pots and then 40 g sand (containing 1000 spores) was added to the hole. After moistening the soil substrate and inoculum with distilled water (500 ml), we gently placed a cherry tomato seedling on the AMF inoculum to ensure that the roots of the seedling were fully exposed to the AM fungus. Then a small amount of substrate was used to cover the fungus and seedling roots, and a small amount of distilled water was sprayed to keep the substrate around the seedling roots moist. In the control treatment, 40 mL water filtrate from non-sterilized AMF mixed inoculum (filtered by 20 μm filter) and 40 g sterilized inoculum were added. After AMF inoculation was finished, the pots were placed in a greenhouse.

All the cherry tomato seedlings were cultured in the greenhouse for 45 days (for the conditions of the greenhouse see below) and then three seedlings of each treatment were inoculated with RKN. Four 2 cm deep holes were dug evenly 1.5 cm away from the stem of each cherry tomato to ensure that the root system would be exposed, and the RKN suspension containing 2000 J2 was evenly injected into the holes. For the control treatment without RKN inoculation, only the same amount of RKN filtrate was added (i.e., the same volume of RKN-containing suspension was sieved through a 500 μm mesh).

Plant cultivation conditions

The greenhouse conditions for cherry tomato cultivation in this experiment are as follows: the photoperiod was 12 h/12 h (light/dark, no supplementary lighting), the optical quantum flux density was 550–600 μmol/m^2s, the temperature was 30/25°C (day/night), and the humidity was 40–50%. Cherry tomato seedlings were checked every day and watered using spray water from a watering pot to keep the substrate moist. The positions of plants were randomly exchanged every week and the growth performance of the cherry tomato seedlings was monitored regularly until the cherry tomato fruits were mature. The entire cultivation duration was 125 days and this experiment was conducted twice with replication in same conditions.

Measurement

The time when the first flower of each cherry tomato opened, and the single flower longevity were recorded. We define flowering time as duration from seedling cultivation to the full opening of the first flower. Flowers in full bloom were sampled to measure their diameters and single flower weight. The pollen number per flower was counted after its anthers were mashed and made into a suspension in 20% sodium hexametaphosphate solution. The pollen viability of cherry tomato was determined by the 2, 3, 5-Triphenyltetrazolium chloride (TTC) method (Sutyemez 2011). We recorded the number of flowers per plant every day until all the flowers withered.

The number of fruits was recorded until the plants were harvested at the 125th day after the cherry tomato seedlings were transplanted (that is the 80th day after inoculation with RKN). The aboveground stem and belowground root system of the cherry tomatoes were separated after being harvested. The root system of each cherry tomato was cleaned before the fresh weights of fruits, root, stem and leaves were measured. The stems, leaves, roots and fruits of each plant were dried at 80 °C for 48 h, then the dry weights were recorded. The root-shoot ratio and reproductive allocation also were calculated. The root-shoot ratio is the ratio of root biomass to aboveground biomass (stem, leaf and fruit) and reproductive allocation is the ratio of the fruit dry biomass to the total dry biomass of each plant. In addition, we separated the seeds from each cherry tomato fruit and record the number of seeds in each fruit after soaking and kneading the fresh fruit. The weight of seeds was determined after air drying. An elemental Analyzer (EA3100, Italy) and the molybdate colorimetry method were used to determine the concentrations of nitrogen and phosphorus in aboveground (stem and leaf) and belowground (root) parts after the dried plant samples were crushed and sieved (100 mesh). Phosphates were extracted by digesting a 0.2 g sample with 5 ml 1.84 g/ml H_2SO_4 and 6 ml 30% H_2O_2 (3 times to join). Then, the neutralized extracts were transferred and 5 ml molybdenum antimony anti indicator was added. Finally, the absorbance value was measured at 700 nm via automated molybdate colorimetry using a Shimadzu UV-1240 ultraviolet spectrophotometer (Sun et al. 2022).

Before drying, cleaned cherry tomato roots were randomly selected and cut into segments of about 1 cm. Mycorrhizal colonization was visualized by Trypan Blue staining, and the colonization of AMF in 100 root segments of each treatment was checked under a stereomicroscope (400×). When obvious arbuscular structures were observed, we considered a root segment to be successfully colonized. Mycorrhizal colonization was calculated as the ratio of the number of colonized root segments to the total number of segments observed (Brundrett et al. 1984).

The numbers of RKN egg masses on the cherry tomato roots under different treatments were counted after being stained with Eosin B solution, which

stains egg masses red and facilitates counting under a stereomicroscope. Due to the large number of galls in the root system (estimated at 2000 to 10,000 galls throughout the root system), to improve the efficiency of the galls count, we counted the galls in 5% (weight) randomly selected samples of the fresh roots and then galls number was divided by 5% fresh root weight (no. / g root) to estimate the infection status of the entire root system. The density of RKN (J2) in soil was determined from 100 g soil (fresh weight) by the modified extraction-tray method, and the total number of RKN was calculated under a stereomicroscope (100×), finally the density was converted to the number of RKN in 100 g of dry soil. The density of AMF spores in soil was measured from 20 g dry soil taken randomly from a well-mixed soil by wet sieving, the total number of AMF spores were counted using a stereomicroscope (100×), and all spores were counted for mixture inoculation treatment (Ma) (Gerdemann and Nicolson 1963; Djian-Caporalino et al. 2019; Detrey et al. 2022).

Data analysis

Before analysis, all data were checked to see whether they conformed to normal distributions with a one-sample Kolmogorov-Smirnov test and whether they conformed to variance homogeneity with either F-test (for two treatments) or Bartlett's test (for three or more treatments). Two-way ANOVA was used to detect the effects of AMF and RKN inoculation on total biomass, root-shoot ratio, reproductive traits, mycorrhizal colonization, AMF spore density and nitrogen and phosphorus concentrations of cherry tomato. One-way ANOVA was used to detect the effects of AMF on RKN density, root gall number and egg mass number. Because only two levels were set for RKN (inoculated and non-inoculated treatments), the *P* value of two-way ANOVA can already explain the difference between treatments, so we did not continue to perform post hoc multiple comparisons for this factor. We choose the Duncan multiple comparison to detect the significance of differences between treatments for AMF inoculation. *P* values were corrected by Benjamini and Hochberg (BH) method after multiple comparison. Differences were considered significant if $P < 0.05$. Statistical data are expressed as mean ± standard errors.

Results

Mycorrhizal colonization, RKN density, gall and egg masses numbers

No mycorrhizal structures were found in the treatments without AMF inoculation, and also no galls or nematode eggs were observed in the treatments without RKN addition. Mycorrhizal colonization and AMF spore density were respectively affected by RKN and AMF (Table S2). The addition of RKN significantly reduced the mycorrhizal colonization of Ma treatment compared with no RKN added (Fig. 1a). In the absence of RKN infection, AMF spore density after Fm inoculation was significantly higher than that of the Ri and Ma inoculation treatments, but there were no significant differences in the AMF spore density in soil under the four AMF treatments after RKN was added (Fig. 1b). Only Fm inoculation treatment significantly reduced the density of RKN in soil. The four AMF treatments did not significantly affected the numbers of gall and egg masses on the root system of cherry tomato (Table 1).

Nitrogen and phosphorus uptake by cherry tomato

AMF, RKN and their interaction significantly affected the uptake of nitrogen by cherry tomato (Table 2). In the absence of RKN, Ri treatment significantly increased the aboveground nitrogen concentration, while Ma treatment significantly decreased it. In the CK and Ri treatments, the aboveground nitrogen concentration with RKN addition significantly decreased compared with that without RKN addition. However, the aboveground nitrogen concentration increased after adding RKN in Ma treatment. When RKN was added, Fm and Gv treatments significantly increased the aboveground nitrogen concentration compared with CK, while Ri treatment significantly decreased it. The belowground nitrogen concentration with the addition of RKN significantly increased compared with that without RKN addition under CK and all four AMF treatments. Under the condition of RKN infection, Gv and Ma treatments significantly increased the belowground nitrogen concentration compared with CK (Fig. 2a).

The phosphorus concentration of cherry tomato was also significantly affected by AMF, RKN and their interaction (Table 2). All four AMF treatments

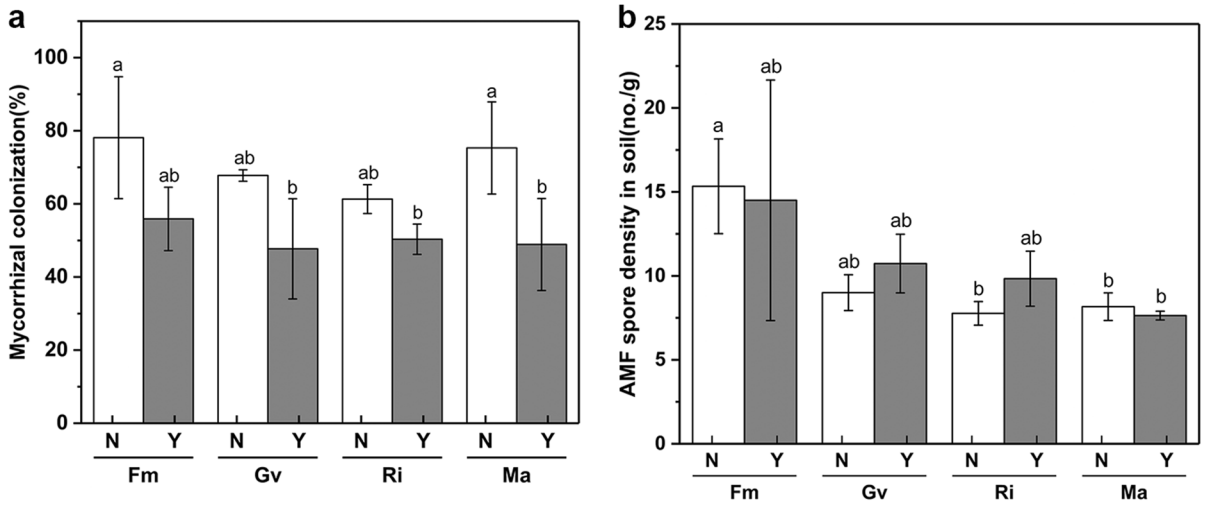

Fig. 1 Effects of AMF and RKN inoculation on mycorrhizal colonization of cherry tomato roots (**a**) and AMF spore density in soil (**b**). Vertical bars indicate ± SE ($n = 6$). N (non-shaded bars) means no RKN were added, and Y (shaded) means 2000 s-stage juveniles of RKN were added. Fm means inoculated *F. mosseae*, Ri means inoculated *R. intraradices*, Gv means inoculated *G. versiforme* and Ma means inoculated mixed inoculum. The different letter means that differences were significant by Duncan test ($P < 0.05$)

Table 1 RKN density, galls number and egg masses number under different AMF inoculation treatments (n ≥ 3)

Treatments	Index		
	RKN density (no. /g soil)	Galls number (no. /g root)	Egg masses number (no. /g root)
CK	437.63 ± 192.386a	172.86 ± 29.247a	53.80 ± 23.199a
Fm	185.99 ± 70.054b	160.49 ± 55.356a	46.95 ± 13.116a
Gv	358.89 ± 77.316ab	120.33 ± 64.213a	69.03 ± 35.224a
Ri	236.66 ± 86.804ab	123.93 ± 45.050a	56.62 ± 27.438a
Ma	296.61 ± 29.259ab	115.08 ± 11.718a	20.63 ± 8.979a

The same letter in the same column means that differences were not significant by Duncan test ($P > 0.05$)

significantly reduced the aboveground phosphorus concentration of cherry tomato with no RKN added. However, Ri and Ma treatments increased the belowground phosphorus concentration of cherry tomato without RKN addition. The phosphorus concentrations in both aboveground and belowground parts were significantly reduced after only RKN was added. However, when RKN were added, Gv, Ri and Ma inoculation treatments significantly reduced the aboveground phosphorus concentration compared with CK, while Fm and Ma significantly increased the belowground phosphorus concentration compared with CK (Fig. 2b).

The growth performance of cherry tomato

The total biomass of cherry tomato was significantly affected by AMF and RKN inoculation (Table 2). Without addition of RKN, the total biomass inoculated with Fm and Gv were significantly increased compared with the CK. The total biomass of cherry tomato infected by RKN was significantly lower than that of plants without RKN infection under all AMF inoculation treatments (Fig. 3a). The root-shoot ratio was significantly affected by AMF, RKN and their interaction (Table 2). Under Fm, Gv, Ma and control

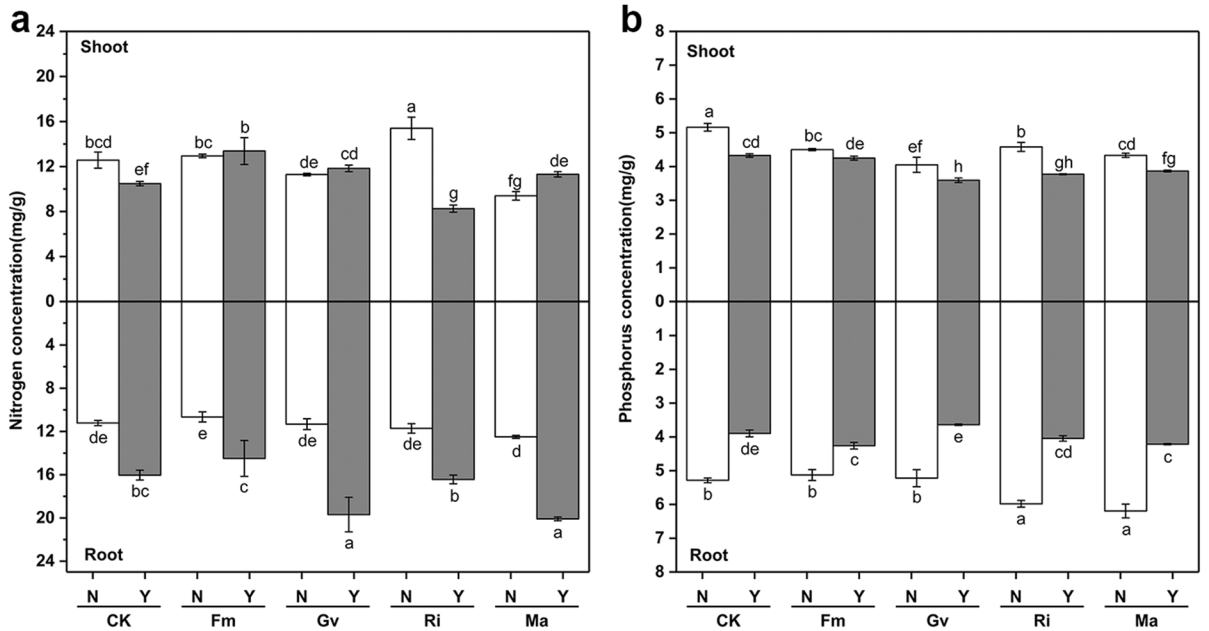

Fig. 2 Effects of AMF and RKN inoculation on nitrogen concentration (**a**) and phosphorus concentration (**b**) in both aboveground and belowground parts of cherry tomato. Vertical bars indicate ± SE ($n = 6$). N (non-shaded bars) means no RKN were added, and Y (shaded) means 2000 s-stage juveniles of RKN were added. CK means not inoculated with any AMF (control), Fm means inoculated *F. mosseae*, Ri means inoculated *R. intraradices*, Gv means inoculated *G. versiforme* and Ma means inoculated mixed inoculum. The different letter means that differences were significant by Duncan test ($P < 0.05$)

Table 2 Effects of AMF colonization, RKN infection and their interactions on growth, nutrient uptake and reproductive traits of cherry tomato ($n = 6$)

Index	AMF ($df = 4$)		RKN ($df = 1$)		AMF×RKN ($df = 4$)	
	F	*P*	*F*	*P*	*F*	*P*
Aboveground N concentration	11.87	**< 0.001**	23.69	**< 0.001**	38.06	**< 0.001**
Belowground N concentration	13.76	**< 0.001**	268.11	**< 0.001**	6.12	**0.002**
Aboveground P concentration	48.18	**< 0.001**	162.58	**< 0.001**	6.44	**0.002**
Belowground P concentration	23.15	**< 0.001**	696.53	**< 0.001**	11.96	**< 0.001**
Total biomass	8.32	**< 0.001**	101.34	**< 0.001**	1.46	0.240
Root-shoot ratio	6.38	**0.001**	83.72	**< 0.001**	4.29	**0.007**
Flowers per plant	2.78	**0.047**	19.51	**< 0.001**	1.46	0.243
Fruits per plant	3.43	**0.021**	9.88	**0.004**	2.30	0.083
Fruits dry weight	5.70	**0.002**	19.14	**< 0.001**	1.97	0.125
Seeds per fruit	4.44	**0.007**	4.84	**0.036**	3.78	**0.014**
Seed weight	30.14	**< 0.001**	104.12	**< 0.001**	2.73	0.058
Reproductive allocation	2.46	0.067	5.74	**0.023**	1.92	0.134

The *P* values with significant differences are bolded

treatments, the root-shoot radio with RKN addition was significantly increased compared with no RKN addition. After RKN addition, except for the Gv treatment, the other three AMF treatments significantly reduced the root-shoot ratio compared with CK (Fig. 3b).

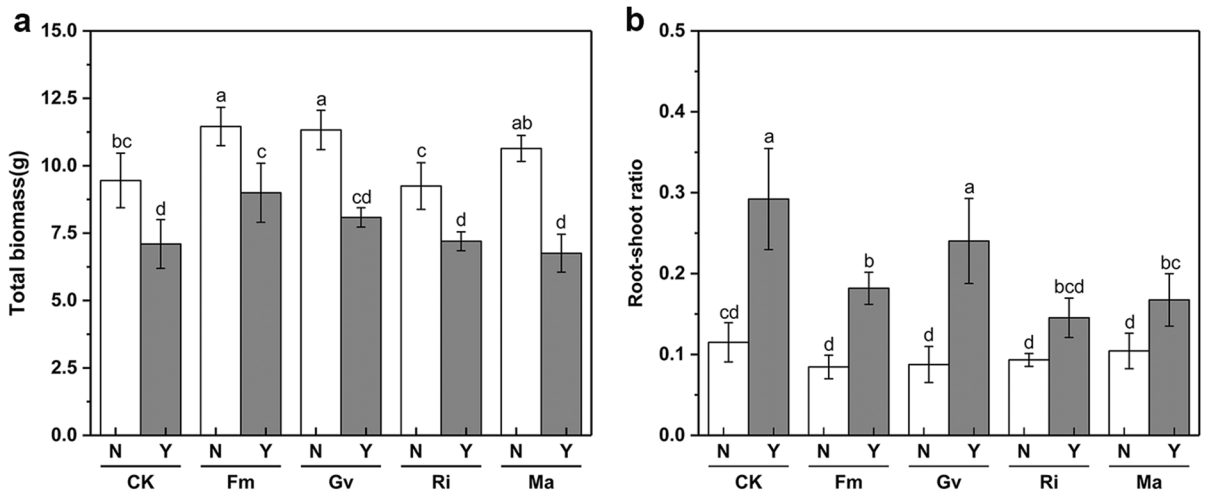

Fig. 3 Total biomass (**a**) and root-shoot ratio (**b**) of cherry tomatoes inoculated with AMF and RKN. Vertical bars indicate ± SE ($n=6$). N (non-shaded bars) means no RKN were added, and Y (shaded) means 2000 s-stage juveniles of RKN were added. CK means not inoculated with any AMF (control), Fm means inoculated *F. mosseae*, Ri means inoculated *R. intraradices*, Gv means inoculated *G. versiforme* and Ma means inoculated mixed inoculum. The different letter means that differences were significant by Duncan test ($P<0.05$)

Cherry tomato reproductive traits

AMF colonization, RKN infection and their interaction did not significantly affected flowering time, flower longevity, flower diameter, flower weight, pollen number or pollen viability of cherry tomato (Fig. S1a-f, Table S2). Flower number was significantly affected by AMF and RKN (Table 2). AMF inoculation alone had no significant effects on flower number compared with CK, while there were significant differences in flower number between the Gv and Ri treatments. The flower number in CK and Gv treatments decreased in the presence of RKN compared with that no RKN added (Fig. 4a). The Fruit number was also significantly affected by AMF and RKN (Table 2). It was only observed that the fruit number of Gv was higher than Ri and Ma inoculation treatments in the absence of RKN. Fruit number under CK, Fm and Gv treatments were significantly reduced when RKN was added compared with that without RKN (Fig. 4b).

Overall, fruit dry weight of cherry tomato was significantly affected by AMF and RKN (Table 2). Fm treatment significantly increased the fruit dry weight without RKN addition, while Ma decreased it. Under CK, Fm and Gv treatments, RKN infection significantly reduced fruit dry weight compared to that with no RKN addition (Fig. 4c). AMF, RKN and their interaction significantly affected seed number per fruit (Table 2). Without addition of RKN, the seed number of cherry tomato inoculated with Fm was significantly increased compared with CK. In the case of no AMF colonization (CK), the seed number in fruit was significantly increased after the addition of RKN. Compared with the CK, Gv and Ma treatments significantly reduced the seed number in fruits under the conditions of infection by RKN (Fig. 4d). The seed weight of cherry tomato was significantly affected by AMF and RKN (Table 2). When the RKN was not added, the seed weight with Gv, Ri and Ma treatments were significantly increased compared with CK. The seed weight with RKN addition was significantly decreased compared with that without RKN addition in all AMF treatments (Fig. 4e). The reproductive allocation of cherry tomato was only significantly affected by RKN (Table 2). The reproductive allocation of CK treatment without RKN addition was significantly higher than that with RKN (Fig. 4f).

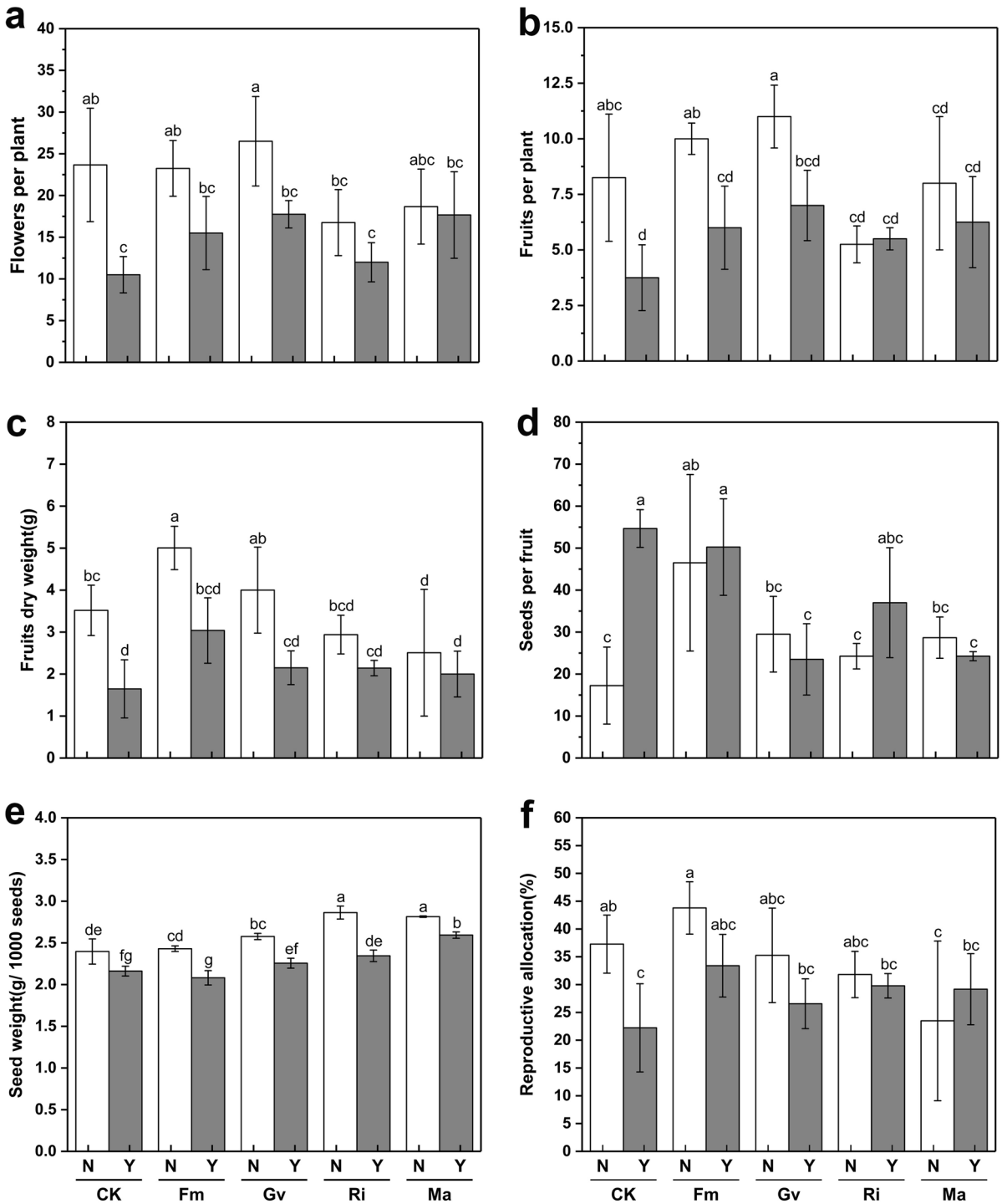

Fig. 4 Effects of AMF inoculation and RKN infection on reproductive traits of cherry tomato. **a** Flower number per plant; **b** Fruit number per plant; **c** Fruit dry weight per plant; **d** Seed number per fruit; **e** Seed weight (1000 seeds); **f** Reproductive allocation (the ratio of fruit dry biomass to whole plant dry biomass). Vertical bars indicate ± SE ($n = 6$). N (non-shaded bars) means no RKN were added, and Y (shaded) means 2000 s-stage juveniles of RKN were added. CK means not inoculated with any AMF (control), Fm means inoculated *F. mosseae*, Ri means inoculated *R. intraradices*, Gv means inoculated *G. versiforme* and Ma means inoculated mixed inoculum. The different letter means that differences were significant by Duncan test ($P < 0.05$)

Discussion

AMF colonization and RKN infection of cherry tomato

Our results showed that RKN infection may reduce mycorrhizal colonization and RKN may be an important factor affecting AMF colonization. Although the mycorrhizal colonization of cherry tomato ranged from 61 to 78%, there were no significant differences among different AMF inoculation treatments. We suggest that the colonization by all fungi probably reached an asymptote at the end of the experiment, which may be why there was no difference in mycorrhizal colonization. The mycorrhizal colonization of all four AMF treatments decreased (47%~55%) in the presence of RKN. According to previous studies, the presence of RKN may increase, decrease, or have no effect on mycorrhizal colonization, and the effect of RKN on mycorrhizal colonization depends on the AMF species (Waceke et al. 2001; Lax et al. 2011). The effect of RKN on arbuscular mycorrhizas may depend on the effects of RKN on plants rather than on the fungi directly (Lax et al. 2011). We also found that the spore density of Fm was highest of all AMF treatments when RKN were not added, but there were no significant differences in spore density after RKN were added. These results suggest that RKN may hinder the nutrient flow between roots and mycorrhizal symbionts, and thus may resist the development and efficiency of mycorrhizal symbionts (Cofcewicz et al. 2001).

We found that only inoculation with Fm reduced the density of RKN in soil. The four AMF treatments had no effects on the number of galls and egg masses in the root system of cherry tomato. Although the presence of AMF did not reduce the infection and reproduction of RKN in roots, it did help to limit the population density of RKN in the soil. In general, the positive effects of AMF on plant infected by RKN mainly were to reduce plant root damage by RKN and to inhibit RKN reproduction (Akhtar and Siddiqui 2008; Marro et al. 2018). Previous studies have shown that mycorrhizal symbiosis can lead to changes in the quantity or quality of plant root exudates such as amino acids, flavonoids, phenolic compounds and organic acids, etc. Because root exudates have negative effects on the chemotaxis, motility or survival of RKN, that might be an important reason for the decrease of RKN density in soil (Vos et al. 2012; Sharma and Sharma 2017). That the effects of AMF colonization on RKN infection response differs among species of AMF was verified in this study, and Fm may have greater potential to control RKN quantity in soil. If AMF colonization and development in the rhizosphere or within plants have a longlasting effect on inhibiting RKN, then then it has an important application prospect sustainable management of soil-borne root diseases (Khalid et al. 2021).

Nitrogen and phosphorus uptake

It is well known that AMF can increase the uptake and utilization of water and inorganic salts, such as nitrogen and phosphate, and increase N and P concentration in host plants (Diaz Franco et al. 2013; Ortas et al. 2013; Baum et al. 2015). In our study, we found that different AMF treatments had different effects on the accumulation of nitrogen and phosphorus in aboveground and belowground parts of cherry tomato. Our results for aboveground parts are consistent with previous studies that showed inoculation with AMF alone can limit the growth and phosphorus uptake of tomato (Facelli et al. 2010). In fact, the symbiotic effects of AMF differ among AMF species. The effect of AMF on nutrient uptake of host plants was also affected by soil substrate conditions. When the availability of phosphate in the environment is high, AMF may inhibit the growth and nutrient uptake of host plants (Koide and Mosse 2004). AMF colonization increased the nitrogen concentration in the belowground parts of cherry tomato inoculated with RKN. This is likely because nitrogen was allocated belowground to form enzymes to resist invasion by RKN (Vos et al. 2013; Przybylska and Obrępalska-Stęplowska 2020). When no AMF was inoculated, the aboveground and belowground phosphorus concentration of cherry tomato decreased after inoculation with RKN, but the presence of AMF could alleviate the decline of belowground phosphorus uptake. Studies have suggested that the biological control mechanism mediated by AMF is that AMF improve the ability of host plants to absorb phosphate which might be attributed to the contribution of fungal external mycelia as it has access to a large volume of soil (Schouteden et al. 2015; Khalid et al. 2021). This study also showed that AMF, especially Fm, had a positive effect on belowground phosphorus uptake. The interaction between AMF and RKN significantly

affected nutrient uptake by cherry tomato. Infection by RKN reduced the uptake of phosphorus, but AMF ameliorated the negative effects of RKN (Sharma and Sharma 2019). It is clear that arbuscular mycorrhizas of cherry tomato may improve host plant resistance to RKN infection by improving mineral uptake.

Growth response of cherry tomato

Our study confirmed that AMF colonization can promote total biomass accumulation of cherry tomato, especially the role of Fm in this aspect is outstanding. The four AMF treatments showed different effects on growth promotion, suggesting that the species of AMF, and the ecological effectiveness and functional compatibility of AMF may be important reasons for the differences in effects among AMFs (Vos et al. 2012; Jin et al. 2017). When facing the stress of RKN, mycorrhizal symbioses formed by pre-inoculation with AMF could effectively protect roots and alleviate the biomass reduction caused by RKN infection. Studies have shown that AMF can affect the development and reproduction of RKN by altering root exudates or producing plant antitoxins (such as glyceraldehyde) in roots (Marro et al. 2014; Vallejos-Torres et al. 2021). Consequently, the presence of AMF reduced the root damage caused by RKN infection and increased the biomass of cherry tomato (Vos et al. 2012). Colonization of AMF will preempt nutrition resources and space when AMF are inoculated prior to RKN. On the one hand, AMF can improve the uptake of mineral nutrients by host plants and regulate the hormone balance in the host plant (Fusconi 2014). On the other hand, AMF colonization may increase the content of defense metabolites in roots, which directly or indirectly leads to a disadvantage of RKN in competition for nutrients. From the perspective of carbon capture, we believe that the carbon capture capabilities of AMF differs from species to species, and correspondingly different AMF species have different biocontrol efficiency against RKN infection by competing for carbon (Dowarah et al. 2021). There were significant differences in cherry tomato biomass between Fm and the other two AMF species treatments when cherry tomatoes were infected by RKN, suggesting that Fm might have greater advantage than the other two species in resisting the negative effects of RKN on cherry tomatoes. Compared with the other AMF and Ma treatments, Fm has the ability of rapid early colonization on cherry tomato which is the main reason why Fm has a beneficial effect on plant performance. Especially, Fm also improved the growth performance of cherry tomato in the presence of RKN stress. Moreover, the interaction effects between AMF and RKN on plant growth is highly variable but generally positive and these effects are dependent on the plant, AMF, and RKN species, as well as prevailing environmental conditions (Campos 2020).

Our study showed that AMF colonization significantly affect the root-shoot ratio of cherry tomato when RKN was added, which indicated that AMF colonization is responsible for changes of the resource investment to the belowground part. We did not consider the effect of RKN weight on the plant biomass calculation here because the total biomass of all RKN in a root after drying is negligible for the dry weight of the root system (average fresh weight of RKN individuals is 1.3×10^{-7} g (Ferris 2010)). The increase in root biomass was mainly due to the increase of the number of giant cell (the main component of gall) caused by RKN infection. Additionally, cherry tomato increased aboveground resource allocation (the root-shoot radio decreased) when AMF and RKN were jointly inoculated, which indicated that the resource trade-off strategy of cherry tomato changed. The increase in the root-shoot ratio after the addition of RKN suggested that the infestation of RKN may induce plants to increase resource investment belowground to alleviate the nutrient absorption obstruction caused by RKN infestation (Nacar and Özarslandan 2021). In this study, AMF colonization could effectively inhibit the downward transfer of resources caused by RKN infection, suggesting that AMF play an important role in eliminating the adverse effects caused by RKN infection. AMF can not only enhance the mineral nutrient uptake capacity of plant, but also can increase its resistance to RKN infection (Rodriguez-Heredia et al. 2020). Furthermore, AMF colonization reduced the belowground biomass allocation of host plant when RKN added, suggesting that the positive feedback generated by AMF could offset the negative feedback caused by RKN infection, and changed the resource allocation strategy of cherry tomato (Wehner et al. 2010). AMF colonization may improve the nutrient accumulation ability of root systems of cherry tomato under RKN stress through reducing belowground resource consumption by entire root systems and increasing resource investment aboveground, so as to

improve photosynthetic ability and meet the resource demand of belowground symbiosis and RKN stress (Lehman and Rilling 2015).

Response of reproductive traits of cherry tomato

Our results showed that AMF alone had positive effects on seed number and seed weight of cherry tomato. A study about tomato found that an increase of phosphorus concentration can promote an increase in the number of plant seeds (Bona et al. 2017). In our study, the positive effects of AMF on seed production of cherry tomato may be driven by the environmental dependency of AMF-host plant symbiosis, such as the availability of phosphorus and N/P ratio (Johnson et al. 2015; Bennett and Meek 2020). Our results, however, showed that AMF did not increase the phosphorus concentration in cherry tomato, instead reducing the phosphorus concentration in the aboveground part which suggested that the increase of seed number in AMF colonized plants may be regulated by other factors. Moreover, AMF may directly affect seed weight by increasing endosperm resource supply, such as starch content which might be an important reason for the increase in seed weight (Bennett and Meek 2020). Our results indicated that single-species AMF inoculation could improve seed production and seed quality of cherry tomato, and was better than combined inoculation in controlled environments.

Our results demonstrated that RKN infection was negative to flower and fruit number, fruit weight and reproductive allocation, AMF symbiosis did not alleviate this stress. But AMF can affect sexual reproduction of cherry tomato after infestation by RKN, likely because of the ability of AMF to transport nutrients in soil. By supplying trace elements (such as zinc, calcium, magnesium, etc.) to host plants, AMFs are beneficial to mineral nutrient absorption, growth and flower bud formation of host plants, and can promote the production of flowers and fruits (Ortas et al. 2011; Nana et al. 2015; He et al. 2017; Herrera-Parra et al. 2021). This study found for the first time that AMF changed the sexual reproductive traits of cherry tomato under the stress of *M. incognita*. In future, understanding the interactions between AMF and RKN is an important challenge to reduce crop yield losses due to RKN (Schouteden et al. 2015).

Conclusion

Our results indicated that symbiosis with AMF plays a positive regulatory role in cherry tomato defense against RKN infection. Mycorrhizal symbionts can alleviate the decline of biomass and reduce the downward transfer of resources of cherry tomato caused by RKN infestation. This study found that AMF colonization can increase cherry tomato's reproductive investment and improve its reproductive capacity after being infected by RKN, and can reduced RKN density in soil and improve nutrient uptake by cherry tomato. Additionally, different AMF species had different benefits in response of cherry tomato to RKN stress, and *Funneliformis mosseae* may be more efficient in assisting host plants to resist RKN stress under this experimental settings. These results provided important references for understanding the role of AMF in controlling RKN invasion and improving the reproductive capacity of a host plant.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

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