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Original Article

A Negative Feedback Regulation of Replanted Soil Microorganisms on Plant Growth and Soil Properties of Peach

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Abstract

Replant disease is one of the main growth limiting factors, interfering with plant growth and yield of stone fruit trees such as peach trees. The ecological feedback mechanisms by replanted soil microbes regulating peach growth and soil structure are rarely known. In our study, rhizosphere soils collected from 18-year-old peach trees were used to plant new peach seedlings, and all soil microbes (R) and soil microbes with the size of < 100 μm ($R_{<100}$) and < 40 μm ($R_{<40}$) were applied into peach rhizosphere. After 90 days of microbial inoculation, compared with no microbe treatment (R_0), the treatments such as R, $R_{<40}$, and $R_{<100}$ reduced plant growth performance (biomass, leaf number, plant height, and stem diameter) and root morphology (total length, projected area, surface area, diameter, and volume), with treatment R being the most inhibition of all other treatments. Similar response of treatment R was observed on changes in concentrations of chlorophyll *a*, chlorophyll *b*, and carotenoid. Interestingly, compared with R_0 treatment, $R_{<100}$ treatment produced a significant increase in glomalin-related soil protein (GRSP), percentage of water-stable aggregates in size of 0.25-0.5 mm, soil polyphenol oxidase activities and soil catalase activities. However, R treatment dramatically decreased the percentage of water-stable aggregates in size of 2-4 mm and soil peroxidase activities. Our results suggested that replanted soil microbes, especially with the size of < 100 μm, played a strong negative role on plant growth and rhizosphere biology of peach.

Keywords: biomass; chlorophyll; GRSP; soil enzymes; soil microbes

Introduction

Peach (*Prunus persica* L. Batsch) is globally a kind of deciduous fruit trees, which has a long history of cultivation. However, peach cultivation often faces a common problem, popularly known as soil replant disease, which results in a variety of symptoms like reduced growth, severe gummosis, leaf chlorosis, root browning, reduced yield, and even tree death (Bent *et al*., 2009; Tewoldemedhin *et al*., 2011). Changes soil microbiome are considered most important driving factor to such problem due to gradual shift from high-fertility bacterial to low-fertility fungal types (Sun *et al*., 2015). According to Benzri *et al*. (2005), soil bacteria such as *Bacillus*, decomposed cyanogenic glycosides under peach roots to produce some toxic substances (i.e., benzoic acid, cyanohydrogen acid, etc.).

Soil microorganisms including bacteria, fungi, actinomycetes, and symbiotic microbes such as rhizobia and mycorrhizae have an important role in process like nutrient acquisition (Sprent, 2001), nitrogen and carbon cycling (Kowalchuk and Stephen, 2001; Hogberg *et al*., 2001), and soil aggregate formation (Rillig and Mummey, 2006). In addition, soil microbes can operate through two major mechanisms, popularly known as positive or negative feedback regulation mechanism in the process of interaction between plants and soils (Lü and Wu, 2018). In positive feedback, roles of soil microbes such as plant growth promoting rhizobacteria (PGPR), phosphate-solubilizing bacteria (PSB), and arbuscular mycorrhizal fungi (AMF) are well established in promoting plant growth, improving soil structure, and strengthening the resistance against biotic and abiotic stress (Bhattacharyya and Jha, 2012; Vimal *et al*., 2017). Zhang *et al*. (2015) further demonstrated that inoculation with an arbuscular mycorrhizal fungus *Funneliformis mosseae* on a replanted peach significantly improved soil structure. In negative feedback, soil microbes accelerate the off-site movement of nutrients, hinder plant growth, and reduce crop productivity. In this regard, large number of pathogens, parasites, and some plant-eating animals compete with plants for the carbon and other nutrients (Bever *et al*., 1997; Burdon *et al*., 2006).

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In this background, the present study was aimed to evaluate the inoculation response of replant soil microbes in plant growth and soil properties of peach (*P. persica* L. Batsch) under controlled potted conditions.

Materials and Methods

Experimental set-up

Seeds of peach provided by the Institute of Fruit and Tea, Hubei Academy of Agricultural Sciences, Wuhan, China, were germinated in autoclaved (121 °C, 0.11 MPa, 2 h) sands with an average day/night temperature of 27/20°C and relative humidity of 80%. After one month, 6-leaf-old peach seedlings with uniform size were transplanted into 2.5-L plastic pots supplied with 2.5 kg autoclaved (121 °C, 0.11 MPa, 2 h) soils. The soil was collected from the rhizosphere of 18-year-old *P. persica* cv. Yuhualu grafted on *P. persica* L. Batsch in the Boksugol (30°25′15.1″N and 112°08′06.6″E) near the west campus of Yangtze University in Jingzhou, Hubei, China. The characteristics of the soil are pH 6.1, available P 12.5 mg/kg, and organic carbon 11.2 mg/kg.

In addition, a portion of collected soil was passed through 2 mm sieve, soaked with sterile water (soil : water = 1 : 2, v/v) for 24 h, filtrated with nylon meshes of Φ 100-μm and Φ 40-μm, and collected the filtrates named respectively, as R<100 and R<40 (Benzri *et al*., 2005).

Experimental design

The experiment was carried out in randomized blocked design with four treatments involving in different sizes of soil microbes: (i) autoclaved (121 °C, 0.11 MPa, 2 h) soils without any native microbes (R_0); (ii) autoclaved (121 °C, 0.11 MPa, 2 h) soils supplied with supernatants of < 40 μm sized microbes ($R_{<40}$); (iii) autoclaved (121 °C, 0.11 MPa, 2 h) soils supplied with supernatants of < 100 μm sized microbes ($R_{<100}$); (iv) collected fresh soils containing all native microbes (R). Each treatment was replicated five times, with a total of 20 pots.

After five days of transplanting, peach seedlings with $R_{<100}$ and $R_{<40}$ were watered with 100 mL supernatants of < 100 μm and < 40 μm microbes into pots at every five days, whilst a 100 mL distilled water/pot was supplied into the R- and R_0-treated pots.

Variable determinations

All the peach seedlings were harvested after 90 days of growth and divided into shoots and roots, whose dry biomass was determined after drying thoroughly. The soil adhered on root surface was collected for onward analysis. Each root system from all treatments was scanned with an EPSON Flat-Scanner (V700, Seiko Epson Corp, Japan) and analyzed with the WinRHIZO 2007d (Regent Instruments Inc., Quebec, Canada) for root morphological traits including root total length, area, volume, and diameter.

Leaf chlorophyll concentration was measured as proposed by Knudson *et al*. (1977) using the extraction with 80% acetone solution.

Distribution of soil water-stable aggregates (WSAs) at the size of 2.00-4.00, 1.00-2.00, 0.50-1.00, and 0.25-0.50 mm was determined using the wet-sieving procedure (Kemper and Rosenau, 1986) with a soil aggregate analyzer (DM200-IV, Shanghai, China). Mean weight diameter (MWD) as an indictor of aggregate stability was calculated by the following formula (Kemper and Rosenau, 1986): $\mathrm{MWD} = \sum_{i=1}^{n} XiWi$, where Xi is mean diameter of the i sieve opening (mm), Wi is proportion of the i size fraction in the total sample mass, and n is number of size fractions.

Soil organic carbon (SOC) was determined by spectrophotometry using dichromate wet oxidation method (Rowell, 1994). Determination of soil easily extractable glomalin-related soil protein (EE-GRSP) and difficulty extractable glomalin-related soil protein (DE-GRSP) was carried out following the protocol as outlined by Wu *et al*. (2015). Total glomalin-related soil protein (T-GRSP) is the sum of EE-GRSP and DE-GRSP.

Determination of soil polyphenol oxidase (PPO), peroxidase (POD), and catalase (CAT) activities was assayed following the procedure as suggested by Yan (1988).

Statistical analysis

The data (means ± SD, n = 5) were statistically analyzed by one-way variance (ANOVA) in SAS v8.1 (SAS Institute Inc., Cary, USA), and the Duncan's Multiple Range Tests were used to compare the significance between treatments at the 0.05 level.

Results and Discussion

Plant growth performance

Plant growth performance is considered as a feedback indicator of rhizosphere properties (Ngullie *et al*., 2015). Compared with R_0 treatment, R treatment registered a lower shoot weight, root weight, and total biomass weight (shoot plus root weight), leaf number, stem diameter, and plant height by 74%, 55%, 69%, 34%, 36%, and 36%, respectively (Table 1), suggesting that replant soil microbes had a negative feedback effect on plant growth parameters of peach. Such reduction in growth of peach plants is attributed to pathogens, parasites, and some plant-eating animals in the replant soil (Jonsson *et al*., 2001; Maherali and Klironomos, 2007; Van Der Heijden *et al*., 2008). While, compared with R_0 treatment, $R_{<100}$ treatment significantly reduced only plant height, shoot weight, and total weight by 11%, 30%, and 25%, respectively. The treatment $R_{<40}$ likewise showed a higher magnitude of reduction in plants height and stem diameter by 20% and 16%, respectively, indicating that replant soil microbes with the size of <100 μm were more inhibitory than <40 μm (Fig. 1). As a result, replant soil microbes mainly including pathogens in nature inhibited plant growth (Griffiths *et al*., 2000; Loreau, 2001; Garbeva *et al*., 2004). Earlier studies by Huang *et al*. (2018) showed that the application of higher concentration of soil water extract from *Angelica sinensis* rhizosphere, produced a distinct reduction in growth response, in terms of plant height, root length, and fresh weight. While, studies by Lau and Lennon (2011) revealed that complex soil microbial community could promote leaf number, above-ground biomass, and flower number in *Brassica rapa*.

These studies are strongly suggestive of the rhizosphere microbial diversity depending upon the nature and properties of crop-specific rhizosphere biology.

Root morphology

Changes in root morphology affect the above-ground plant growth. An inhibitive effect of exogenously applied replant soil microbes (Fig. 1; Table 2) was observed over R_0. Compared to R_0 treatment, R treatment significantly reduced the total root length, projected area, and root volume by 22%, 17%, and 35%, respectively (Table 2). The treatment $R_{<100}$ though, decreased these growth parameters to a lesser extent compared to R treatment by 20%, 15%, and 25%, respectively. However, $R_{<40}$ treatment failed to induce any change in these root traits. It seems that replant soil microbes, especially with Φ < 100 μm, but not Φ < 40 μm, exhibited strong negative effects on root morphology of replanted peach. The soil microbe size of Φ < 100 μm directly hindered the root development possibly by producing toxic exudates to restrict the root growth (Caffaro *et al*., 2011; Sugiyama and Yazaki, 2012). On the other hand, $R_{<40}$ treatment did not induce changes in growth root parameters such as root length, root area, root diameter, and root volume compared with R_0 treatment, suggesting that Φ < 40 μm size soil microbes are less growth inhibitive on root growth. In previous studies, soil beneficial microbes, for example, AMF (Φ 10 μm) recorded much higher magnitude of growth response than Φ < 40 μm (Allen, 2009). These microbes stimulated the root growth by reducing the relative abundance of toxic substances and producing auxins and polyamines, much to the added advantage in accelerating the root growth (Van Der Heijden *et al*., 2008; Zou *et al*., 2015; Lü and Wu, 2017).

Table 1. Effects of different sized soil microbes on plant growth performance of replanted peach (*Prunus persica*) seedlings

Treatments	Dry weight (g/plant)			Leaf number	Plant height	Stem diameter
	Shoot	Root	Total	(No/plant)	(cm)	(mm)
R_0	2.20±0.27a	0.98±0.27a	3.18±0.48a	32.4±5.9a	44.2±4.2a	3.60±0.60a
$R_{<40}$	1.90±0.18a	0.94±0.14a	2.84 ±0.20a	27.6±5.0a	35.5±4.4b	3.02±0.35b
$R_{<100}$	1.54±0.30b	0.84±0.33a	2.38±0.47b	27.2±3.3ab	39.2±1.9b	3.54±0.30a
R	0.57±0.06c	0.44±0.17b	1.00 ± 0.22c	21.4±2.3b	28.4±1.6c	2.30±0.14c

Note: Data (means ± SD, n = 5) followed by different letters among treatments indicate significant differences at 5% level. Abbreviations: R_0 = autoclaved replanted soil without any microbes; $R_{<40}$ = autoclaved replanted soil treated by Φ <40 μm soil microbes; $R_{<100}$ = autoclaved replanted soil treated by Φ <100 μm soil microbes; R = non-autoclaved replanted soil.

Fig. 1. Effects of replanted soil microbes on plant growth and root architecture system of replanted peach (*Prunus persica*) seedlings

Table 2. Effects of different sized soil microbes on root morphological traits of replanted peach (*Prunus persica*) seedlings

Treatments	Total length (cm)	Projected area (cm^2)	Surface area (cm^2)	Average diameter (mm)	Volume (cm^3)
R_0	222.91±13.35a	13.17±0.49a	16.94±1.07ab	0.46±0.02ab	1.07±0.16a
$R_{<40}$	217.35±10.35a	12.38±0.76ab	17.58±0.54a	0.48±0.04a	0.99±0.24ab
$R_{<100}$	178.61±19.73b	11.15±1.23b	16.02±0.42b	0.41±0.03b	0.80±0.17c
R	173.70±35.46b	10.88±1.67b	15.90±1.49b	0.33±0.03c	0.70±0.15c

Note: Data (means ± SD, n = 5) followed by different letters among treatments indicate significant differences at 5% level. Abbreviations: R_0 = autoclaved replanted soil without any microbes; $R_{<40}$ = autoclaved replanted soil treated by Φ < 40 μm soil microbes; $R_{<100}$ = autoclaved replanted soil treated by Φ < 100 μm soil microbes; R = non-autoclaved replanted soil.

Chlorophyll concentrations

Response on plant biomass is by and large regulated through changes in chlorophyll concentration. Our results displayed that compared to R_0 treatment, both $R_{<40}$ and $R_{<100}$ did not produced no significance difference in concentration of leaf chlorophyll *a*, chlorophyll *b*, and carotenoid concentrations (Fig. 2). While, R treatment drastically reduced the leaf chlorophyll *a*, chlorophyll *b*, and carotenoid concentration.

These results are in agreement with Huang *et al*. (2018) in *Angelica membranaceu* and *Cannabis sativa*. Lau and Lennon (2011) on the other hand, reported that complex microbial community significantly improved chlorophyll concentrations of *Brassica rapa* through increase photosynthetic efficiency, compared to simple microbial community. Our observations suggested that all soil microbes derived from fresh replant soil produce a negative feedback regulation on chlorophyll synthesis of peach plants, possibly related to reduce availability of nutrients like Mg, N, and Fe.

Glomalin-related soil protein (GRSP), WSAs and SOC

GRSP produced by AMF is closely related to soil organic matter and plays an important role in the formation of soil aggregates, soil carbon budget and resistance to stresses in plants (Barea *et al*., 2013). GRSP is considered to be the focal point of structural stability of soil (Wu *et al*., 2016). The concentration of soil EE-GRSP, DE-GRSP and T-GRSP were observed to increase by 9%, 8%, and 8% with $R_{<40}$ treatment, by 91%, 32%, and 47% with $R_{<100}$ treatment, and by 55%, 5%, and 19% with R treatment, compared to R_0 treatment (Fig. 3). These observations further suggested that peach rhizosphere soils with $R_{<100}$ treatment produced relatively higher soil GRSP levels, due to stimulation in PGPR via spore germination and mycelium elongation of AMF, leading to better production efficiency of GRSP (Driver *et al*., 2005; Bedini *et al*., 2009; Wu *et al*., 2016), however, in agreement with replanted peach inoculated with *Funneliformis mosseae* (Zhang *et al*., 2015). Soil microorganisms such as nematodes and collembolan are reported to have a negative effect on GRSP production by AM hyphae to reduce further proliferation and spread of hyphae network (Bedini *et al*., 2009).

Changes in soil structure are directly guided by SOC. Soil WSAs are closely associated with water infiltration rate, tilth and aeration in soils (Kemper and Rosenau, 1986). WSAs are an important index of soil structural stability, which is regulated by a variety of aggregate stabilizing agents like roots, SOC, soil enzymes, and soil microbial community (Rillig, 2004; Rillig and Mummey, 2006; Wu *et al*., 2012; Peng *et al*., 2013). SOC plays an adhesion role in the initial formation of soil aggregates (Bronick and Lal, 2005). Soil microbes can potentially affect soil WSAs at different levels through hyphae network and their secreted organic polymers (Rillig and Mummey, 2006; Griffiths *et al*., 2008; Wang *et al*., 2014). In our study, compared to R_0 treatment, R treatment significantly reduced $WSA_{2.00\text{-}4.00\ mm}$ by 65% and increased $WSA_{0.50\text{-}1.00\ mm}$ and $WSA_{0.25\text{-}0.50\ mm}$ by 38% and 54% (Table 3). $R_{<100}$ treatment significantly reduced $WSA_{2.00\text{-}4.00\ mm}$ and $WSA_{0.50\text{-}1.00\ mm}$ by 48% and 31%, and increased $WSA_{0.25\text{-}0.50\ mm}$ by 62%, over R_0 treatment. Soil MWD and SOC respectively, declined by 41% and 19% with R and 38% and 10% with $R_{<100}$, compared with R_0 treatment (Table 3). Although a distinct increase in soil GRSP level was observed in inoculated seedlings, a lower soil WSA distribution, SOC, and MWD in inoculated seedlings showed that microbial release of GRSP is not the deciding factor in soil structural improvement, because root surface, root exudates, SOC, and soil enzymes all modulate soil structure formation (Wu *et al*., 2015).

Table 3. Effects of different sized soil microbes on distribution of water-stable aggregate (WSA), mean weight diameter (MWD), and soil organic carbon (SOC) concentrations of replanted peach (*Prunus persica*) seedlings

Treatments	Distribution of WSAs (%)				MWD (mm)	SOC (mg/g)
	2.00-4.00 mm	1.00-2.00 mm	0.50-1.00 mm	0.25-0.50 mm		
R_0	0.31±0.10a	0.14±0.06a	0.13±0.03b	0.13±0.05b	1.28±0.22a	11.97±0.30a
$R_{<40}$	0.24±0.09ab	0.15±0.05a	0.15±0.01ab	0.20±0.08a	1.15±0.22a	11.17±0.67b
$R_{<100}$	0.16±0.10bc	0.12±0.08a	0.09±0.03c	0.21±0.08a	0.80±0.25b	10.80±0.21b
R	0.11±0.04c	0.14±0.04a	0.18±0.02a	0.20±0.03a	0.75±0.13b	9.73±0.54c

Note: Data (means ± SD, n = 5) followed by different letters among treatments indicate significant differences at 5% level. Abbreviations: R_0 = autoclaved replanted soil without any microbes; $R_{<40}$ = autoclaved replanted soil treated by Φ < 40 μm soil microbes; $R_{<100}$ = autoclaved replanted soil treated by Φ < 100 μm soil microbes; R = non-autoclaved replanted soil.

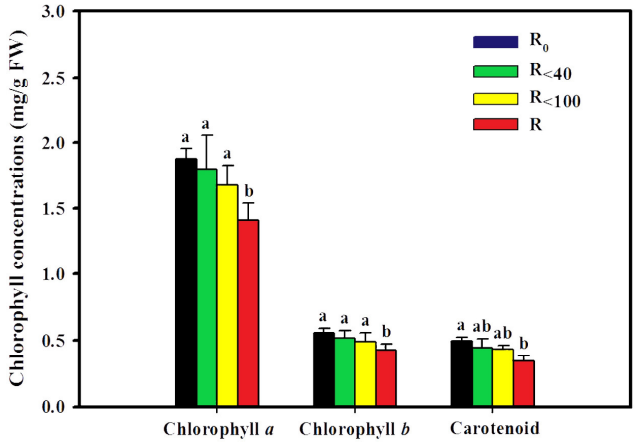

Fig. 2. Effects of different sized replanted soil microbes on chlorophyll *a*, chlorophyll *b* and carotenoid concentrations of peach (*Prunus persica*) seedlings. Data (means ± SD, n = 5) followed by different letters among treatments indicate significant differences at the 5% level

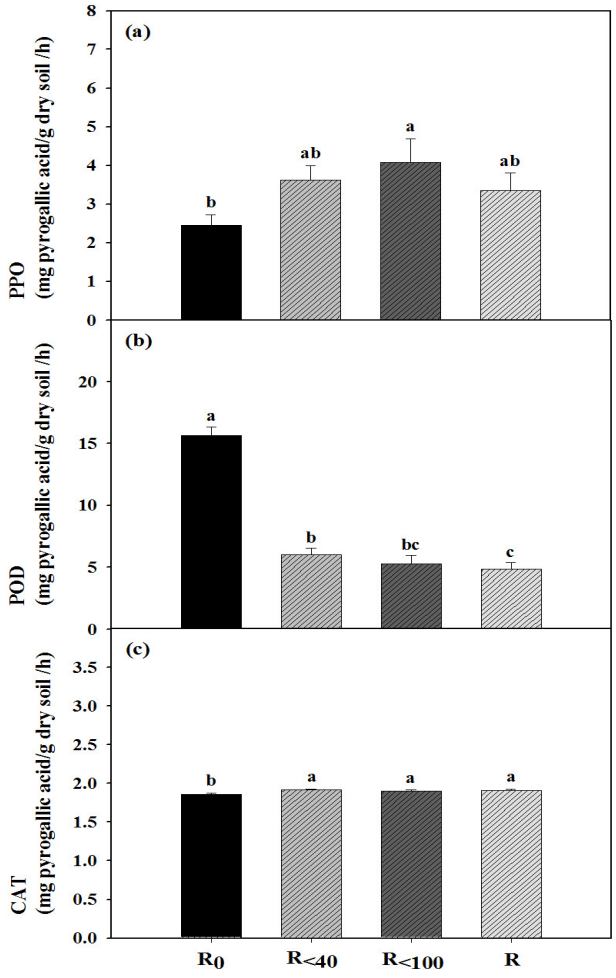

Fig. 4. Effects of different sized replanted soil microbes on activities of polyphenol oxidase (PPO) (a), peroxidase (POD) (b) and catalase (CAT) (c) of peach (*Prunus persica*) seedlings. Data (means ± SD, n = 5) followed by different letters among treatments indicate significant differences at the 5% level

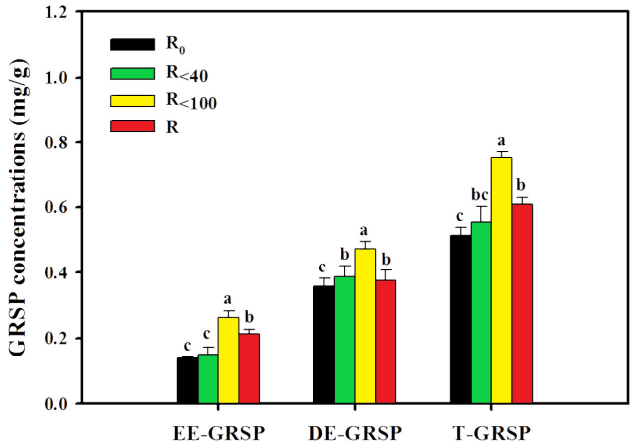

Fig. 3. Effects of different sized replanted soil microbes on easily extractable glomalin-related soil protein (EE-GRSP), difficulty extractable glomalin-related soil protein (DE-GRSP), and total glomalin-related soil protein (T-GRSP) concentrations of peach (*Prunus persica*) seedlings. Data (means ± SD, n = 5) followed by different letters among treatments indicate significant differences at the 5% level

Soil antioxidant enzyme activities

Soil enzymes play an important role in energy transformation and nutrient cycling in soil-based ecosystems (Bowles *et al*., 2014). Soil enzymatic activities are closely related to soil microbial flora, quantity and biodiversity, heavily promoting soil metabolic processes (Taylor *et al*., 2002; Finkenbein *et al*., 2013). Soil PPO can oxidize the aromatic compounds in soil and generate organic matters and pigments, thus completing the soil aromatic compounds cycle (Toscano *et al*., 2003). PPO on the other hand, holds an equally important role in transforming heterocyclic compounds (i.e., PAHs) in soils, coupled with positive effects of GRSP on the availability of PAHs (Sun *et al*., 2012; Gao *et al*., 2017). Hence, soil microbes, especially with the size of Φ <100 μm significantly increased soil PPO activities, in association with an increase of GRSP (Fig. 4a). Soil POD mainly comes from soil microorganisms, which plays an important role in the formation of humus (Wang *et al*., 2010). Our results indicated that three soil microbial treatments significantly reduced soil POD activities (Fig. 4b). This is in agreement with Zhang *et al*. (2015) earlier reported similar response on soil POD and soil PPO activities of replanted peach. Toxic substances released by roots or soil microbes required POD to perform degradation, thereby, resulted a decrease in soil POD activity (Kong, 2007; Wang *et al*., 2010). Soil CAT is derived from the decomposition of plants and exerts effects on removing the toxic effect of soil hydrogen peroxide (Liu *et al*., 2008). CAT is closely related to soil microbial abundance and plant roots biomass, which breaks down hydrogen peroxide in the soil to reduce its toxic effects on plants (Liu *et al*., 2008). Such a considerable increase in soil CAT activities by soil microbial treatments (Fig. 4c) as seen through our observations would partly alleviate toxic effects of hydrogen peroxide on plants.

Furthermore, $R_{<100}$ treatment represented strong inhibitory effects on biomass production, root development

and soil physicochemical traits, relative to $R_{<40}$ treatment. It might be due to the fact that $R_{<100}$ treatment contained a mass of pathogenic organisms with the size of 40-100 μm, such as *Rhizoctonia solani* (Qin *et al*., 2014), *Ralstonia solanacerum* (Chen *et al*., 2011), *Fusarium wilt* (Akköprü and Demir, 2005), *Pythium*, *Phytophthora* (Spies *et al*., 2011), etc. Therefore, such pathogens of $R_{<100}$ treatment might trigger the inhibitive effect.

Conclusions

Replant soil microbes inhibited plant growth performance, root growth, soil aggregation, SOC, and soil PPO activities, especially the soil microbes locked within the size of $\Phi < 100$ μm showed the heaviest negative response. With peach as continuous rotation, soil microbes with $\Phi <$ 100 μm need to be eliminated to mitigate the issues related to soil replant disease. However, it remains to be seen, after how many rotations (cropping seasons) such replant issue becomes more distinctive in a given crop-soil-climate setup, alongside the associated biochemistry involved.

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