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Mycorrhizal colonization represents functional equilibrium on root morphology and carbon distribution of trifoliate orange grown in a split-root system

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ABSTRACT

Trifoliate orange seedlings were grown in perspex pots of a split-root system, where one half of the split roots was inoculated with or without arbuscular mycorrhizal fungi (AMF, *Acaulospora scrobiculata* or *Funneliformis mosseae*). Five months after inoculation, the growth performance, leaf, stem and root biomass and photosynthetic rate were generally significantly higher in AM than in non-AM seedlings. Greater root morphological traits were observed in the AM root side than in the non-AM side for the same plant and in AM than in non-AM plants. AM seedlings had significantly higher leaf sucrose and glucose contents and total (leaf + root) glucose and fructose contents as compared to non-AM ones. In the split roots, the AM side displayed substantially higher sucrose, glucose and fructose contents than the non-AM side for the same plant, and in AM than in non-AM plants. These results showed greater C movement into the non-AM side from an AM-colonized plant than from a non-AM-colonized plant. These results conclude that the presence of AM in one side of the split roots benefited C acquisition and root development to another half non-AM side, suggesting functional equilibrium and resource allocation of AM within a root system.

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1. Introduction

Arbuscular mycorrhizal fungi (AMF), belonging to the phylum Glomeromycota, can form the mutualistic symbioses, arbuscular mycorrhizas (AMs), with roots of more than 80% terrestrial plants (Smith and Read, 2008). The formation of AMs provides multiple benefits to the fungal partner, including uptake of mineral nutrients and water, while consumes ~20% of plant photosynthetically fixed carbon (C) to sustain the symbiosis life cycle (Smith and Read, 2008). AMs thus function as a metabolic C-sink causing basipetal mobilization of photosynthates to roots.

Sucrose, a major photosynthate, is transported by sucrose transporters from source leaves to sink tissues such as AMs, where it is cleaved by invertases and sucrose synthases (degraded direction) into hexoses, further into trehalose and glycogen for the storage and utilization of C in AMs (Bago et al., 2003; Doidy et al., 2012b). Meanwhile, glucose, one of hexoses, is preferentially taken up by the mycobiont (Doidy et al., 2012a), though the percentage of hexoses allocated to AM versus non-AM roots is unknown. As a consequence, AM growth is a C-limited process, whilst the host plants have ultimate control over fungal activity through the regulation of carbohydrate transfer to the roots (Miller et al., 2002). Root AM colonization was generally linearly correlated with the C-sink strength of roots (Lerat et al., 2003). A higher plant C assimilation rate would hence compensate for their greater below-ground C expenditure in AM symbioses (Eissenstat et al., 1993). Foraging strategies of AMs and roots for energy are linked to plant C source (Gavito and Olsson, 2003). Even so, the cost of an AM formation involved in C partitioning between AMs and plants is poorly understood (Doidy et al., 2012a).

Plant root systems exhibit highly plastic characteristics while are affected by various abiotic and biotic factors, including AMF (Hodge et al., 2009). AMF had been confirmed to improve root morphology in strawberry, rice and citrus plants (Norman et al., 1996;

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Gutjahr et al., 2009; Wu et al., 2011, 2012), which would consume more root carbohydrates for root respiration and root biomass production (Liu et al., 2006). The presence of AM would lead to an increase of carbohydrates in the non-AM root sides in the split-root citrus seedlings (Koch and Johnson, 1984). Early studies showed a 3–4% higher transfer of carbohydrates in AM root sides than in non-AM root sides of split roots (Douds et al., 1988).

Citrus, one of the most planted fruit trees worldwide is strongly dependent on the AM symbiosis because of lacking of root hairs (Wu et al., 2011). Trifoliate orange [*Poncirus trifoliata* (L.) Raf.], a close relative to *Citrus*, is widely used as a rootstock of citrus plantation in Asia, including China, India, and Japan. In field, root colonization of citrus trees by native AMF is less than 10% in China (Zeng et al., 2004) and ~20% in Japan (Ishii and Kadoya, 1996). It seems that in whole root systems, a large proportion of citrus roots in the field are not colonized by native AMF. As a result, we do not know whether these non-AM roots in whole root systems obtain some carbohydrates for better root development.

Split-root system approaches can provide differential treatments for separate and independent root side of the whole root system but share a conjunct aerial part (Larrainzar et al., 2014). Split-root experiments have been extensively used to study the effects of AMF colonization on the production of carbohydrates and biomass (Koch and Johnson, 1984; Vierheilig et al., 2000; Lerat et al., 2003). Using this technique, the root system of a plant is divided into two parts, one of which is inoculated with an AM fungus, allowing a comparison of the C-sink strength between the AM and non-AM root halves of the same plant (Lerat et al., 2003). However, these studies considered C allocation only, while neglecting the root modification between AM and non-AM root sides. Here, we thus hypothesized that the non-AM root of split roots could gain a certain amount of carbohydrates from C pools of AM root side to support better root development, though how carbohydrates are distributed in roots to ensure the fungal metabolism and greater root growth is poorly understood. To confirm this hypothesis, in the present study, with one half of trifoliate orange root colonized by AMF or not, we firstly compared differences in root morphology and carbohydrate contents in two root sides, and then addressed if AM root side represent functional equilibrium and resource allocation in non-AM root side.

2. Materials and methods

2.1. Biological materials

Two AMF strains, *Acaulospora scrobiculata* Trappe and *Funneliformis mosseae* (Nicol. and Gerd.) Schüßler and Walker, respectively isolated from the rhizosphere of *Bauhinia blakeana* in Hongkong and of *Incarvillea younghusbandii* in Tibet in China, were used. The inocula were propagated from the identified fungal spores and cultivated with host plant of *Sorghum vulgare* (*A. scrobiculata*) or *Trifolium repens* (*F. mosseae*) for 16 weeks. After harvesting, the growth substrate contained 21 or 23 spores g^{-1} for *A. scrobiculata* or *F. mosseae*, respectively.

Seeds of trifoliate orange were collected from a Citrus Orchard on the Yangtze University campus, surface-sterilized with 70% ethanol for 10 min, and germinated in a plastic box containing autoclaved sands in a controlled growth chamber at 28/20 °C and 16/8 photoperiod hours (day/night) for 3 weeks under 80% relative humidity and 1200 μmol m^{-2} s^{-1} photosynthetic photon flux density. Fresh taproots of four-leaf-old (under sterilization) trifoliate orange seedlings were excised and kept 3-cm long. Subsequently, these treated seedlings were re-planted into the plastic box for 7 weeks for inducing the formation of lateral roots.

2.2. Experimental set-up

Perspex pots (20 × 10 × 18 cm = length × width × height) were separated in the middle by a 15-cm-height perspex to form two equal sized compartments (see Fig. 1). At the top of the separated perspex, a semicircle of 1-cm diameter was designed to arrange nearly equal lateral roots of the seedlings into two halve compartments. A 5 × 3 × 2 cm (length × width × height) foam board was placed in the shoot bottom of a seedling to fix the seedlings for upright growth. Such plants were defined as the split-root plants. Each compartment was filled with 1550 g autoclaved (121 °C, 0.11 Mpa, 2 h) soil. The soil (Xanthi-Udic Ferralsols, FAO system) was collected from the same Citrus Orchard on the Yangtze University campus. The soil chemical properties were pH 6.1, 9.7 g kg^{-1} organic carbon, 11.8 mg kg^{-1} available nitrogen, 15.3 mg kg^{-1} Oslen-P, and 21.5 mg kg^{-1} available potassium.

The AMF inoculated split-root compartment (M) received 50 g AMF inocula, and the other compartment (NM) of the pot received the same amount of autoclaved (121 °C, 0.11 Mpa, 2 h) inocula plus 2 mL filtrate (25 μm) of AMF inocula to keep similar other microorganisms. The experiment consisted of a completely randomized design with three mycorrhizal treatments (*A. scrobiculata*, *F. mosseae*, and non-AMF control). Each treatment replicated four times, creating a total of 12 pots.

The seedlings were grown in an environment controlled plastic greenhouse from April to September, 2013, where photosynthetic photon flux density was 965 μmol m^{-2} s^{-1}, day/night temperature 28/21 °C, and relative humidity 85%. The seedlings were watered in an interval of three days with distilled water to avoid waterlogging at the bottom of the compartment. A 30 mL standard Hoagland solution was biweekly supplied into each compartment.

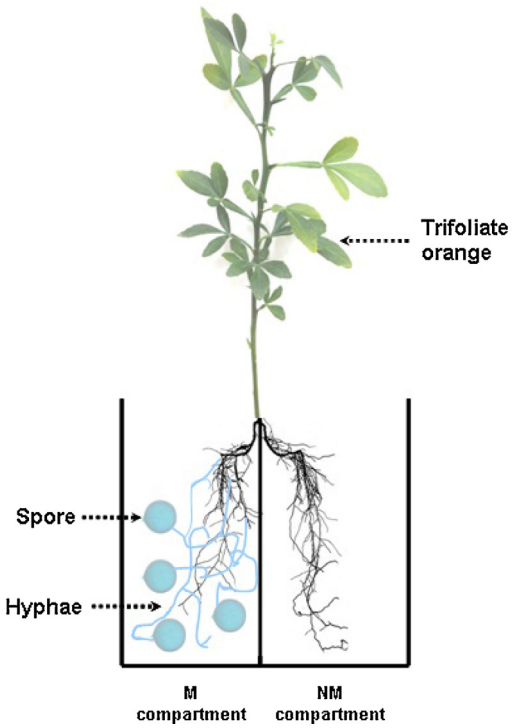

Fig. 1. Schematic diagram of a two-chambered split-root system to grow trifoliate orange seedlings with or without *Acaulospora scrobiculata* or *Funneliformis mosseae* colonization. *Abbreviations*: NM, non-AMF inoculation; M, AMF inoculation.

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