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The better suppression of pepper *Phytophthora* blight by arbuscular mycorrhizal (AM) fungus than *Purpureocillium lilacinum* alone or combined with AM fungus

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Abstract

Purpose *Phytophthora* blight caused by *Phytophthora capsici* (*Pc*) is one of the most economically destructive soilborne diseases of pepper (*Capsicum annum* L.) on a global scale. Biocontrol using antagonistic microbes, such as *Purpureocillium lilacinum* (*Pl*) and arbuscular mycorrhizal (AM) fungus *Funneliformis caledonium* (*Fc*), is one of the significant strategies for ecologically sound plant disease management. The purpose of this work was to investigate the sole and combined suppression of pepper *Phytophthora* blight by *Fc* and *Pl*.

Materials and methods The 14-week pot experiment with three pepper plants per pot included five treatments: control (non-inoculation), inoculation with *Pc*, inoculation with *Pc* and *Pl* (*Pc* + *Pl*), inoculation with *Pc* and *Fc* (*Pc* + *Fc*), and inoculation with *Pc*, *Pl*, and *Fc* (*Pc* + *Pl* + *Fc*). Pots were randomly arranged with eight replicates per treatment. The incidence and severity of *Phytophthora* blight at plant full productive stage were recorded. The biomasses and N, P, and K concentrations of pepper shoots, roots, and fruits were all measured. In addition, root mycorrhizal colonization rate and soil pH, phosphatase activity, and available P concentration were also tested.

Results and discussion The inoculation of *Pc* induced both high incidence (92%) and severity (33%) of pepper *Phytophthora* blight, and the alleviating effects of *Pl*, *Fc*, and *Pl* + *Fc* were 46%, 79%, and 59%, respectively. The *Fc* significantly increased ($P < 0.05$) root mycorrhizal colonization, nutrient (N, P, and K) acquisition, plant biomass, and fruit yield of pepper, while *Pl* only significantly increased ($P < 0.05$) plant nutrient (N and P) acquisition and tended to increase the fruit yield. The *Pc*, *Pl*, and *Fc* all had additive effects on decreasing soil pH, but only *Fc* significantly increased ($P < 0.05$) soil phosphatase activity and available P concentration, contributing partly to the elevated P acquisition as well as the increased P concentrations in both shoot and root.

Conclusions Compared with the sole inoculation of *Fc*, the extra inoculation of *Pl* had negative effects on mycorrhizal colonization, soil P mobilization, and plant growth and nutrient acquisition. It suggests that AM fungus (*Fc*) has the superiority of formatting symbioses with plant roots and enhancing soil P mobilization for the suppression of pepper *Phytophthora* blight compared with *Pl*, and the joint application of different fungal agents to improve plant health needs careful consideration.

Keywords *Funneliformis caledonium* · Nutrient acquisition · *Phytophthora capsici* · Soil phosphatase · Soil available P · Soil pH

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1 Introduction

Pepper (*Capsicum annum* L.), which contains not only significant amount of vitamins A and C but also considerable antioxidant and anti-cancer capacity (Podsedek 2007; Chuah et al. 2008), is widely used in food, spices, and traditional medicine and has become a vital and highly profitable vegetable across the world. However, continuous monocropping of pepper often results in various cultivation obstacles like increase of soil pathogen populations (Khan et al. 2015), leading to severe plant disease and enormous yield loss. For example, *Phytophthora* blight, caused by *Phytophthora capsici*

Leonian and deemed as one of the most economically destructive soilborne diseases of pepper on a global scale, is difficult to control and often be a factor limiting pepper production in tropical areas with hot and humid climates (Reifschneider et al. 1992; Li et al. 2019). The application of germicides before the appearance of a disease, instead of once symptoms have appeared, is the most common practice for farmers to control diseases in conventional agriculture (Holmes et al. 2015). However, the excessive use of germicides has produced pathogen resistance (Bellón-Gómez et al. 2014) and has an effect not only on pathogens but also on non-target microbes (Santísima-Trinidada et al. 2018). Since disease control through chemicals (i.e., germicides) is becoming problematic, a number of alternative ways are proposed to alleviate the trend of chemical usage (Majid et al. 2016).

By comparison, overall speaking, biocontrol using antagonistic microbes, achieved through niche/nutrient competition, plant growth promotion, induced systemic resistance, antibiotic production, and colonization or parasitism against target pathogens, is one of the significant strategies for ecologically sound plant disease management (Sang et al. 2013). Yau et al. (2013) isolated a number of strains that can protect plants against blight caused by the *Phytophthora* species in greenhouse-grown pepper. Majid et al. (2016) tried to focus on all recommended strategies that might be effective against *P. capsici* but there is still a need to discover more antagonistic microbes. Furthermore, different biocontrol agents often do not show consistent disease suppression, and thus it is quite urgent to screen effective microbial strains or even consortium for future practical applications in the biocontrol of pepper *Phytophthora* blight.

Among soil microbes, arbuscular mycorrhizal (AM) fungi are ubiquitous mutualists that can form symbiotic associations with the roots of the majority of terrestrial plant species (Smith and Read 2008), including pepper (Hu et al. 2019). The most important of the symbiotic benefits is attributed to increased plant uptake of growth-limiting resources, notably P (Cobb et al. 2016). AM fungi are also antagonistic to plant pathogens via competing space/nutrients in the rhizosphere which constructs a defense barrier against pathogens, changing the patterns of root exudation which promotes the establishment of beneficial microbes, and inducing systematic resistance through which plant could counterattack pathogens in any area of the vegetal tissue (Azcón-Aguilar and Barea 1996; Hu et al. 2010). The protection degree varies with the pathogen involved and can be modified by soil and environmental conditions. With regard to pepper *Phytophthora* blight, the biocontrol by AM fungus has been well documented (Nemec et al. 1996; Ozgonen and Erkilic 2007; Reyes-Tena et al. 2017), but it is not clear if the prophylactic ability of AM fungi can be exploited in cooperation with other antagonists to improve plant growth and health.

On the other hand, *Purpureocillium lilacinum* (Thom.) Samson (formerly *Paecilomyces lilacinus*) is mainly considered as a typical entomopathogenic fungus with excellent performance in reducing nematode populations (Luangsa-ard et al. 2011; Rao et al. 2012). Apart from its pathogenicity to insects, *P. lilacinum* also possesses a plant growth promotion ability, leading to significantly larger plant sizes (Mansoor et al. 2007; Singh et al. 2013; Lopez and Sword 2015). This powerful growth vigor can lead to a greater tolerance towards pathogens and has got momentous achievement in biocontrol of plant diseases, such as tomato (*Lycopersicon esculentum* Mill.) *Fusarium* wilt (Munawar et al. 2015), and eggplant (*Solanum melongena* L.) *Verticillium* wilt (Lan et al. 2017), caused by *Fusarium oxysporum* f. sp. *Lycopersici* and *Verticillium dahliae*, respectively. Recently, the bioactivity of *P. lilacinum* in inhibiting the growth of notorious *P. capsici* was observed via confronting incubation (Wang et al. 2016). However, there is rare research focusing on the control of pepper *Phytophthora* blight by *P. lilacinum*.

With the information above, it was hypothesized that there would be an opportunity, which might be sound in theory, for exploiting a synergism between *P. lilacinum* and AM fungi in protecting pepper plants grown on *P. capsici*-enriched soils. However, the potential contributions of AM fungi and *P. lilacinum* in controlling pepper *Phytophthora* blight have not been systematically compared, and information regarding their cooperation is fragmented. Therefore, the present study was conducted to investigate the incidence and severity of *Phytophthora* blight, and plant biomass, fruit yield, and nutrient accumulation of pepper, in a sterilized soil inoculated with *P. capsici* in response to AM fungal and/or *P. lilacinum* inoculation, based on a greenhouse pot trial. The major aim of this study was to address the additive or exclusionary efforts of AM fungi and *P. lilacinum* on biocontrol of pepper *Phytophthora* blight. This work may contribute to developing application strategies of AM fungi and *P. lilacinum* for dealing with vegetable fields that is accumulated with pathogens.

2 Materials and methods

2.1 Soil, inocula, and seedling preparation

A surface soil sample was collected from a glasshouse with the continuous planting of pepper at Shizhu County (30°08′N, 108°11′E), Chongqing city, China. The soil is classified as Orthic Anthrosol. The air-dried soil sample was ground and homogenized using a wooden pestle and a 5-mm sieve and was autoclaved at 121 °C for 1 h on three successive days. The soil had a pH of 7.03 (H_2O) and contained 11.1 g kg^{-1} of organic C, 1.24 g kg^{-1} of total N, 0.550 g kg^{-1} of total P, 17.8 g kg^{-1} of total K, 3.65 mg kg^{-1} of mineral N,

58.6 mg kg^{-1} of available P (i.e., Olsen-P), and 345 mg kg^{-1} of available K.

The tested AM fungus *Funneliformis caledonium* (Nicol. & Gerd.) Trappe & Gerdemann 90036 was deposited at Institute of Soil Science, Chinese Academy of Sciences, Nanjing, China, and was propagated by a cycle of white clover (*Trifolium repens* L.) and a cycle of sudangrass (*Sorghum sudanese* (Piper) Stapf.) grown in an autoclaved (121 °C for 1 h on three successive days) substrate (4 months each cycle). The final inocula were a mixture of rhizospheric soil containing mycorrhizal root fragments, hyphae, and spores (> 100 g^{-1}) and were air-dried and sieved (2 mm). Meanwhile, the non-mycorrhizal inoculum was also prepared with the same sterilized substratum on which plant was cultivated under the same conditions.

The tested *Purpureocillium lilacinum* (Thom.) Samson was provided by Fujian Desheng Bioengineering Co., Ltd., Quanzhou, China. The tested *Phytophthora capsici* Leonian 36279 was obtained from Agricultural Culture Collection of China, Beijing, China. Both of them were cultured with a potato dextrose medium at 28 °C for 4 days and filtered into a piece of sterilized gauze, and then the mycelial paste was made by blender (MJ-25BM01A, Guangdong Midea, China) with sterilized water (m/v 1: 20 and 1: 4, respectively).

The seeds of chili pepper (Sujiao 5) were purchased from Jiangsu Seed CO. Ltd., Jiangsu province, China. Pepper seeds were sterilized with 0.5% NaClO, washed with distilled water, and then germinated in a hole tray filled with sterilized peat moss for 5 weeks.

2.2 Pot experiment

There were five treatments in this experiment: control (non-inoculation), inoculation with *P. capsici* (*Pc*), inoculation with *P. capsici* and *P. lilacinum* (*Pc* + *Pl*), inoculation with *P. capsici* and *F. caledonium* (*Pc* + *Fc*), and inoculation with *P. capsici*, *P. lilacinum*, and *F. caledonium* (*Pc* + *Pl* + *Fc*). Soil samples, 2.4 kg each, were put in a polyvinyl chloride pot (18 cm diameter × 18 cm depth), followed with a thin layer of 150 g AM inocula or non-mycorrhizal inoculum, 20 ml mycelial paste (1 g hypha) of *P. lilacinum* or not, 30 ml mycelial paste (7.5 g hypha) of *P. capsici* or not, and thereby three seedlings of pepper with eight leaves and 0.6 kg casing soils. The soil samples were completely mixed with chemical fertilizers (i.e., urea, superphosphate, and potassium sulfate) with the application rates of 135, 108, and 162 kg ha^{-1} of N, P_2O_5, and K_2O, respectively. Pots were randomly arranged with eight replicates per treatment. Plants were grown in a sunlit glasshouse with 30/22 °C day/night temperature, 40–60% relative humidity, and 75–85% water-holding capacity. After growing for 14 weeks, both the incidence of *Phytophthora* blight per pot and the disease category of each individual plant at full productive stage were recorded, followed with the harvest of fruits and plants and the collection of soil samples.

2.3 Blight analysis

The *Phytophthora* blight incidence was calculated as the number of wilted plants divided by the total number of plants, multiplied by 100%. The disease category was evaluated based on a 0–5 scale according to Sunwoo et al. (1996), where 0 = no visible disease symptoms, 1 = leaves slightly wilted with brownish lesions beginning to appear on stems, 2 = 30–50% of entire plant diseased, 3 = 50–70% of entire plant diseased, and 4 = 70–90% of entire plant diseased, and 5 = plant dead. Then, the *Phytophthora* blight severity was calculated for each pot as $[(1 \times n_1 + 2 \times n_2 + 3 \times n_3 + 4 \times n_4 + 5 \times n_5) / N \times (n_1 + n_2 + n_3 + n_4 + n_5)] \times 100\%$, where n_1–n_5 indicate the plant numbers with the respective disease category, and N indicates the highest disease category (Ren et al. 2015).

2.4 Plant analysis

The fresh pepper fruits were weighed immediately. The plants were divided into shoots and roots. All roots were thoroughly rinsed with tap water before drying, and weighed subsamples of fresh roots were used for mycorrhizal colonization assessment by the grid-line intersect method (Giovannetti and Mosse 1980) after clearing with 10% (*m*/*m*) KOH and staining with acid fuchsin (Phillips and Hayman 1970). All left root samples and shoot and fruit samples were weighed after oven drying at 70 °C for 48 h. Subsamples of dried and pulverized fruits, shoots, and roots were taken for acid (H_2SO_4–H_2O_2) digestion, followed by Kjeldahl digestion, molybdenum-ascorbic acid colorimetry, and flame photometry to measure N, P, and K concentrations (Lu 1999). To this end, the total N, P, and K acquisitions by pepper plant per pot were calculated.

2.5 Soil analysis

Soil samples were air-dried and homogenized by sieving through a 0.841-mm-mesh sieve. Soil pH was determined with a glass electrode using a soil-to-water ratio of 1: 2.5 (m/m). Soil phosphatase activity was determined according to the method of Tabatabai (1982) and is given in units of mg *p*-nitrophenol produced g^{-1} soil 24 h^{-1}. Soil-available P was extracted by sodium bicarbonate and determined by molybdenum blue spectrophotometry (Olsen et al. 1954). All these results were expressed on an oven-dried soil weight basis by correcting for water content in the soil (105 °C, 24 h).

2.6 Statistical analysis

The means and standard deviations of four replicates were computed. An analysis of variance was carried out using the

one-way ANOVA procedure with SPSS software. The comparison of mean effects was based on Duncan's new multiple range method ($P < 0.05$). The redundancy analysis was calculated by Canoco to elucidate the relationships between plant parameters, soil/mycorrhizal properties, and different treatments. The Pearson correlation coefficients were also calculated among plant, soil, and mycorrhizal parameters.

3 Results

3.1 The incidence and severity of *Phytophthora* blight, plant biomass, and fruit yield

Compared with the control, the *P. capsici*-inoculated (*Pc*) soil greatly increased ($P < 0.05$) both incidence and severity of *Phytophthora* blight (Fig. 1a, b) significantly decreased ($P < 0.05$) both shoot and root biomasses of pepper (Fig. 1c), and also tended to decrease the fruit yield (Fig. 1d). Compared with *Pc*, inoculation with *P. lilacinus* (+*Pl*) and/or *F. caledonium* (+*Fc*) significantly decreased ($P < 0.05$) both incidence and severity of *Phytophthora* blight, and the average alleviating effect was higher with +*Fc* (79%) than with +*Pl* (46%) or +*Pl* + *Fc* (59%). Meanwhile, only +*Fc* significantly increased ($P < 0.05$) both shoot and root biomasses and fruit yield of pepper, while +*Pl* and +*Pl* + *Fc* only tended to increase the fruit yield.

3.2 The tissue concentrations and total acquisitions of N, P, and K

Compared with the control, *Pc* significantly decreased ($P < 0.05$) the total acquisitions of N, P, and K by pepper (Fig. 2d) as well as P concentration in fruit (Fig. 2c) and tended to decrease both N and K concentrations in fruit and P concentrations in both shoot and root (Fig. 2a, b) but tended to increase N concentration in shoot. Compared with *Pc*, +*Fc* rather than +*Pl* and +*Pl* + *Fc* significantly increased ($P < 0.05$) both N and P concentrations in both shoot and root, and +*Pl* and +*Pl* + *Fc* rather than +*Fc* significantly increased ($P < 0.05$) both N and P concentrations in fruit. Meanwhile, +*Pl* and/or +*Fc* significantly decreased ($P < 0.05$) K concentration in shoot, and +*Pl* rather than +*Fc* and +*Pl* + *Fc* significantly increased ($P < 0.05$) K concentration in fruit. Therefore, the total acquisitions of N and P were significantly increased ($P < 0.05$) by +*Fc*, and also by +*Pl* and +*Pl* + *Fc*, while the total acquisition of K was significantly increased ($P < 0.05$) only by +*Fc*.

3.3 Mycorrhizal colonization rate and soil pH, phosphatase activity, and available P concentration

Mycorrhization was shown in the two *F. caledonium*-inoculated treatments (Fig. 3a), and the colonization rate with +*Fc* was significantly higher ($P < 0.05$) than with +*Pl* + *Fc*.

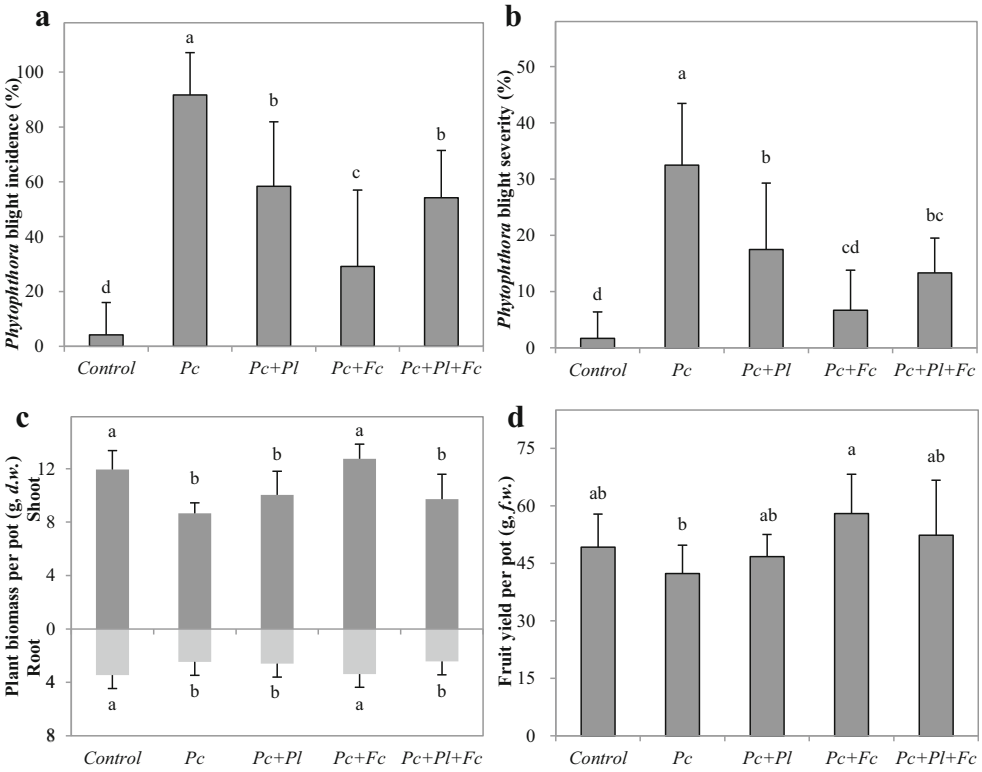

Fig. 1 The incidence (**a**) and severity (**b**) of *Phytophthora* blight and plant biomass (**c**) and fruit yield (**d**) of pepper (*Capsicum annum* L.). Control, non-inoculation; *Pc*, inoculation with *Phytophthora capsici*; *Pc* + *Pl*, inoculation with *P. capsici* and *Purpureocillium lilacinum*; *Pc* + *Fc*, inoculation with *P. capsici* and *Funneliformis caledonium*; *Pc* + *Pl* + *Fc*, inoculation with *P. capsici*, *P. lilacinum*, and *F. caledonium*. Vertical T bars indicate standard deviations. Values not topped by a same letter differ significantly ($P < 0.05$)

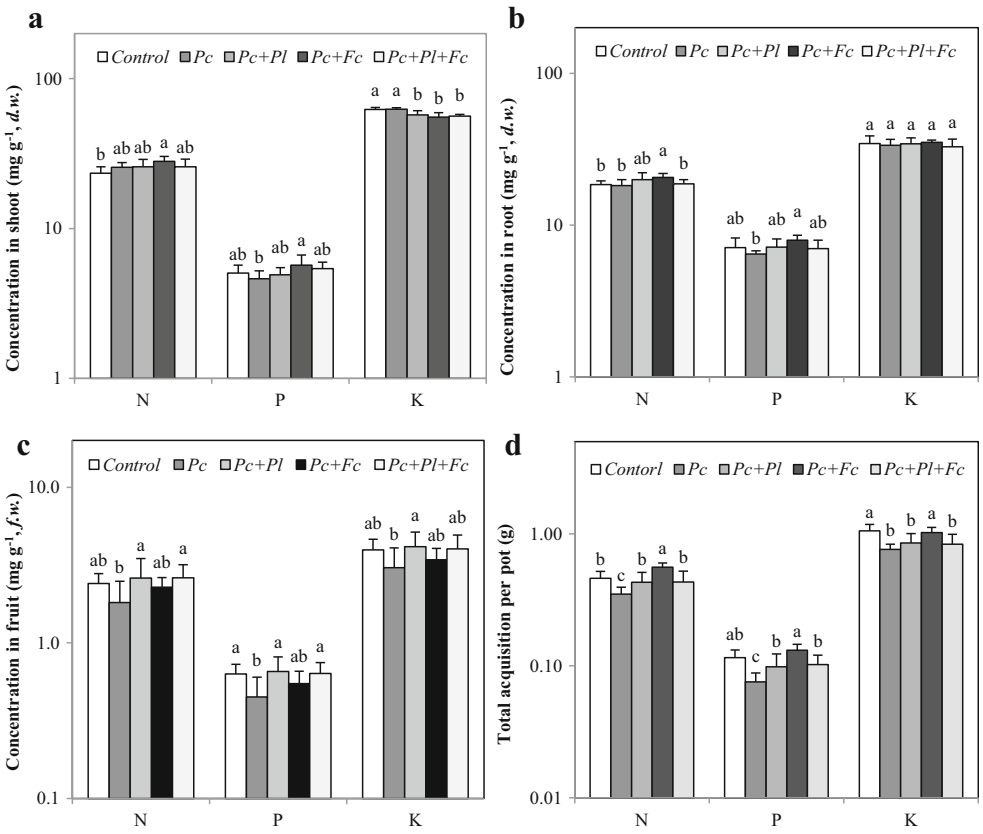

Fig. 2 The N, P, and K concentrations in shoot (**a**), root (**b**), and fruit (**c**) of pepper (*Capsicum annum* L.) and their total acquisition amounts per pot (**d**). Control, non-inoculation; *Pc*, inoculation with *Phytophthora capsici*; *Pc* + *Pl*, inoculation with *P. capsici* and *Purpureocillium lilacinum*; *Pc* + *Fc*, inoculation with *P. capsici* and *Funneliformis caledonium*; *Pc* + *Pl* + *Fc*, inoculation with *P. capsici*, *P. lilacinum*, and *F. caledonium*. Vertical T bars indicate standard deviations. Values not topped by a same letter differ significantly ($P < 0.05$)

Compared with control, *Pc* significantly decreased ($P < 0.05$) soil pH (Fig. 3b), but had no effect on soil phosphatase activity (Fig. 3c) and available P concentration (Fig. 3d). Compared with *Pc*, both + *Pl* and + *Fc* tended to decrease soil pH, but only + *Fc* significantly increased ($P < 0.05$) phosphatase activity and available P concentration, while + *Pl* + *Fc* significantly decreased ($P < 0.05$) soil pH and tended to increase phosphatase activity and available P concentration.

3.4 Redundancy analysis results

The inoculation of *Pc* had positive effects on both incidence and severity of blight, while *Pc* + *Fc* had the greatest negative influences on blight and the greatest positive effect on fruit yield (Fig. 4). Both blight incidence and severity negatively but closely corrected ($P < 0.05$ and 0.01, respectively) to total K acquisition, and both shoot and root biomasses significantly correlated ($P < 0.01$) to total K acquisition (Table 1). Both fruit yield and shoot biomass significantly correlated to total N ($P < 0.05$) and P ($P < 0.05$ and 0.01, respectively) acquisitions, and both total K and N acquisitions significantly correlated ($P < 0.05$ and 0.01, respectively) to total P acquisition. The fruit yield also significantly correlated ($P < 0.05$) to mycorrhizal colonization rate, soil phosphatase activity, and available P concentration, which were significantly correlated ($P < 0.01$) to each other.

4 Discussion

Keeping a balanced plant pathosystem with beneficial soil microbes to increase plant disease tolerance and suppress soilborne disease biologically is the major purpose of disease management by biocontrol in sustainable vegetable production systems (Lan et al. 2017). For example, Chen et al. (2016) suggested that *Streptomyces plicatus*, which showed 75% crown rot disease reduction in pot test, could be a good biocontrol agent to be integrated in the *Phytophthora* blight management program. The objectives of this study were to compare the suppression of pepper *Phytophthora* blight by arbuscular mycorrhizal (AM) fungus and *Purpureocillium lilacinum* and to investigate whether there was an additive biocontrol effort of AM fungus and *P. lilacinum*. The inoculation of *Phytophthora capsici* induced both high incidence (92%) and severity (33%) of pepper *Phytophthora* blight (Fig. 1a, b), and AM fungus showed a better biocontrol performance (with an alleviating effect of 79%) than *P. lilacinum* alone or combined with AM fungus, with the alleviating effects of 46% and 59%, respectively. Mechanisms causing such differential effectiveness between AM fungus and *P. lilacinum* are not fully understood but seem to be due to their physiological variances. Although both of them might compete space and nutrients against *P. capsici* in plant rhizosphere (Ozgonen and Erkilic 2007; Lan et al. 2017), AM fungus

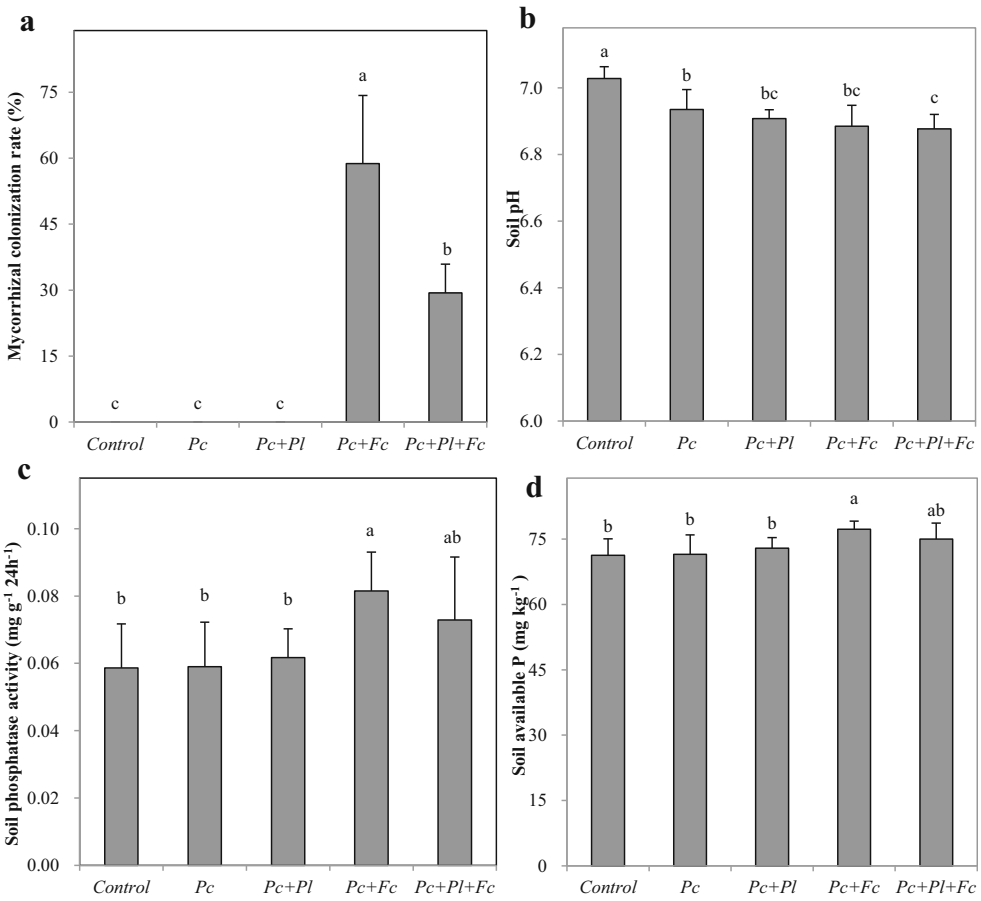

Fig. 3 The mycorrhizal colonization (**a**) in pepper (*Capsicum annum* L.) root, and soil pH (**b**), phosphatase activity (**c**), and available P concentration (**d**). Control, non-inoculation; *Pc* + *Pc*, inoculation with *P. capsici* and *Phytophthora capsici*; *Pc* + *Pl*, inoculation with *Purpureocillium lilacinum*; *Pc* + *Fc*, inoculation with *P. capsici* and *Funneliformis caledonium*; *Pc* + *Pl* + *Fc*, inoculation with *P. capsici*, *P. lilacinum*, and *F. caledonium*. Vertical T bars indicate standard deviations. Values not topped by a same letter differ significantly ($P < 0.05$)

could form good symbioses with plant roots (Fig. 3a), creating a defense barrier on roots, as well as the extraradical hyphal networks, both of which could block pathogen transmission (Reyes-Tena et al. 2017).

Besides the direct action upon high mycorrhizal colonization (Fig. 3a), AM fungus also induced higher plant nutrient acquisitions than *P. lilacinum* did (Fig. 2d), achieving structural functional compensation (Fig. 1c) in the diseased plants (Vierheilig et al. 2008). Although K was the crucial factor controlling blight incidence, P and K codetermined the blight severity (Table 1). Furthermore, P seemed to be the limiting nutrition factor, since there was no significant correlation between total K and total N acquisitions, but both of them significantly correlated to total P acquisition (Table 1). Then, take P for example, AM fungal inoculation also significantly increased soil phosphatase activity (Fig. 3c), leading to the release of P (Nannipieri et al. 2011) and the increase of available P concentration (Fig. 3d), contributing partly to the elevated P acquisition as well as the increased P concentrations in both shoot and root (Fig. 2a, b). In some cases, biocontrol has been regarded as an effective means of controlling plant diseases by altering soil enzymatic activities (Wang et al. 2015). The enhancement of soil phosphatase activity involve AM fungi directly and indirectly: AM fungal propagules themselves synthesize enzymes, and mycorrhizal roots release more root exudates containing enzymes (Wang et al. 2006). Although *P. lilacinum* had no similar effect on soil phosphatase activity and available P concentration, it significantly increased plant P acquisition as well. Various biocontrol agents possess properties to promote nutrient uptake via physiological and biochemical routes, and the improvement of soil microenvironment and thereby root vigor, which mirrors plant's ability of water and nutrient uptake as well as synthesis and storage of metabolites, may be a possible reason (Lan et al. 2017). Further research is thus needed to explore the growth-promoting ability of *P. lilacinum*, followed by a study on the mechanisms of secretase, resistance signal transduction, and so on. An alternative pathway to increase P phytoavailability in neutral or alkaline soils is to decrease soil pH by producing H^+ or by exuding organic acid (Li et al. 1991). In this study, *P. capsici*, *P. lilacinum*, and AM fungus all had additive effects on decreasing soil pH (Fig. 3b), but the increase of available P level was inconsistent with the decrease of pH (Fig. 4; Table 1), suggesting the mild acidification was not the major factor influencing P phytoavailability under this condition.

It is noteworthy that the combined biocontrol effects were lower than by AM fungus alone (Fig. 1a, b), suggesting an exclusionary but not additive effort between AM fungus and

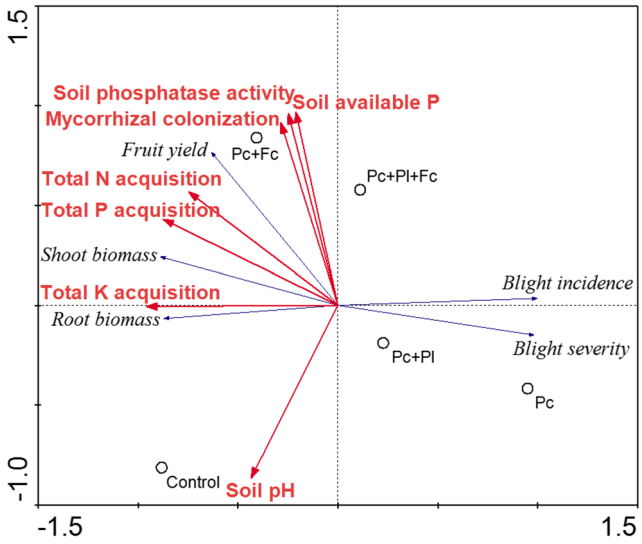

Fig. 4 Redundancy analysis of soil, mycorrhizal, and plant parameters with different experimental treatments. Control, non-inoculation; *Pc*, inoculation with *Phytophthora capsici*; *Pc* + *Pl*, inoculation with *P. capsici* and *Purpureocillium lilacinum*; *Pc* + *Fc*, inoculation with *P. capsici* and *Funneliformis caledonium*; *Pc* + *Pl* + *Fc*, inoculation with *P. capsici*, *P. lilacinum*, and *F. caledonium*. Projecting an object (treatment) at right angle on a response (blue) or an explanatory (red) variable approximates the value of the object along that variable; the angles between response and explanatory variables or between response variables themselves reflect their correlations, and the relationship between the centroid of a qualitative explanatory variable and a response variable is also found by projecting the centroid at right angle on the variable

P. lilacinum. Compared with the inoculation of AM fungus (+ *Fc*), the extra inoculation of *P. lilacinum* (+ *Pl*) had negative effects on mycorrhizal colonization, soil P mobilization, and plant nutrient acquisition and biomass (Fig. 3a, c; 2d; and 1c). Therefore, *P. lilacinum* might compete space and nutrients against AM fungus in rhizosphere due to the similar niche and biological features of fungi, inhibiting the mycorrhizal performance. In contrast, the combined application of *P. lilacinum* with *Pseudomonas aeruginosa* (a bacterium) resulted in greater shoot weight of pepper (Sultana et al. 2006) and greater suppression of tomato root knot (Siddiqui et al. 2000) than either component alone, and the co-inoculation of an AM fungal consortium and two actinomycete strains also had synergetic effects in vegetal growth promotion and protection against pepper wilt caused by *P. capsici* (Reyes-Tena et al. 2017). However, application of *P. lilacinum* had no effect on the frequency and intensity of tomato root colonization by AM fungus, and the extra inoculation of AM fungus did not enhance root protection from *Meloidogyne incognita* compared to single application of *P. lilacinum* (Rumbos et al. 2006). In contrast, application of both biocontrol agents significantly enhanced growth and yield of tomato plants (Udo et al. 2013). These results demonstrated that both AM fungus and *P. lilacinum* can be exploited in cooperation with antagonistic bacteria or each other, but the joint usage of different

Table 1 The Pearson correlation coefficients between plant, soil, and mycorrhizal parameters

	Blight incidence	Blight severity	Shoot biomass	Root biomass	Fruit yield	Total N acquisition	Total P acquisition	Total K acquisition	Mycorrhizal colonization rate	Soil pH	Soil phosphatase activity
Total N acquisition	− 0.728	− 0.794	0.931*	0.752	0.927*						
Total P acquisition	− 0.860	− 0.908*	0.966**	0.823	0.897*	0.975**					
Total K acquisition	− 0.959**	− 0.911*	0.959**	0.975**	0.627	0.799	0.891*				
Mycorrhizal colonization rate	− 0.255	− 0.386	0.559	0.318	0.908*	0.782	0.676	0.341			
Soil pH	− 0.467	− 0.277	0.206	0.507	− 0.369	− 0.165	0.008	0.457	− 0.601		
Soil phosphatase activity	− 0.215	− 0.373	0.493	0.214	0.906*	0.754	0.646	0.267	0.986**	− 0.692	
Soil available P concentration	− 0.177	− 0.341	0.476	0.179	0.885*	0.754	0.632	0.233	0.968**	− 0.741	0.992**

*Correlation is significant at the 0.05 level (two-tailed); **correlation is significant at the 0.01 level (two-tailed)

fungal agents to improve plant growth and health needs careful consideration.

5 Conclusions

AM fungus (*Funneliformis caledonium*) had a better biocontrol of pepper *Phytophthora* blight (caused by *Phytophthora capsici*) than *Purpureocillium lilacinum* alone or combined with AM fungus. AM fungus significantly increased mycorrhizal colonization, nutrient (N, P, and K) acquisition, plant biomass, and fruit yield of pepper, while *P. lilacinum* only significantly increased plant nutrient (N and P) acquisition and tended to increase fruit yield. The formation of symbioses with plant roots and the enhancement of soil P mobilization seemed to be the superiority of AM fungus. In addition, AM fungus and *P. lilacinum* might compete space and nutrients against each other in the rhizosphere, inducing an exclusionary but not additive effort on biocontrol. It demonstrated that the joint usage of different fungal agents to improve plant health needs careful consideration.

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