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Soil moisture legacy effects: Impacts on soil nutrients, plants and mycorrhizal responsiveness

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ABSTRACT

Although most land-plants form associations with arbuscular mycorrhizal fungi (AMF) as a means of optimising nutrient capture, legacy effects of altered soil moisture regimes on plant responses to arbuscular mycorrhizas (AM) have not been studied. As rainfall patters change with climate change, soil moisture legacy effects, and their impact on plants, soil and microbes may become increasingly important. Results of an experiment are presented in which soil was subjected to a range of different soil moisture regimes prior to planting a mycorrhiza-defective tomato mutant and its mycorrhizal wild-type progenitor. There were clear legacy effects of the soil moisture regime prior to planting on soil physicochemical properties, plant growth and nutrition, the formation of AM and mycorrhizal responsiveness. For example, in the Dry treatment the plants were well colonized by AM, there was a clear benefit to the plants in terms of mycorrhizal growth responses and mycorrhizal P responses. In contrast, in the Intermediate treatment AM colonisation was lower, there was little benefit in terms of mycorrhizal responses. Finally, in the Wet and Wet/Dry treatments AM colonization levels were similar (albeit lower) to those in the Dry treatment, but mycorrhizal growth responses were lower and more variable. Together, these results clearly indicate that soil nutrients, plant growth and nutrition and mycorrhizal responsiveness are affected by soil moisture legacy effect. Consequently, as we move into a period where more variable and intense rainfall amounts and patterns have been projected, we need to consider soil moisture legacy effects.

1. Introduction

Climate models are projecting a drier and/or a more variable (in terms of rainfall) climate for many regions of the world (Jentsch et al., 2007; IPCC, 2013). More frequent extreme weather events associated with climate change (Jentsch et al., 2007; IPCC, 2013) are expected to increase abiotic and biotic stress on plants. In addition to the direct impacts of changes in the amount, timing and intensity of rainfall events on plants, indirect impacts can also occur (Knapp and Smith, 2001). For example, nutrient availability and soil microbial community composition, both of which affect plant growth (van der Heijden et al., 1998; Bardgett and Wardle, 2010), can change in response to soil moisture (Franzluebbers et al., 1994; Meisnera et al., 2013) (Drenovsky et al., 2010; Brockett et al., 2012). These indirect effects can result in the establishment of "soil moisture legacy effects" where plants are impacted by conditions prior to plant establishment (Meisnera et al., 2013).

Plants have evolved many strategies and traits for optimising nutrient acquisition (Lynch, 2007), including the formation of arbuscular mycorrhizas (AM) (Lambers et al., 2008; Smith and Read, 2008). Under nutrient limiting conditions, the formation of AM can increase plant fitness and competitiveness, which has important consequences for ecosystem productivity and biodiversity (van der Heijden et al., 1998; Facelli et al., 1999; Cavagnaro et al., 2004). Although most land-plants form AM, soil moisture legacy effects (Meisnera et al., 2013) on the formation of AM and plant responses to arbuscular mycorrhizal fungi (AMF) have not been studied.

Although the impact of soil moisture legacy effects on AM formation and functioning remain unknown, some predictions can be made. For example, the wetting of soils in the absence of plants may trigger germination of spores of AMF, but in the absence of a suitable host plant, this may see a reduction in the inoculum potential of the soil (Giovannetti et al., 2002). Thus, a consequence of soil

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moisture legacy effects may be a reduction in the colonisation of roots by AMF. Additionally, if soil moisture legacy effects result in a reduction in soil nutrient availability (e.g. via stimulation of denitrification under wet conditions leading to gaseous soil N loss), the relative benefit of forming AM may be higher. Conversely, if soil moisture legacy effects result in an increase in plant-available nutrients (e.g. via stimulation of mineralization N and P), the role of AM may be diminished. Taken together, a consequence of soil moisture legacy effects on AM may be a change in the balance between the costs and benefits of forming AM, with shift from negative, neutral or positive mycorrhizal responses resulting (Johnson et al., 1997).

Since most plants form AM, and these associations can have a major impact on plant growth and nutrient acquisition, the impact of soil moisture legacy effects on the formation and functioning of AM could potentially be very significant. Here, are presented results of a study testing the hypothesis that a history of dry, wet, intermediate or variable (wet/dry cycles) soil moisture conditions prior to planting will affect the formation and functioning (in terms of impacts on plant nutrition and growth) of AM, due to changes in soil nutrient availability. The experiment involved growing a mycorrhiza defective tomato mutant, and its mycorrhizal wildtype progenitor (Barker et al., 1998) in soils with (experimentally established) different soil moisture legacies. This genotypic approach for controlling the formation of AM was selected as it allows for the comparison of mycorrhizal and non-mycorrhizal plants with the wider soil biota intact (Rillig, 2004; Watts-Williams and Cavagnaro, 2015), and because the two genotypes exhibit very similar growth patterns when grown in the absence of AMF (Watts-Williams and Cavagnaro, 2014).

2. Materials and methods

The soil used in this experiment was an Urrbrae red-brown earth (Alfisol), collected from the 0–10 cm soil layer of The University of Adelaide's Waite Campus Arboretum, South Australia, in April 2014 (Austral Autumn). This soil was selected as it has previously been shown to have high levels of AM inoculum potential and provides a good growth medium for our model plant, tomato (see below). The soil was air-dried and sieved to <2 mm prior to use to homogenise the soil and remove rocks and coarse woody debris. The soil has a pH (1:5 soil:water extract) of 6.3 ± 0.01 and a total C concentration of 4.7 ± 0.3%. The $NH_4^+ - N$ concentration of the soil, which was measured colorimetrically on 2 M KCl extracts (Forster, 1995), was 7.3 ± 0.2 (μg/g dry soil), and the $NO_3^- - N$ concentration, also measured colorimetrically on 2 M KCl extracts (Miranda et al., 2001), was 3.1 ± 0.1 (μg/g dry soil). The plant-available (Colwell) P concentration of the soil was 3.0 ± 0.04 (μg/g dry soil). The field capacity of the soil was determined using a sintered glass funnel connected to a 100 cm water column ($\Psi_m = -10$ kPa). Soil was packed in the glass funnel to the same bulk density as the field site from which it was collected (1.36 g/cm^3), saturated with water and allowed to drain for 48 h and weighed. The soil was then dried at 105 °C for 48 h and gravimetric moisture content calculated. The gravimetric moisture content at field capacity was 0.35 g water/g dry soil.

To each of 40 plastic bags was added 884 g of dry soil. Reverse Osmosis (RO) water was then added to the bags in varying amounts to establish the following four soil moisture treatments (i.e. 10 bags per treatment). Dry treatment: water added to 25% of water holding capacity (gravimetric moisture content of 0.9 g water/g dry soil). Intermediate treatment: water added to 50% of water holding capacity (gravimetric moisture content of 0.18 g water/g dry soil). Wet treatment: water added to 75% of water holding capacity (gravimetric moisture content of 0.27 g water/g dry soil). Wet/Dry treatment: water added to 75% of water holding capacity (gravimetric moisture content of 0.27 g water/g dry soil). These moisture contents were selected as 75% of water holding capacity provides optimal conditions for plant growth in the soil, and 25% of water holding capacity can be achieved when the soil is left to dry under typical glasshouse conditions in a reasonable amount of time (preliminary data not shown, but see Fig. 1). N.B. the Wet/Dry treatment was subjected to drying and re-wetting later in the experiment, as outlined below. Immediately following the addition of water to the soil in the bags the soil was mixed thoroughly to ensure an even distribution.

One day after water was added to the soil in the plastic bags, the soil was transferred to plastic, non-draining pots. These pots were then moved to a glasshouse facility on the Waite campus where they remained for the remainder of the experiment. Conditions in the glasshouse were set to 22–26 °C and daytime light levels, with supplemental lighting were 950 μmol m^{-2} s^{-1} with a 16/8 day/night photoperiod. The pots in the Dry, Intermediate and Wet treatments were weighed thrice weekly and water added to the pots to maintain them at their target moisture content for a period of 93 days (Fig. 1). Pots in the Wet/Dry treatment were also weighed thrice weekly and water loss (by mass) recorded; however, in this treatment, they were maintained at 75% of water holding capacity (by adding water) for 14 days, at which time watering was ceased until the soil reached 25% of water holding capacity (35 d). From day 35–45 the pots were maintained at 25% of water holding capacity by adding water as required. On day 45 the pots were then re-watered up to 75% of water holding capacity and maintained at this moisture content until day 49. On day 49 watering was again ceased until the soil reached 25% of water holding capacity (73 d). From day 73–82 the pots were maintained at 25% of water holding capacity. On day 82 the pots were then re-watered up to 75% of water holding capacity and maintained at this moisture content until day 94 (see Fig. 1).

On day 94, all pots in all treatments were watered up to 75% of water holding capacity, and seedlings planted into the pots on the same day, as follows. In the middle of each pot a small soil core was taken (approx. 10 g) using a 10 mm diameter stainless steel cork borer. The soil from the core was analysed for concentrations of $NH_4^+ - N$, $NO_3^- - N$ and plant available (Colwell) P, as described above. Into each hole one three week old tomato seedling (i.e. either of two different genotypes, as follows) was planted. The tomato genotypes were a reduced mycorrhiza colonisation tomato (*Solanum lycopersicum* L.) mutant genotype (*rmc*, hereafter), and its AM mycorrhizal progenitor (76R, hereafter) (Barker et al., 1998). The seedlings were raised by surface-sterilising the seeds, pre-germinating them on moist filter paper for 5 days (following Cavagnaro et al., 2010), and sowing the seeds into individual seed raising containers, each containing approx. 50 g of sterile sand. The seedlings were transplanted by gently washing them from the sand in which they were sown and then placing them in the hole created in the centre of each pot. The small void surrounding the roots of the seedlings was then gently backfilled using sterile sand. Immediately after planting, all pots were watered to 75% of water holding capacity, at which moisture content they were maintained for the remainder of the experiment.

Thirty-seven days after the seedlings were transplanted into the pots, all plants were destructively harvested; this time was selected as plants have had sufficient time for roots to be colonised by AMF and have not begun to senesce. The plants were carefully washed from the soil with RO water. All the shoots and a sub-sample of the roots were oven-dried (50 °C) until a constant mass was achieved, and dry weights determined. The dried plant material was then ground to a fine powder and P concentrations determined by radial view inductively coupled plasma-optical emission spectroscopy