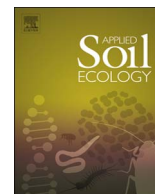




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Contrasting communities of arbuscule-forming root symbionts change external critical phosphorus requirements of some annual pasture legumes

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ABSTRACT

Annual pasture legumes with a superior ability to acquire soil phosphorus (P) and a low external critical P requirement could reduce the need for P fertiliser. Roots of pasture legumes grown in field soil will commonly be colonised by arbuscular mycorrhizal fungi (AMF). However, recent research suggests a second community of arbuscule-forming root-colonising fungi may be present: fine root endophytes (FRE). AMF are known to enhance P acquisition by plants under certain conditions, whereas very little is known about FRE and their impact on plant P status. We, therefore, grew plants at seven levels of P supply to determine and compare the external critical P requirements of two species of *Ornithopus* and two cultivars of *Trifolium subterraneum* when colonised predominantly by FRE (FRE-dominant treatment) or both FRE and AMF (mixed treatment). As expected from previous studies, the *Ornithopus* species had a lower critical P requirement than the *T. subterraneum* cultivars. However, for the *Ornithopus* species only, the FRE-dominant community had a significantly lower external critical P requirement (24–31 mg P kg⁻¹ soil) than the mixed community (50–58 mg P kg⁻¹ soil). Moreover, at low-P supply (≤ 15 mg applied P kg⁻¹ soil), *Ornithopus* species in the FRE-dominant treatment had longer specific root length, smaller average root diameter, 45–128% greater total root length, and lower shoot and root P concentration than in the mixed treatment. We concluded that comparisons among experiments of root morphological traits and external critical P requirements can be affected by the presence of different communities of arbuscule-forming root-colonising fungi and that these effects may vary among plant species.

1. Introduction

There is a need for high yielding pasture legume cultivars or species with lower phosphorus (P) requirements than existing commercial cultivars to maintain productivity with lower P fertiliser use and increase the profitability of pasture systems (Simpson et al., 2011a; 2014; 2015; Weaver and Wong, 2011). The external critical P requirement, defined as the extractable soil-P concentration necessary for 90% maximum growth, is considered to be a useful breeding target and is often calculated in P-response experiments screening pasture species for improved P-acquisition (Haling et al., 2016a,b; Simpson et al., 2014). *Ornithopus sativus* (French serradella), *O. compressus* (yellow serradella) and *Trifolium subterraneum* (subterranean clover) are economically important annual pasture legumes (Nichols et al., 2007) and form the backbone of many pasture systems in southern Australia and similar

Mediterranean climates due to their climatic suitability and biological nitrogen fixation abilities (Loi et al., 2005; Nichols et al., 2007, 2012). A focussed search for annual pasture legumes with lower critical P requirements (Bolland and Paynter, 1994; Haling et al., 2015; 2016a,b; Maxwell et al., 2013; Pinkerton and Randall, 1994; Weaver and Wong, 2011) has identified *Ornithopus* species as having lower external critical P requirements than *T. subterraneum* as a result of their longer, thinner roots and long root hairs (Haling et al., 2016a).

Arbuscular mycorrhizal fungi (AMF) colonise the roots of most plant species and are ubiquitous in Australian pastures (Simpson et al., 2011b). It has been found that AMF decrease the external critical P requirement of annual pasture legumes (Schweiger et al., 1995) in low-P soils, presumably by enhancing P-uptake via greater soil exploration by fungal hyphae, compared to uncolonised roots (Bolan, 1991; Nazeri et al., 2014). In Schweiger et al. (1995) and many similar glasshouse

Abbreviations: AMF, Arbuscular mycorrhizal fungi; DM, dry mass; FRE, fine root endophytes; RMF, root mass fraction; SRL, specific root length; TRL, total root length and 0, 8, 15, 30, 60, 120, 180 mg P kg⁻¹ dry soil (P0, P8, P15, P30, P60, P120 and P180)

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experiments, plants growing in pasteurised soil were inoculated with single isolates of AMF. However, this approach lacks relevance to field conditions as pastures host a diverse community of AMF (Simpson et al., 2011b), which may differ in host plant specificity and the rate of colonisation (Abbott and Robson, 1982; Ryan et al., 2016). For instance, at a single pasture site in Western Australia, ~20 species of morphologically different AMF were observed and the three most abundant species of AMF (identified from spores) in the rhizosphere soil differed among five perennial pasture legumes (Tibbett et al., 2008).

Recent research has suggested additional complexity in the mycorrhizal community through the proposition that there may be two distinct groups of arbuscule-forming root-colonising fungi in agricultural systems (Orchard et al., 2016; Ryan and Kirkegaard, 2012). This finding stems from the discovery that fine root endophytes (FRE), currently classified as *Glomus tenue* under the phylum Glomeromycota, likely belong to the subphylum Mucoromycotina (Orchard et al., 2017a). It seems probable that phylogenetic divergence could also correspond with functional divergence. A recent review by Orchard et al. (2017b) highlights that FRE are widely distributed in agricultural soils of Australia (Abbott and Robson, 1982; McGee, 1989; Orchard et al., 2016; Ryan and Kirkegaard, 2012) and likely the world (Christie and Kilpatrick, 1992; Gnekow and Marschner, 1989; Hooker et al., 2007; Jeffries et al., 1988). Indeed, in Western Australian pasture systems, especially those containing *T. subterraneum* (Abbott et al., 1983), FRE sometimes colonise a greater proportion of root length than AMF (Abbott and Robson, 1982; Orchard et al., 2016) and were more widely found across 20 pasture-crop rotation paddocks than any other mycorrhizal fungus (Abbott and Robson, 1982). Under waterlogging, FRE were more persistent than AMF for *Lotus*, but not ryegrass (Orchard et al., 2016); similar reports from regions which experience extreme cold (Newsham et al., 2009) also support suggestions that FRE may dominate the root-endophyte community in extreme environmental conditions, but only for specific host species (Orchard et al., 2017b).

Despite their common occurrence in agricultural soils, FRE are poorly understood due to the difficulty of isolating their spores and, hence, producing spore-based cultures (Orchard et al., 2017b; Thippayarugs et al., 1999). As such, much of what is known about FRE is based on observations rather than targeted research. Consequently, the impact of endophyte communities differing in the relative dominance of FRE and AMF on the host plant has not been examined. Therefore, we compared the effect of two contrasting communities (a FRE-dominant treatment and a mixed treatment of FRE and AMF) on the external critical P requirement and root morphological traits of two *Ornithopus* species and two *T. subterraneum* cultivars.

2. Materials and methods

2.1. Experimental design

This glasshouse study examined the impact of three factors and their interactions on morphological and symbiotic root traits related to P acquisition. The factors were genotype (four annual pasture legumes), endophyte community (two contrasting communities of arbuscule-forming root-colonising fungi) and P supply (seven levels). There were five replicates of each combination of factors, and pots were arranged in a randomised block design. Canopies were constrained to mimic photosynthetic conditions in a dense pasture sward where lower leaves experience shading from higher leaves of the same or neighbouring plants (Haling et al., 2016b; Hill et al., 2005; Jeffery et al., 2017b). The inclusion of seven rates of P application allowed the calculation of the external critical P requirement (Haling et al., 2016a).

2.2. Genotypes

Four economically important annual pasture legumes were included in the experiment: *Ornithopus sativus* Brot. (French serradella) cv.

Margurita, *O. compressus* L. (yellow serradella) cv. Santorini, *Trifolium subterraneum* L. cv. Woogenellup (ssp. *subterraneum*), and *T. subterraneum* cv. Riverina (ssp. *yanninicum*). These were selected based on their previous inclusion in similar P-response experiments (Haling et al., 2016b; Jeffery et al., 2017a,b).

2.3. Soil and endophyte community

An unfertilised, sandy loam collected at 0–40 cm depth from The University of Western Australia Future Farm, Pingelly, Western Australia (32°30'23"S, 116°59'31"E) on 13 April 2015 was sieved to < 5 mm, pasteurised at 63 °C for 90 min on three consecutive days, oven-dried at 40 °C for seven days and allowed to cool for four hours prior to potting up. Half of the pots were then filled with this soil, which contained inoculum of the indigenous arbuscule-forming root-colonising fungi known as fine root endophytes (FRE) that had survived the pasteurisation treatments. This treatment is referred to as the 'FRE-dominant treatment'. The remaining soil was then mixed thoroughly with a commercial AMF inoculum (Microbe Smart start-up super VAM inoculum) stated to contain four species: *Claroideoglomus etunicatum*, *Funneliformis mosseae*, *F. coronatum* and *Rhizophagus irregularis*. This treatment is referred to as the 'mixed treatment', as roots were highly colonised by both FRE and AMF.

Pasteurised soil was analysed by CSBP analytical laboratories (Bibra Lake, Australia) and methods, unless otherwise specified, followed those of Rayment and Lyons (2011); method numbers supplied. The soil was a sandy loam (9% clay, 79% sand and 12% silt) with low plant-available bicarbonate-extractable P (7.2 mg P kg⁻¹ dry soil) (9-B) (Colwell, 1965), a high P-buffering index (PBI = 337) (912-C), a pH in CaCl₂ of 5.6 (4-A1, 4-B3, 3-A1), and contained 8 mg kg⁻¹ nitrate-N, 10 mg kg⁻¹ ammonium-N (7-C, 2-B) and 104 mg kg⁻¹ bicarbonate-extractable K (18-A1).

2.4. Phosphorus supply

Cylindrical free-draining PVC pots (90 mm diameter × 200 mm depth) were filled with 700 g of oven-dried soil, which was then wet with 200 ml of deionised water; 300 g of dry soil was then added on top of the wetted soil. Seven P treatments were established prior to sowing. An 80 ml solution of KH₂PO₄, sufficient to saturate the top 300 g of soil, was applied at either 0, 8, 15, 30, 60, 120 or 180 mg P kg⁻¹ dry soil (P0, P8, etc.) to concentrate P in the topsoil as occurs under pastures (McLaughlin et al., 2011). Total K was balanced to 120 mg kg⁻¹ soil among P treatments with KCl (Pang et al., 2010) and all essential nutrients except P were provided at final concentrations of (mg kg⁻¹ dry soil): N 30, S 50, Ca 45, Mg 10, Cu 0.5, Zn 7, Mn 4, B 0.12, Mo 0.4 and Fe 5. Nitrogen was added as a mixture of NH₄NO₃ and Ca(NO₃)₂ with a molar ratio of 1 and was intended to provide an initial supply of N following germination, prior to nodulation.

2.5. Growth and maintenance

Micro-swards were established by sowing ten seeds per pot and thinning to six seedlings after emergence. Seeds were inoculated with a slurry of peat-based inoculum of Group C rhizobia (*Rhizobium leguminosarum* bv. *trifolii*) for *T. subterraneum* and Group S¹ rhizobia (*Bradyrhizobium* spp.) for *Ornithopus* species (Becker Underwood, Somersby, New South Wales, Australia). White alkanethene beads were placed on the soil surface to minimise evaporation.

Plants were grown for seven weeks from 4 May 2015 in a glasshouse maintained between 17 °C and 25 °C at The University of Western Australia, Perth, Australia (31°98'S, 115°81'E). Reflective sleeves around pots were raised to shoot height daily to constrain the shoot canopy and mimic photosynthetic conditions experienced within a dense pasture sward (Hill et al., 2005; Jeffery et al., 2017b). Pots were randomised within replicates to minimise the effects of temperature

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