
Article:
Magkourilou, E., Durant, E., Bell, C. et al. (3 more authors) (2024) Plant pests influence the movement of plant-fixed carbon and fungal-acquired nutrients through arbuscular mycorrhizal networks. Functional Ecology. ISSN 0269-8463

https://doi.org/10.1111/1365-2435.14693

Received: 4 March 2024 | Accepted: 24 September 2024

DOI: 10.1111/1365-2435.14693

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Mycorrhizal Networks

Plant pests influence the movement of plant-fixed carbon and fungal-acquired nutrients through arbuscular mycorrhizal networks

E. Magkourilou[1] | E. K. Durant[1] | C. A. Bell[2] | T. J. Daniell[3] | P. E. Urwin[2] | K. J. Field[1]

[1]Plants, Photosynthesis and Soil, School of Biosciences, University of Sheffield, Sheffield, UK

[2]Faculty of Biological Sciences, School of Biology, University of Leeds, Leeds, UK

[3]Molecular Microbiology: Biochemistry to Disease, School of Biosciences, University of Sheffield, Sheffield, UK

Correspondence
E. Magkourilou
Email: emagkourilou1@sheffield.ac.uk

K. J. Field
Email: k.j.field@sheffield.ac.uk

Funding information
Biotechnology and Biological Sciences Research Council, Grant/Award Number: BB/T007222/1 and BB/X009823/1; European Research Council, Grant/Award Number: 865225

Handling Editor: Petar Jovanovic

Abstract

1. Plants typically interact with multiple, co-occurring symbionts, including arbuscular mycorrhizal (AM) fungi which can form networks, connecting neighbouring plants. A characteristic aspect of the mycorrhizal symbiosis is the bidirectional exchange of nutrients between host plants and fungal partners. Concurrent interactions with competing organisms such as aphids or potato cyst nematodes (PCN) can disrupt the carbon-for-nutrient exchange between plants and AM fungi. However, the role of mycorrhizal networks (MNs) in mediating these interactions remains unclear.
2. Using isotope tracing in multi-plant experimental systems, we investigated the movement of plant photosynthates and fungal-acquired soil phosphorus through MNs and the interactive effects of PCN infection on this.
3. We found evidence of preferential allocation of fungal-acquired phosphorus to plants that were not infected by PCN compared with infected neighbours. Contrary to previous findings using single plants, we did not detect a PCN-induced reduction in the amounts of plant carbon delivered to AM fungi in multi-plant systems. However, the MN(s) moved plant-fixed carbon away from PCN-infected host plants, regardless of the PCN infection status of the neighbouring plant host.
4. Our work highlights the responsiveness of MNs to interactions with below-ground organisms. It also strengthens the argument for a more mycocentric view of AM–plant symbioses. Experimental designs of increasing ecological complexity are needed for a more comprehensive understanding of the carbon-for-nutrient dynamics in AM fungi–plant networks. This will, in turn, elucidate the role of AM fungi in terrestrial carbon cycling and their function in agricultural systems.

KEYWORDS
arbuscular mycorrhizal fungi, biological markets, carbon-for-nutrient exchange, mycorrhizal networks, potato cyst nematode, soil carbon, symbiosis

1 | INTRODUCTION

The intimate associations formed between the roots (or rhizoids) of plants and symbiotic soil fungi, together known as mycorrhizas, evolved at the dawn of plant terrestrialisation >450 million years ago (Redecker et al., 2000). Today, mycorrhizal symbioses are formed by the vast majority of land plants across nearly all terrestrial ecosystems (Brundrett & Tedersoo, 2007). At least 72% of vascular plant species (Brundrett & Tedersoo, 2018), including many crops (Wang & Qiu, 2006), form mycorrhizal symbioses with arbuscular mycorrhizal (AM) fungi of the subphylum Glomeromycotina (Spatafora et al., 2016). AM fungal hyphae extend beyond the roots of host plants into the surrounding soil to form a complex web of extraradical mycelium, also known as a 'mycorrhizal network' (MN). MNs can reach and colonise additional neighbouring plants, sometimes involving the fusion of separate fungal hyphae by anastomosis (de Novais et al., 2017; Giovannetti et al., 2004; Mikkelsen et al., 2008), forming what is then often referred to as a 'common mycorrhizal network' (CMN; Wipf et al., 2019).

Through their MNs, AM fungi supply up to 80% of phosphorus (P; Bago & Bécard, 2002) and ~30% of nitrogen (N; Govindarajulu et al., 2005) of their host plants' requirements alongside other micronutrients (Hamilton & Smith, 2000; Lehmann et al., 2014), offering a vital ecosystem service to plant communities. AM fungi are obligate biotrophs, unable to produce and exude the necessary degradative enzymes for the decomposition of complex soil organic materials (Tisserant et al., 2012, 2013), relying entirely on their plant hosts for their carbon (C) nutrition (Bago & Bécard, 2002). Up to 30% of a plant host's photosynthetically fixed C can be allocated to AM fungi (Drigo et al., 2010). As such, together with other types of mycorrhizal fungi, AM fungi are important regulators of global C dynamics (Averill et al., 2014; van der Heijden et al., 2015; Wurzburger et al., 2017). According to recent estimates, plants allocate 13.12 Gt of CO_2e to mycorrhizal fungi globally, an amount equivalent to around 36% of current annual CO_2 emissions from fossil fuels (Hawkins et al., 2023).

The evolutionary drivers and mechanisms that underpin bidirectional nutrient exchange between AM fungi and their host plants are often discussed using a 'biological markets' framework (e.g., Noë & Kiers, 2018; Werner et al., 2014; Werner & Kiers, 2015; Wyatt et al., 2014). According to this, plant C is preferentially allocated to AM fungal partners that offer the most 'generous' supply of fungal-acquired nutrients (Kiers et al., 2011). In return, it is hypothesised that AM fungi also discriminate between alternative partners, 'rewarding' more 'generous' hosts by supplying them with more nutrients (Bücking & Shachar-Hill, 2005; Fellbaum et al., 2012; Kiers et al., 2011). However, the regulation and control of mycorrhizal resource exchange remains a topic of hot debate with source–sink regulation presented as an alternative or a complementary mechanism (Kiers et al., 2016; van der Heijden & Walder, 2016; Walder & van der Heijden, 2015). An important, yet often overlooked, factor in mycorrhizal resource exchange is that plants rarely interact only with mutualistic symbionts (Magkourilou et al., 2024). Instead, they exist as part of complex, multi-kingdom ecosystems, interacting with a myriad of co-occurring organisms and with neighbouring plants usually interconnected underground by one or more MNs. When these complex symbiotic scenarios are considered, the evidence suggests that co-occurring, competing organisms such as aphids (Charters et al., 2020) and plant-parasitic nematodes (Bell et al., 2022) drive asymmetry in C-for-nutrient exchange where infected plants reduce the allocation of C to their AM fungal symbionts, but nutrient supplies from AM fungi to plants are maintained. However, these studies still do not reflect ecologically relevant scenarios in which the regulation of plant C and soil nutrient flows is modulated across multiple hosts of various infection statuses by CMNs (Bell et al., 2021).

Experiments assessing the impacts of changing C source–sink strengths across a CMN, either by shading (Fellbaum et al., 2012; Weremijewicz et al., 2016) or by altering nutrient gradients in vitro (Lekberg et al., 2010; van't Padje et al., 2021; Whiteside et al., 2019) suggest that CMN can modulate resource regulation. Moreover, results from experiments employing multitrophic interactions (e.g., Alaux et al., 2020; Babikova et al., 2013; Durant et al., 2023; Song et al., 2014) point to the responsiveness and resilience of CMNs and their ability to potentially ameliorate some plant stresses. Despite these advances in understanding nutrient dynamics in plant–AM fungal networks, the relative C contribution of each plant partner into the MN(s) remains unclear. An important consideration should be the spatial distribution and movement of C by AM fungal hyphae through the soil. An aspect of the responsiveness of MNs is likely their ability to move resources away from 'poor' hosts, increasing AM hyphal proliferation and subsequent exploration of the soil profile; potentially in search of alternative, more 'generous' hosts.

To address these important knowledge gaps, we investigated the movement of fungal-acquired P from the soil and plant-fixed C across MNs formed between two neighbouring plants, manipulating the resource dynamics of the symbioses using the potato cyst nematode (PCN), a common pest that feeds on the roots of potatoes and is responsible for 9% of yield losses worldwide (Turner & Rowe, 2006). We tested the hypothesis that AM fungi provide more P to host plants not infected with PCN because uninfected plants would provide the MN with more photosynthetically fixed C (Kiers et al., 2011; Werner & Kiers, 2015).

2 | MATERIALS AND METHODS

2.1 | Mesocosm design and plant growth

Plants were grown in mesocosms (37 cm length × 26 cm width × 22 cm height) that were divided into two equal compartments by a 35 µm pore nylon mesh barrier (no air gap) affixed centrally using hot glue. This mesh excluded plant roots but allowed mycorrhizal hyphae to cross (Johnson et al., 2001). A single, non-sterile tuber from *Solanum tuberosum* cv. Désirée (Denholm Seed Potatoes, UK) was planted in the middle of each compartment within each mesocosm, containing a total of ~10 kg of non-sterile coarse sand: topsoil (50:50) mix (sand

acquired from RHS Enterprise Ltd., UK for coarse sand and topsoil from East Riding Horticulture Ltd., UK). The distance between the two plant stems was ~18 cm.

Both compartments of all mesocosms received 100 g of a commercially available mixed species mycorrhizal fungal inoculum (*Funneliformis mosseae*, *Funneliformis geosporus*, *Claroideoglomus clarodeum*, *Rhizophagus intraradices*, *Glomus aggregatum*, *Diversispora* spp. and *Scleroderma citrinum*; PlantWorks Limited, UK). Three treatment combinations were established based on the presence or absence of the PCN *Globodera pallida* (population Lindley) in each compartment of the mesocosms (Figure 1). The PCN-containing compartments were established by mixing in stock soil of known PCN density to achieve a final density of ~10 eggs per gram of substrate. These relatively low levels of infection reflected the conditions of most infected fields in England (Minnis et al., 2002) and ensured that plants would not be severely damaged by PCN. Mesocosms were established in a randomised block layout, in the same controlled environment glasshouse (16°C night–18°C day, 16 h day length, 60% humidity) and grown for a total of 7 weeks.

2.2 | Tracing fungus-to-plant ^{33}P transfer

Mesocosms ($n = 12$ per treatment combination shown in Figure 1) were established in three identical blocks across subsequent weeks. Two soil-filled PVC cores (18 mm diameter × 130 mm length; Barkston Ltd., UK) with 35 µm pore nylon mesh-lined windows (70 mm × 16 mm) affixed using Tensol 12 acrylic adhesive (Bostik Ltd., Stafford, UK) were positioned in the middle of each mesocosm (Figure S1). A 1 mm diameter silicone capillary tube (Smiths Medical Ltd., Ashford, UK) perforated every 0.5 cm using a mounted needle was also fixed centrally in each core to allow for the distribution of ^{33}P through one core in each pot, with water added to the control cores. Specifically, 5 weeks after planting, 150 µL of ^{33}P-orthophosphate (1.5 MBq; [^{33}P]-orthophosphate; Hartmann Analytic, Braunschweig, Germany) was supplied to one of the two cores in each pot via the capillary tube. In half of the mesocosms per treatment combination ($n = 6$; Figure 1), the ^{33}P-labelled cores were rotated every other day to sever hyphal connections between the core and plant roots (Figure S1). The non-labelled cores in these pots remained static to preserve the hyphal links between the core contents and the plant roots. In the remaining pots ($n = 6$ per treatment combination), ^{33}P-labelled cores remained static with non-labelled cores rotated (Figure S1). This allows fungal-acquired ^{33}P transfer to plants to be estimated by excluding the transfer of ^{33}P via alternative means such as by diffusion or alternative microbial nutrient cycling processes (see below for more details; Johnson et al., 2001). The experiment was harvested 2 weeks following the application of ^{33}P (Figure S2a).

2.3 | Tracing plant-to-fungus C transfer

Mesocosms ($n = 6$ for each shown in Figure S3) were established in two identical blocks across subsequent weeks. Seven weeks after planting (Figure S2b), the above-ground tissue of all plants was enclosed within polythene bags (Polybags Ltd., London, UK), sealed airtight using anhydrous lanolin and cable ties at the base of the plant stem. One plant per mesocosm was labelled with $^{14}CO_2$, with plants for labelling selected randomly where appropriate (Figure S3). At the beginning of the photoperiod, one of the two soil-filled, meshed-walled cores on each side of the mesh barrier separating the plants was rotated to sever the hyphal connection between the core and plant roots (Figure S3). $^{14}CO_2$ was liberated into the chamber by adding 2 mL 10% lactic acid to a cuvette containing 190 µL ^{14}C-sodium bicarbonate (specific activity: 1.62 GBq mmol^{-1}; total activity released: 1 MBq; Perkin Elmer, USA). Plants were left in situ for 24 h post-labelling (Figure S2b), at which point 2 mL of 2 M KOH was added to vials within each labelled chamber to capture any remaining gaseous $^{14}CO_2$. At the end of the experiment, soil sub-samples

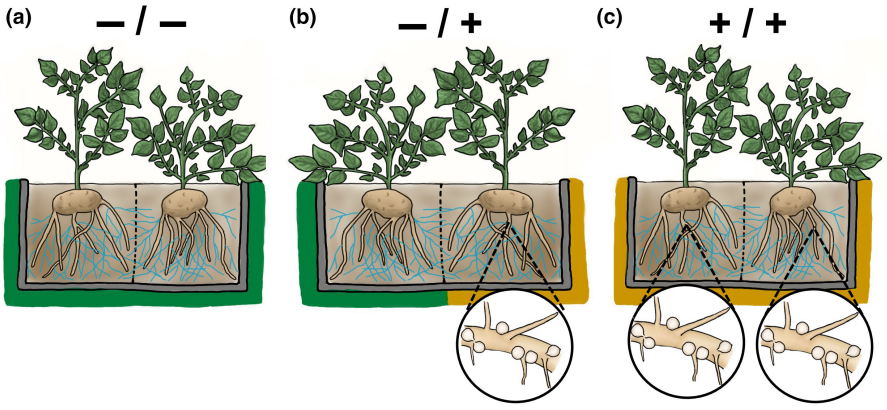

FIGURE 1 Treatment combinations were used to test the effect of potato cyst nematodes (PCN; illustrated by the beige shapes on the magnified portions of the roots) on the carbon-for-phosphorus exchange between plants and arbuscular mycorrhizal fungi. All plants were connected by one or more mycorrhizal networks (illustrated by the blue lines) across a root-excluding 35 µm pore mesh. Plants without PCN are indicated by '–' and green borders, whereas plants with PCN are indicated by '+' and orange borders. Three treatment combinations were deployed: (a) PCN-/PCN-; (b) PCN-/PCN+; (c) PCN+/PCN+.

from within the cores were used to estimate the amount of recently fixed plant C provided to the fungus (i.e., fungal C; see below for more details).

2.4 | Preparation and harvest of plants and soils

The week of harvest, using leaves of similar size, the photochemical activity of photosystem II characterised by FvP/FmP and the relative chlorophyll content (SPAD; Photosynthesis RIDES protocol, MultispeQ 2.0, PhotosynQ; Kuhlgert et al., 2016) was recorded in a subset of plants as a functional indicator of plant photosynthetic efficiency and plant stress (Cessna et al., 2010). Two weeks after the introduction of ^{33}P tracer or 24 h after the release of $^{14}CO_2$, soil and plant material were separated into shoots, roots, and tubers, as well as the soil from each compartment and the soil from within each core. Roots were cleaned with tap water and sub-samples (~5–10 g) of a subset of plants were taken and stored in 50% ethanol (v/v) at 4°C for AM colonisation counts. All of the soil in each compartment was weighed fresh and the measurements were used to extrapolate the hyphal counts to the equivalent compartments. All other components (i.e., the above-ground portion of plants, tubers, remaining roots, and soil from within the cores) were stored at −20°C until they were freeze-dried (CoolSafe 55-4; LaboGene, Allerød, Denmark) and dry mass of each was recorded. All freeze-dried plant materials were then homogenised using a hand-blender and stored at room temperature until subsequent analysis.

2.5 | Quantification of fungal-acquired ^{33}P and total P in plant shoots

To quantify ^{33}P in plant shoots, ~100–200 mg of the homogenised freeze-dried samples were processed as per Cameron et al. (2007). Briefly, samples were digested in duplicate in 2 mL concentrated sulphuric acid (H_2SO_4) at 365°C for 15 min (Grant BT5D; Grant Instruments Ltd., St Ives, UK), cleared in hydrogen peroxide (H_2O_2; 300–600 μL), diluted to 10 mL with distilled water (dH_2O) and then a 2 mL sub-sample was added to 10 mL of the liquid scintillant (Emulsify-safe; PerkinElmer). Sample radioactivity was quantified through liquid scintillation counting (Tri-Carb 3100TR; PerkinElmer) and ^{33}P quantified using previously published equations (Cameron et al., 2007). ^{33}P budgets were calculated using established equations (see Durant et al., 2023 for detailed equations as adapted from Cameron et al., 2007). For each of the three experimental blocks, the mean ^{33}P content of plants with no direct hyphal access to the isotopes ('rotated' core pots) was subtracted from the individual measured ^{33}P content of each plant with hyphal access to the isotopes ('static' core pots). This accounts for the movement of isotopes out of the cores by diffusion or alternative microbial nutrient cycling processes. The total P content (i.e., plant and fungal-acquired) of plant shoot material from a subset of plants was also determined using an adapted method of Murphy and Riley (1962). Sample optical density was recorded at 822 nm using a spectrophotometer (Jenway 6300, Staffordshire, UK). A 10 mg/mL standard P solution was used to produce a standard curve against which total sample P was calculated.

2.6 | Quantification of host-fixed C in fungi

About 100–250 mg of freeze-dried soil from within each core was weighed in duplicate into Combusto-cones (PerkinElmer, Beaconsfield, UK). ^{14}C was measured following sample oxidation (Model 307 Packard Sample Oxidiser; Isotech, Chesterfield, UK) with released $^{14}CO_2$ from burnt soil samples trapped in 10 mL of the liquid scintillant CarbonTrap and mixed with 10 mL CarbonCount (Meridian Biotechnologies Ltd., Tadworth, UK). Radioactivity was quantified by liquid scintillation counting (Packard Tri-Carb 4910TR; PerkinElmer). The total C (i.e., $^{12}CO_2$ and $^{14}CO_2$) contained in each soil sub-sample was calculated by quantifying the total CO_2 volume and content mass in the labelling chamber and the proportion of the supplied $^{14}CO_2$ that was photosynthetically fixed by the plant during the 24 h labelling period (see Durant et al., 2023 for detailed equations as adapted from Cameron et al., 2008).

To account for the movement of ^{14}C via diffusion and to estimate the amount of plant-fixed C transferred from the ^{14}C-labelled plants to the MN (i.e., fungal C), the rotated core C values (i.e., soil and severed hyphae) were subtracted from the static core (i.e., soil and intact hyphae) for each mesocosm compartment. These values were then extrapolated to the entire compartment and expressed relative to the soil hyphal density measurements for each compartment. To calculate the percentage (%) of fungal C that moved from the ^{14}C-labelled plant compartment to the unlabelled plant compartment of the same mesocosm, the following equation was used:

$$\%\ \text{of fungal C that moved} = \frac{\text{fungal C in the compartment of the unlabelled plant}}{\left(\text{fungal C in the compartment of the unlabelled plant} + \text{fungal C in the compartment of the } ^{14}\text{C - labelled plant}\right)} \times 100$$

2.7 | Fungal colonisation of roots and soil

Root samples that had been stored for colonisation assessment were stained using the 'ink and vinegar' staining method (Vierheilig et al., 1998) at 70°C for 20 min. Roots were de-stained in 1% acetic acid at room temperature and mounted on microscope slides using polyvinyl lacto-glycerol (16.6 g polyvinyl alcohol powder, 10 mL glycerol, 100 mL lactic acid, 100 mL dH_2O). Assessment of percentage root length colonisation (including intraradical hyphae, arbuscules, and vesicles) was made using the magnified intersection methodology (around 150 intersects per mesocosm, 100× magnification; McGonigle et al., 1990).

Fungal hyphae were extracted from soil from each of the two compartments of the mesocosms used for ^{33}P tracing and from

within the static cores of each compartment for the mesocosms used for ^{14}C labelling. 4.5–5 g of dried soil sub-samples were first suspended in 500 mL H_2O. A 10 mL aliquot was filtered through a cellulose nitrate membrane filter (47 mm diameter, 0.45 μm pore size; CYTIVA, Whatman™, Germany) and stained with a few drops of ink and vinegar solution (Vierheilig et al., 1998). Filter papers were halved and mounted on microscope slides using polyvinyl lacto-glycerol and oven-dried at 65°C for an hour. Hyphal lengths (excluding only a few unstained, thick, and highly septate hyphae) per mesocosm were calculated using the gridline-intersection methodology (50 fields of view per half filter paper, 100× magnification; Tennant, 1975).

2.8 | PCN infection

Upon harvest, PCN cysts were removed from the roots by vigorously shaking the roots. The cysts were then extracted from a sub-sample of soil (minimum 250 g) from each mesocosm compartment used for ^{33}P tracing using Fenwick's (1940) method. Briefly, soil was washed through a 1 mm mesh into the Fenwick can (i.e., a metal can with a sloped base at the top and a sloping collar below the rim). Heavy soil particles sink to the bottom of the water-filled can, whereas cysts and light soil debris float to the surface and are siphoned over the rim into a 250 mm sieve. The contents of the sieve were then washed through a filter paper which was in turn examined under a dissecting microscope for the collected cysts to be counted and PCN infection to be expressed as cysts per gram of soil (Figure S4).

2.9 | Statistical analysis

All statistical analyses and figure construction were performed in R studio (RStudio Team, 2022) using the R programming language (R Core Team, 2023). For the ^{33}P tracing experiment, one or both plants did not grow sufficiently in two mesocosms, so these were removed from all analyses. For all comparisons, linear mixed-effects models were performed including a block effect (i.e., week of planting) and the PCN infection treatment of a plant and/or the PCN infection treatment of its neighbouring plant as fixed effects. A random intercept for the mesocosm was included to account for non-independence among pairs of plants from the same mesocosm. After visual evaluation of the data for the fungal-acquired ^{33}P concentration in the shoots, a further mixed-effects model with the same parameters as explained above was performed on the intermediate treatment combination (i.e., '−PCN/+PCN'). The significance of all model parameters was assessed using the 'anova' function in R and the *lmerTest* package (Kuznetsova et al., 2017). Assumptions for the use of general linear models were validated by plotting residuals versus fitted values, square root residuals versus fitted values, normal qq plot, and constant leverage using the 'autoplot' function of the *ggplot2* package (Wickham, 2014). The data for soil hyphal counts did not satisfy assumptions so these were ($\log_{10}+1$) transformed.

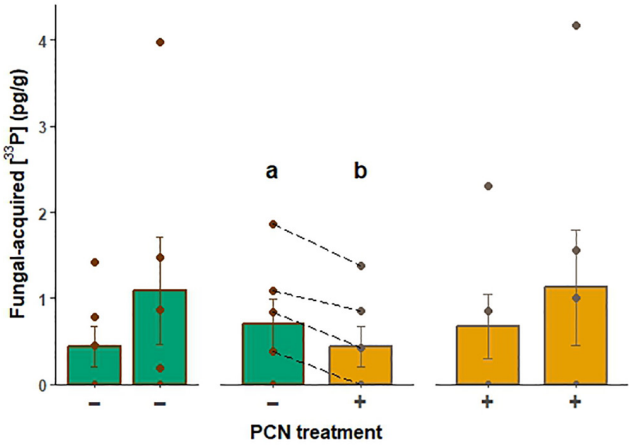

FIGURE 2 Concentration of arbuscular mycorrhizal (AM) fungal-acquired ^{33}P in plant shoots for each potato cyst nematode (PCN) treatment. Letters and dashed lines between data points indicate paired plants within the same mesocosm when significant effects were observed ($p < 0.05$; linear mixed-effects model). Barplots denote mean ± SE. Plants without PCN are indicated by '–' and green bars, whereas plants with PCN are indicated by '+' and orange bars.

Data for the percentage of fungal C that moved across the mesocosm showed an unequal variance, so a Welch two-sample *t*-test was performed to assess the effect of the PCN infection on the ^{14}C-labelled plant.

3 | RESULTS

3.1 | Impact of PCN infection on AM fungi and plant growth

The soil PCN population (Figure S4), total root colonisation (Figure S5a), and soil hyphal length density (Figure S5d) were not influenced by either the PCN infection of the plants or the PCN infection in their neighbours (Table S1). Shoot dry biomass upon harvest (Figure S6a), as well as FvP/FmP (Figure S7a) and SPAD (Figure S7b) measured during the weeks of harvest, were also not significantly affected by the PCN infection of the plants or the PCN infection of their neighbouring plants (Table S1).

3.2 | Total P in plant shoots and AM fungal-acquired ^{33}P

The total concentration of P (plant and AM fungal-acquired; Figure S8) in plant shoots did not differ overall based on the PCN infection of the plants ($p = 0.71$, $F = 0.14$) nor the PCN infection of their neighbours ($p = 0.19$, $F = 1.82$). The concentration of fungal-acquired ^{33}P in the shoots (Figure 2) was also not overall influenced by either the presence of PCN on the plants ($p = 0.86$, $F = 0.03$) or the presence of the PCN on their neighbours ($p = 0.57$, $F = 0.32$). However,

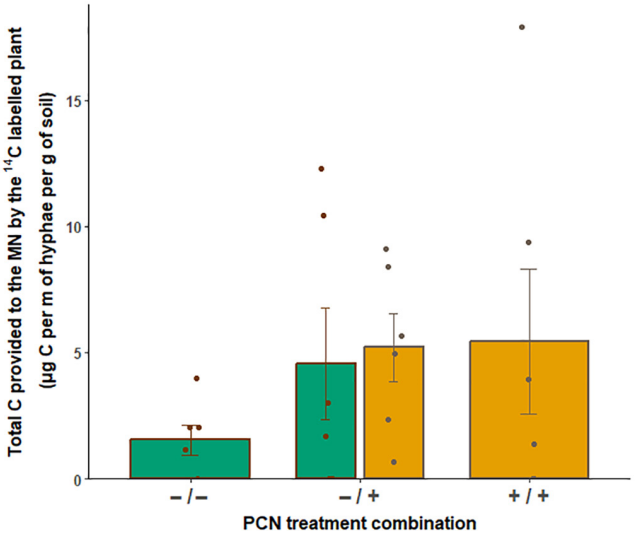

FIGURE 3 The total amount of recently-fixed plant-derived C detected in the mycorrhizal network (MN; µg C per metre of hyphae per gram of dry soil) across both compartments of the mesocosm based on the potato cyst nematode (PCN) treatment combination. Barplots denote mean ± SE. Treatments without PCN are indicated by '–' and green bars, whereas treatments with PCN are indicated by '+' and orange bars.

within the same mesocosms, when an uninfected plant was grown next to a PCN-infected plant (i.e., '–/+'), the uninfected plants consistently acquired more fungal ^{33}P in the shoots relative to their PCN-infected neighbours ($p = 0.03$, $F = 8.38$; Figure 2).

3.3 | Plant-fixed C transfer to AM fungal networks

The total recently-fixed plant-derived C in extraradical hyphae (i.e., fungal C) across the whole mesocosm (Figure 3) did not significantly differ based on the PCN infection of the ^{14}C-labelled plant ($p = 0.27$, $F = 1.30$) nor the infection of the neighbouring plant ($p = 0.42$, $F = 0.68$).

However, the percentage of fungal C that moved across the mesocosms (i.e., from the ^{14}C-labelled to the unlabelled compartment; Figure 4) was significantly influenced by the PCN infection of the ^{14}C-labelled plant ($p = 0.02$, $t = 2.74$), with more C moving away from infected plants (i.e., 46% or 38% depending on whether the plant on the other side was also infected or uninfected) than from uninfected plants (0% or 6% depending on whether the plant on the other side was also uninfected or PCN-infected).

4 | DISCUSSION

Despite the near-ubiquity of plant symbioses with AM fungi, our understanding of their function in complex, ecologically relevant scenarios is not often addressed experimentally. Interacting or interconnected MNs can modulate resource allocation below-ground (Durant et al., 2023; Mikkelsen et al., 2008) and facilitate the transmission of defence signals between neighbouring plants (Alaux et al., 2020; Babikova et al., 2013; Song et al., 2014). In this way, MNs influence wider ecological processes and dynamics, including plant competition and subsequent community structure and function (Tedersoo et al., 2020) as well as global C cycling (Hawkins et al., 2023). However, the function and responsiveness of MNs to biotic perturbation, such as that caused by a disruption of the C supply by pests or pathogens, which is common in natural ecosystems, remains unexplored. Here, using a dual tracer approach, we determined the allocation of P from the MN to plant hosts of contrasting PCN infection, as well as the relative contribution of C made by the two neighbouring plants and the movement of C through the MN.

Despite relatively low levels of PCN infection (Minnis et al., 2002) and no obvious PCN-induced physiological impact on the plants (Figures S6a and S7a,b; Table S1), AM fungi in our experiments transferred more ^{33}P to uninfected plants compared with PCN-infected plant neighbours ('–/+'; Figure 2). However, in line with previous experiments using single plants (Bell et al., 2022), fungal-acquired P transfer to PCN-infected hosts was overall maintained, regardless of PCN treatment (Figure 2). Together, these findings suggest a degree of preference in the allocation of fungal-acquired resources towards non-infected plants, but only when the MN is linked to plant hosts of contrasting parasitism. However, this effect does not appear to be universal across plant and pest species, as another experiment that also used paired plants with interconnected or interacting MNs detected no differences (between or within treatments) in fungal-acquired P between aphid-infested and uninfested plants (Durant et al., 2023).

Although there were differences in the levels of fungal-acquired ^{33}P in shoots within the '–/+' PCN treatment combination (Figure 2), this was not matched by a PCN-induced difference in the total amount of C each plant contributed to the MN (Figure 3). Contrary to a previous experiment using single plants, where plant C provision to AM fungi decreased in the presence of PCN (Bell et al., 2022), a similar level of PCN infection in our experiment did not impact the overall amount of plant C delivered to the MN. This difference may be driven by plant–plant interactions modifying the amounts of plant resources invested below-ground (Weiner & Thomas, 1992). CMNs can increase competition between plants (Merrild et al., 2013; Weremijewicz et al., 2016) and host plants connected to the same CMN, or even interacting MNs, may partially adjust C resource allocation below-ground according to each other's C provision (Wyatt et al., 2014). For example, in our '–/+' treatment combination, uninfected plants could have reduced their C allocation to the MN to mimic that of their infected neighbours. It is also worth noting that although we do not know the exact effect of the temporary pulse of $^{14}CO_2$ on the labelled plants, these results suggest that PNC-infected and uninfected plants reacted similarly in terms of total C provision below-ground.

Another important consideration is that adjustments in C resource provision by host plants could be reflected in the quantity and

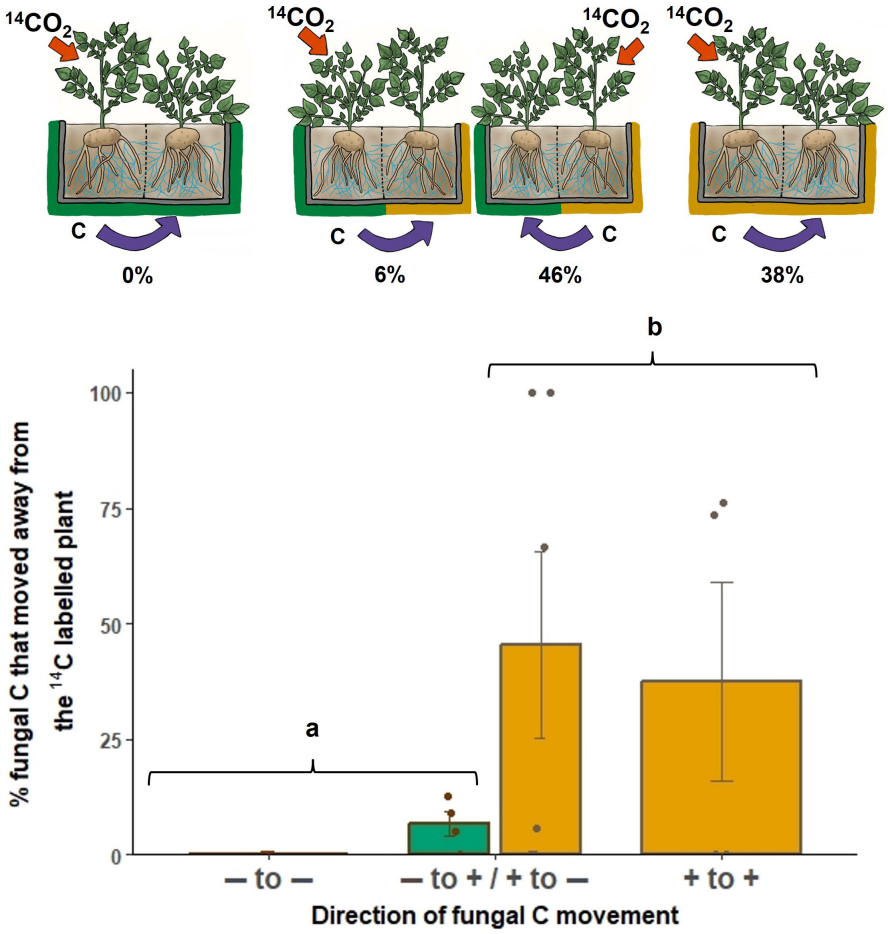

FIGURE 4 Percentage of fungal C (amount per metre of hyphae in a gram of dry soil) that moved from the ^{14}C-labelled compartment to the unlabelled compartment of the mesocosm according to the potato cyst nematode (PCN) treatment of both plants. Numbers underneath the visual schematics represent means. Brackets indicate the significantly different groups ($p < 0.05$). Barplots denote mean ± SE. Treatments without PCN are indicated by '–' and the green colour, whereas treatments with PCN are indicated by '+' and the orange colour.

as well as the quality of C resources allocated to AM fungi. Using single plants in split root experimental systems, transcriptomic analysis has revealed that expression of mycorrhizal-induced hexose transporters is reduced when plants are coinfected with either an above or a below-ground parasite (Bell et al., 2024). However, host plants appear to maintain C transfer to AM fungi by maintaining the expression of fatty acid biosynthesis and transportation pathways (Bell et al., 2024). A similar mechanism could be in play here, whereby AM fungi in and around PCN-infected roots could be receiving more C in the form of fatty acids, whereas AM fungi in uninfected compartments could be receiving more C in the form of glucose. The former would likely be more suitable for longer-term storage rather than for immediate metabolism and mycelium growth (Salmeron-santiago et al., 2022) and thus may not be detected in our experiments which capture the fate of recently-fixed plant C.

Any PCN-induced changes in plant C could also affect the composition of the AM fungal community (Frew et al., 2024). Such changes in the AM fungal community can be induced by other root herbivores (e.g., Frew, 2022), and recently it has been suggested that in addition to C availability driving changes in mycorrhizal species composition, the ability of mycorrhizal species to support the plant hosts' defence mechanisms might also act as a selection pressure (Frew et al., 2024). In other words, the impact of plants on AM fungi could be, at least partly, driven indirectly by PCN-induced differences in the composition and functionality of the AM fungal community, rather than directly by differences in plant C inputs.

The movement of P from 'rich' to 'poor' patches has been observed in in vitro experiments using AM root organ cultures (Whiteside et al., 2019). However, Whiteside et al. (2019) did not resolve how the AM fungus itself might redistribute C across the network. Our experimental design allowed us to explore this in soil, where we detected below-ground movement of plant-fixed C resources away from plants infected with PCN (Figure 4). The movement of plant-derived C resources could have promoted AM fungal mycelium expansion and exploration of the soil, away from the 'drain' on plant C resources caused by PCN. However, a greater accumulation of plant C did not translate into increased fungal hyphal density within the soil in our experiments (Figure S5d). It is important to note that absorptive AM hyphal networks are typically ephemeral, with hyphae disintegrating 5–7 days after formation (Friese & Allen, 1991); as such differences might not have been captured within the timescale of these experiments.

In our experiment, the capacity of the MN to detect parasitism of host plants and move C according to the C source–sink strength seems to be limited spatially. Specifically, although we detected an overall movement of C away from PCN-infected hosts, there was no clear indication that this movement was more pronounced when the plant in the other compartment was uninfected (+ to –) rather than

infected (+ to +; Figure 4). Therefore, it appears that extraradical AM fungal hyphae may be able to 'perceive' parasitism of their proximal plant host and move C away if that host is infected, but the direction of C movement thereafter appears to be 'blind' to infection of the more distal plant host. Similarly to what has been suggested for plants (Veresoglou et al., 2022), AM fungi may thus be 'hedging their bets'; moving C away from infected hosts in case of a future physiological decline of those same hosts. In the field, PCN infection tends to be heterogeneous (Been & Schomaker, 2000), so any movement of C and mycelium growth away from infected plants would increase the chances of the MN associating with an uninfected host.

To date, many studies investigating the AM fungi–plant symbiosis focus on plant benefits or conceptualise the C-for-nutrient regulation using a rigid 'reciprocal rewards' framework. Here, we have shown evidence of a fungal-mediated movement of C based on the pest-infection status of the host plants. From a fungal perspective, resources could be distributed evenly across MNs to compensate for C losses due to competing plant symbionts (Durant et al., 2023), or alternatively, resources could be invested more readily in parts of the networks that might be more 'profitable'. Our data on C movement support the latter hypothesis; however, any differences in perceived 'profitability' between PCN-infected and uninfected hosts by AM fungi remain to be determined, as we did not detect a reduction in plant C delivery under PCN infection. A better understanding of the physiology and evolution of AM fungi, as well as the varied benefits they receive from their plant hosts, would help further elucidate our results.

In the long term, any fungal-mediated C movement is likely to influence plant hosts themselves via effects on the growth and functioning of MNs. As pointed out by Finlay and Söderström (1992) and later by Pfeffer et al. (2004), the distribution of C within MNs may be significant to plants even in the absence of net transfer of C from fungus to plants. This is because the C demand of the fungal mycelium would be reduced, and newly colonised plants would gain access to nutrients from the mycelium without contributing as much C in return. Overall, our findings reveal a new dimension which lines with a more mycocentric view of MNs (Fitter et al., 1998), whereby fungi move C to satisfy their own needs as well as those of their plant hosts. More research, using a range of plant species and different organisms that might impact AM fungi function, is needed to better understand the role of MNs in modulating the C-for-nutrient exchange of the symbiosis. Increasing the temporal and spatial resolution of experimental studies is also paramount to fully appreciate the importance of AM fungi and MNs for ecosystem functioning (reviewed by Alaux et al., 2021), especially their role in C cycling and storage (e.g., Averill et al., 2014; Hawkins et al., 2023; van der Heijden et al., 2015; Wurzburger et al., 2017) as well as their role in agricultural systems (Rillig et al., 2019; Thirkell et al., 2017).

AUTHOR CONTRIBUTIONS

Emily Magkourilou and Katie J. Field conceived and designed the study, with contributions from P. E. Urwin and Tim J. Daniell. Emily Magkourilou set up the experiment, collected and analysed data, and Emily K. Durant assisted with the experimental work. Emily Magkourilou led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Dr. Besiana Sinanaj and Dr. Alex Williams (University of Sheffield) for their assistance in harvesting. We thank Prof. Dylan Childs (University of Sheffield) for feedback on the initial statistical analyses performed. E.M. is supported by a BBSCR White Rose DTP studentship (BB/T007222/1). C.A.B. is supported by a BBSRC Discovery Fellowship (BB/X009823/1). K.J.F. is supported by an ERC CoG (MYCOREV—865225). We thank the de Laszlo Foundation for generously supporting postgraduate student research.

CONFLICT OF INTEREST STATEMENT

K. J. Field is a senior editor of Functional Ecology but took no part in the peer review or decision-making processes for this article. The authors declare no other conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from Dryad: https://doi.org/10.5061/dryad.905qfttt3 (Magkourilou et al., 2024).

ORCID

E. Magkourilou https://orcid.org/0000-0003-0195-5653
C. A. Bell https://orcid.org/0000-0002-7437-2793
P. E. Urwin https://orcid.org/0000-0002-3469-2549
K. J. Field https://orcid.org/0000-0002-5196-2360

REFERENCES

Alaux, P. L., Naveau, F., Declerck, S., & Cranenbrouck, S. (2020). Common mycorrhizal network induced JA/ET genes expression in healthy potato plants connected to potato plants infected by *Phytophthora infestans*. *Frontiers in Plant Science*, *11*, 503121. https://doi.org/10.3389/fpls.2020.00602

Alaux, P. L., Zhang, Y., Gilbert, L., & Johnson, D. (2021). Can common mycorrhizal fungal networks be managed to enhance ecosystem functionality? *Plants, People, Planet*, *3*(5), 433–444. https://doi.org/10.1002/ppp3.10178

Averill, C., Turner, B. L., & Finzi, A. C. (2014). Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature*, *505*(7484), 543–545. https://doi.org/10.1038/nature12901

Babikova, Z., Gilbert, L., Bruce, T. J. A., Birkett, M., Caulfield, J. C., Woodcock, C., Pickett, J. A., & Johnson, D. (2013). Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecology Letters*, *16*(7), 835–843. https://doi.org/10.1111/ELE.12115

Bago, B., & Bécard, G. (2002). Bases of the obligate biotrophy of arbuscular mycorrhizal fungi. In S. H. S. Gianinazzi, J. M. Barea, & K. Haselwandter (Eds.), *Mycorrhizal technology in agriculture* (pp. 33–48). Birkhäuser Verlag. https://doi.org/10.1007/978-3-0348-8117-3_3

Been, T. H., & Schomaker, C. H. (2000). Development and evaluation of sampling methods for fields with infestation foci of potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*). *Phytopathology*, *90*(6), 647–656. https://doi.org/10.1094/PHYTO.2000.90.6.647

Bell, C. A., Magkourilou, E., Ault, J. R., Urwin, P. E., & Field, K. J. (2024). Phytophagy impacts the quality and quantity of plant carbon resources acquired by mutualistic arbuscular mycorrhizal fungi. *Nature Communications*, *15*(1), 1–14. https://doi.org/10.1038/s41467-024-45026-3

Bell, C. A., Magkourilou, E., Urwin, P. E., & Field, K. J. (2021). The influence of competing root symbionts on below-ground plant resource allocation. *Ecology and Evolution*, *11*(7), 2997–3003. https://doi.org/10.1002/ECE3.7292

Bell, C. A., Magkourilou, E., Urwin, P. E., & Field, K. J. (2022). Disruption of carbon for nutrient exchange between potato and arbuscular mycorrhizal fungi enhanced cyst nematode fitness and host pest tolerance. *New Phytologist*, *234*(1), 269–279. https://doi.org/10.1111/NPH.17958

Brundrett, M. C., & Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist*, *220*(4), 1108–1115. https://doi.org/10.1111/NPH.14976

Bücking, H., & Shachar-Hill, Y. (2005). Phosphate uptake, transport and transfer by the arbuscular mycorrhizal fungus *Glomus intraradices* is stimulated by increased carbohydrate availability. *New Phytologist*, *165*(3), 899–912. https://doi.org/10.1111/J.1469-8137.2004.01274.X

Cameron, D. D., Johnson, I., Leake, J. R., & Read, D. J. (2007). Mycorrhizal acquisition of inorganic phosphorus by the green-leaved terrestrial orchid *Goodyera repens*. *Annals of Botany*, *99*(5), 831–834. https://doi.org/10.1093/AOB/MCM018

Cameron, D. D., Johnson, I., Read, D. J., & Leake, J. R. (2008). Giving and receiving: Measuring the carbon cost of mycorrhizas in the green orchid, *Goodyera repens*. *New Phytologist*, *180*(1), 176–184. https://doi.org/10.1111/J.1469-8137.2008.02533.X

Cessna, S., Demmig-Adams, B., Adams, W. W., & Cessna, I. S. (2010). Exploring photosynthesis and plant stress using inexpensive chlorophyll fluorometers. *Journal of Natural Resources and Life Sciences Education*, *39*(1), 22–30. https://doi.org/10.4195/JNRLSE.2009.0024U

Charters, M. D., Sait, S. M., Correspondence, K. J. F., & Field, K. J. (2020). Aphid herbivory drives asymmetry in carbon for nutrient exchange between plants and an arbuscular mycorrhizal fungus. *Current Biology*, *30*, 1801–1808.e5. https://doi.org/10.1016/j.cub.2020.02.087

de Novais, C. B., Pepe, A., Siqueira, J. O., Giovannetti, M., & Sbrana, C. (2017). Compatibility and incompatibility in hyphal anastomosis of arbuscular mycorrhizal fungi. *Scientia Agricola*, *74*(5), 411–416. https://doi.org/10.1590/1678-992X-2016-0243

Drigo, B., Pijl, A. S., Duyts, H., Kielak, A. M., Gamper, H. A., Houtekamer, M. J., Boschker, H. T. S., Bodelier, P. L. E., Whiteley, A. S., van Veen, J. A., & Kowalchuk, G. A. (2010). Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO_2. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(24), 10938–10942. https://doi.org/10.1073/PNAS.0912421107

Durant, E., Hoysted, G. A., Howard, N., Sait, S. M., Childs, D. Z., Johnson, D., & Field, K. J. (2023). Herbivore-driven disruption of arbuscular mycorrhizal carbon-for-nutrient exchange is ameliorated by neighboring plants. *Current Biology*, *33*(12), 2566–2573.e4. https://doi.org/10.1016/J.CUB.2023.05.033

Fellbaum, C. R., Gachomo, E. W., Beesetty, Y., Choudhari, S., Strahan, G. D., Pfeffer, P. E., Kiers, E. T., & Bücking, H. (2012). Carbon availability triggers fungal nitrogen uptake and transport in arbuscular mycorrhizal symbiosis. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(7), 2666–2671. https://doi.org/10.1073/PNAS.1118650109

Fenwick, D. W. (1940). Methods for the recovery and counting of cysts of *Heterodera schachtii* from soil. *Journal of Helminthology*, *18*(4), 155–172. https://doi.org/10.1017/S0022149X00031485

Finlay, R., & Söderström, B. (1992). Mycorrhiza and carbon flow to the soil. In M. F. Allen (Ed.), *Mycorrhizal functioning: An integrative plant-fungal process* (pp. 134–160). Springer Science & Business Media.

Fitter, A. H., Graves, J. D., Watkins, N. K., Robinson, D. G., & Scrimgeour, C. (1998). Carbon transfer between plants and its control in networks of arbuscular mycorrhizas. *Functional Ecology*, *12*(3), 406–412. https://doi.org/10.1046/J.1365-2435.1998.00206.X

Frew, A. (2022). Root herbivory reduces species richness and alters community structure of root-colonising arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, *171*, 108723. https://doi.org/10.1016/J.SOILBIO.2022.108723

Frew, A., Weinberger, N., Powell, J., Watts-Williams, S. J., & Aguilar-Trigueros, C. A. (2024). Community assembly of root-colonising arbuscular mycorrhizal fungi: Beyond carbon and into defence? *The ISME Journal*, *18*, 4592. https://doi.org/10.1093/ismejo/wrae007/7584592

Friese, C. F., & Allen, M. F. (1991). The spread of VA mycorrhizal fungal hyphae in the soil: Inoculum types and external hyphal architecture. *Mycologia*, *83*(4), 409–418. https://doi.org/10.1080/00275514.1991.12026030

Giovannetti, M., Sbrana, C., Avio, L., & Strani, P. (2004). Patterns of below-ground plant interconnections established by means of arbuscular mycorrhizal networks. *New Phytologist*, *164*(1), 175–181. https://doi.org/10.1111/J.1469-8137.2004.01145.X

Govindarajulu, M., Pfeffer, P. E., Jin, H., Abubaker, J., Douds, D. D., Allen, J. W., Bücking, H., Lammers, P. J., & Shachar-Hill, Y. (2005). Nitrogen transfer in the arbuscular mycorrhizal symbiosis. *Nature*, *435*(7043), 819–823. https://doi.org/10.1038/nature03610

Hamilton, A. C. L. H. R. I., & Smith, B. L. D. L. M. (2000). Acquisition of Cu, Zn, Mn and Fe by mycorrhizal maize (*Zea mays* L.) grown in soil at different P and micronutrient levels. *Mycorrhiza*, *9*, 331–336. https://doi.org/10.1007/s005720050277

Hawkins, H.-J., Cargill, R. I. M., van Nuland, M. E., Hagen, S. C., Field, K. J., Sheldrake, M., Soudzilovskaia, N. A., & Kiers, E. T. (2023). Mycorrhizal mycelium as a global carbon pool. *Current Biology*, *33*(11), 560–573. https://doi.org/10.1016/J.CUB.2023.02.027

Johnson, D., Leake, J. R., & Read, D. J. (2001). Novel in-growth core system enables functional studies of grassland mycorrhizal mycelial networks. *New Phytologist*, *152*(3), 555–562. https://doi.org/10.1046/J.0028-646X.2001.00273.X

Kiers, E. T., Duhamel, M., Beesetty, Y., Mensah, J. A., Franken, O., Verbruggen, E., Fellbaum, C. R., Kowalchuk, G. A., Hart, M. M., Bago, A., Palmer, T. M., West, S. A., Vandenkoornhuyse, P., Jansa, J., & Bücking, H. (2011). Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science*, *333*(6044), 880–882. https://doi.org/10.1126/SCIENCE.1208473

Kiers, E. T., West, S. A., Wyatt, G. A. K., Gardner, A., Bücking, H., & Werner, G. D. A. (2016). Misconceptions on the application of biological market theory to the mycorrhizal symbiosis. *Nature Plants*, *2*(5), 1–2. https://doi.org/10.1038/nplants.2016.63

Kuhlgert, S., Austic, G., Zegarac, R., Osei-Bonsu, I., Hoh, D., Chilvers, M. I., Roth, M. G., Bi, K., TerAvest, D., Weebadde, P., & Kramer, D. M. (2016). MultispeQ Beta: A tool for large-scale plant phenotyping connected to the open PhotosynQ network. *Royal Society Open Science*, *3*(10), 160592. https://doi.org/10.1098/RSOS.160592

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/JSS.V082.I13

Lehmann, A., Veresoglou, S. D., Leifheit, E. F., & Rillig, M. C. (2014). Arbuscular mycorrhizal influence on zinc nutrition in crop plants – A meta-analysis. *Soil Biology and Biochemistry*, *69*, 123–131. https://doi.org/10.1016/J.SOILBIO.2013.11.001

Lekberg, Y., Hammer, E. C., & Olsson, P. A. (2010). Plants as resource islands and storage units – Adopting the mycocentric view of

arbuscular mycorrhizal networks. *FEMS Microbiology Ecology*, *74*(2), 336–345. https://doi.org/10.1111/J.1574-6941.2010.00956.X

Magkourilou, E., Bell, C. A., Daniell, T. J., & Field, K. J. (2024). The functionality of arbuscular mycorrhizal networks across scales of experimental complexity and ecological relevance. *Functional Ecology*, 1–16. https://doi.org/10.1111/1365-2435.14618

McGonigle, T. P., Miller, M. H., Evans, D. G., Fairchild, G. L., & Swan, J. A. (1990). A new method which gives an objective measure of colonization of roots by vesicular—Arbuscular mycorrhizal fungi. *New Phytologist*, *115*(3), 495–501. https://doi.org/10.1111/J.1469-8137.1990.TB00476.X

Merrild, M. P., Ambus, P., Rosendahl, S., & Jakobsen, I. (2013). Common arbuscular mycorrhizal networks amplify competition for phosphorus between seedlings and established plants. *New Phytologist*, *200*(1), 229–240. https://doi.org/10.1111/NPH.12351

Mikkelsen, B. L., Rosendahl, S., & Jakobsen, I. (2008). Underground resource allocation between individual networks of mycorrhizal fungi. *New Phytologist*, *180*(4), 890–898. https://doi.org/10.1111/J.1469-8137.2008.02623.X

Minnis, S. T., Haydock, P. P. J., Ibrahim, S. K., Grove, I. G., Evans, K., & Russell, M. D. (2002). Potato cyst nematodes in England and Wales – Occurrence and distribution. *Annals of Applied Biology*, *140*(2), 187–195. https://doi.org/10.1111/J.1744-7348.2002.TB00172.X

Murphy, J., & Riley, J. P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, *27C*, 31–36. https://doi.org/10.1016/S0003-2670(00)88444-5

Noë, R., & Kiers, E. T. (2018). Mycorrhizal markets, firms, and co-ops. *Trends in Ecology & Evolution*, *33*(10), 777–789. https://doi.org/10.1016/J.TREE.2018.07.007

Pfeffer, P. E., Douds, D. D., Bücking, H., Schwartz, D. P., & Shachar-Hill, Y. (2004). The fungus does not transfer carbon to or between roots in an arbuscular mycorrhizal symbiosis. *New Phytologist*, *163*(3), 617–627. https://doi.org/10.1111/J.1469-8137.2004.01152.X

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org

Redecker, D., Kodner, R., & Graham, L. E. (2000). Glomalean fungi from the Ordovician. *Science*, *289*(5486), 1920–1921. https://doi.org/10.1126/science.289.5486.1920

Rillig, M. C., Aguilar-Trigueros, C. A., Camenzind, T., Cavagnaro, T. R., Degrune, F., Hohmann, P., Lammel, D. R., Mansour, I., Roy, J., van der Heijden, M. G. A., & Yang, G. (2019). Why farmers should manage the arbuscular mycorrhizal symbiosis. *New Phytologist*, *222*(3), 1171–1175. https://doi.org/10.1111/NPH.15602

RStudio Team. (2022). *RStudio: Integrated development for R*. RStudio. http://www.rstudio.com/

Salmeron-santiago, I. A., Martínez-trujillo, M., Valdez-alarcón, J. J., Pedraza-santos, M. E., Santoyo, G., Pozo, M. J., & Chávez-bárcenas, A. T. (2022). An updated review on the modulation of carbon partitioning and allocation in arbuscular mycorrhizal plants. *Microorganisms*, *10*(1), 75. https://doi.org/10.3390/MICROORGANISMS10010075

Song, Y. Y., Ye, M., Li, C., He, X., Zhu-Salzman, K., Wang, R. L., Su, Y. J., Luo, S. M., & Zeng, R. (2014). Hijacking common mycorrhizal networks for herbivore-induced defence signal transfer between tomato plants. *Scientific Reports*, *4*(1), 1–8. https://doi.org/10.1038/srep03915

Spatafora, J. W., Chang, Y., Benny, G. L., Lazarus, K., Smith, M. E., Berbee, M. L., Bonito, G., Corradi, N., Grigoriev, I., Gryganskyi, A., James, T. Y., O'Donnell, K., Roberson, R. W., Taylor, T. N., Uehling, J., Vilgalys, R., White, M. M., & Stajich, J. E. (2016). A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia*, *108*(5), 1028–1046. https://doi.org/10.3852/16-042

Tedersoo, L., Bahram, M., & Zobel, M. (2020). How mycorrhizal associations drive plant population and community biology. *Science*, *367*(6480), eaba1223. https://doi.org/10.1126/science.aba1223

Tennant, D. (1975). A test of a modified line intersect method of estimating root length. *The Journal of Ecology*, *63*(3), 995. https://doi.org/10.2307/2258617

Thirkell, T. J., Charters, M. D., Elliott, A. J., Sait, S. M., & Field, K. J. (2017). Are mycorrhizal fungi our sustainable saviours? Considerations for achieving food security. *Journal of Ecology*, *105*(4), 921–929. https://doi.org/10.1111/1365-2745.12788

Tisserant, E., Kohler, A., Dozolme-Seddas, P., Balestrini, R., Benabdellah, K., Colard, A., Croll, D., da Silva, C., Gomez, S. K., Koul, R., Ferrol, N., Fiorilli, V., Formey, D., Franken, P. H., Helber, N., Hijri, M., Lanfranco, L., Lindquist, E., Liu, Y., … Martin, F. (2012). The transcriptome of the arbuscular mycorrhizal fungus *Glomus intraradices* (DAOM 197198) reveals functional tradeoffs in an obligate symbiont. *New Phytologist*, *193*(3), 755–769. https://doi.org/10.1111/J.1469-8137.2011.03948.X

Tisserant, E., Malbreil, M., Kuo, A., Kohler, A., Symeonidi, A., Balestrini, R., Charron, P., Duensing, N., Frei Dit Frey, N., Gianinazzi-Pearson, V., Gilbert, L. B., Handa, Y., Herr, J. R., Hijri, M., Koul, R., Kawaguchi, M., Krajinski, F., Lammers, P. J., Masclaux, F. G., … Martin, F. (2013). Genome of an arbuscular mycorrhizal fungus provides insight into the oldest plant symbiosis. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(50), 20117–20122. https://doi.org/10.1073/pnas.1313452110

Turner, S. J., & Rowe, J. A. (2006). Cyst nematodes. In R. N. Perry & M. Moens (Eds.), *Plant nematology* (pp. 90–122). CAB International.

van der Heijden, M. G. A., Martin, F. M., Selosse, M. A., & Sanders, I. R. (2015). Mycorrhizal ecology and evolution: The past, the present, and the future. *New Phytologist*, *205*(4), 1406–1423. https://doi.org/10.1111/NPH.13288

van der Heijden, M. G. A., & Walder, F. (2016). Reply to 'Misconceptions on the application of biological market theory to the mycorrhizal symbiosis'. *Nature Plants*, *2*(5), 1. https://doi.org/10.1038/nplants.2016.62

van't Padje, A., Werner, G. D. A., & Kiers, E. T. (2021). Mycorrhizal fungi control phosphorus value in trade symbiosis with host roots when exposed to abrupt 'crashes' and 'booms' of resource availability. *New Phytologist*, *229*(5), 2933–2944. https://doi.org/10.1111/NPH.17055

Veresoglou, S. D., Johnson, D., Mola, M., Yang, G., & Rillig, M. C. (2022). Evolutionary bet-hedging in arbuscular mycorrhiza-associating angiosperms. *New Phytologist*, *233*(5), 1984–1987. https://doi.org/10.1111/NPH.17852

Vierheilig, H., Coughlan, A. P., Wyss, U., & Piché, Y. (1998). Ink and vinegar, a simple staining technique for arbuscular-mycorrhizal fungi. *Applied and Environmental Microbiology*, *64*(12), 5004–5007. https://doi.org/10.1128/aem.64.12.5004-5007.1998

Walder, F., & van der Heijden, M. G. A. (2015). Regulation of resource exchange in the arbuscular mycorrhizal symbiosis. *Nature Plants*, *1*(11), 1–7. https://doi.org/10.1038/nplants.2015.159

Wang, B., & Qiu, Y.-L. (2006). Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza*, *16*(5), 299–363. https://doi.org/10.1007/S00572-005-0033-6

Weiner, J., & Thomas, S. C. (1992). Competition and allometry in three species of annual plants. *Ecology*, *73*(2), 648–656. https://doi.org/10.2307/1940771

Weremijewicz, J., da Sternberg, L. S., & Janos, D. P. (2016). Common mycorrhizal networks amplify competition by preferential mineral nutrient allocation to large host plants. *New Phytologist*, *212*(2), 461–471. https://doi.org/10.1111/NPH.14041

Werner, G. D. A., & Kiers, E. T. (2015). Partner selection in the mycorrhizal mutualism. *New Phytologist*, *205*(4), 1437–1442. https://doi.org/10.1111/NPH.13113

Werner, G. D. A., Strassmann, J. E., Ivens, A. B. F., Engelmoer, D. J. P., Verbruggen, E., Queller, D. C., Noë, R., Johnson, N. C., Hammerstein, P., & Kiers, E. T. (2014). Evolution of microbial markets. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(4), 1237–1244. https://doi.org/10.1073/PNAS.1315980111

Whiteside, M. D., Werner, G. D. A., Caldas, V. E. A., van't Padje, A., Dupin, S. E., Elbers, B., Bakker, M., Wyatt, G. A. K., Klein, M., Hink, M. A., Postma, M., Vaitla, B., Noë, R., Shimizu, T. S., West, S. A., & Kiers, E. T. (2019). Mycorrhizal fungi respond to resource inequality by moving phosphorus from rich to poor patches across networks. *Current Biology*, *29*(12), 2043–2050.e8. https://doi.org/10.1016/J.CUB.2019.04.061

Wickham, H. (2014). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. https://ggplot2.tidyverse.org

Wipf, D., Krajinski, F., van Tuinen, D., Recorbet, G., & Courty, P. E. (2019). Trading on the arbuscular mycorrhiza market: From arbuscules to common mycorrhizal networks. *New Phytologist*, *223*(3), 1127–1142. https://doi.org/10.1111/NPH.15775

Wurzburger, N., Brookshire, E. N. J., McCormack, M. L., & Lankau, R. A. (2017). Mycorrhizal fungi as drivers and modulators of terrestrial ecosystem processes. *New Phytologist*, *213*(3), 996–999. https://doi.org/10.1111/NPH.14409

Wyatt, G. A. K., Toby Kiers, E., Gardner, A., & West, S. A. (2014). A biological market analysis of the plant-mycorrhizal symbiosis. *Evolution*, *68*(9), 2603–2618. https://doi.org/10.1111/EVO.12466

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. The experimental design used to test the effect of potato-cyst nematodes (PCN) on the transfer of fungal-acquired ^{33}P to pairs of potato plants.

Figure S2. A simplified experimental timeline for (a) the tracing of ^{33}P from fungus to plant and (b) the tracing of plant (c) from plant to fungus.

Figure S3. The experimental design used to test the effect of potato-cyst nematodes on the transfer of recently-fixed plant carbon across the mycorrhizal network.

Figure S4. Soil potato-cyst nematode (PCN) population at the end of the experiments expressed as the number of cysts per gram of soil.

Figure S5. (a) Percentage total root colonisation, (b) percentage arbuscular root colonisation, (c) percentage vesicular root colonisation and (d) hyphal lengths expressed as metres in a gram of soil ($\log_{10}+1$ transformed), for each potato cyst nematode (PCN) treatment.

Figure S6. (a) Shoot dry biomass in grams, (b) total number of harvested tubers, and (c) dry tuber yield expressed in grams, for each potato cyst nematode (PCN) treatment.

Figure S7. The photochemical activity of photosystem II characterised by the FvP/FmP (a) and the relative chlorophyll content [SPAD; (b)] values at the week of harvest for each potato cyst nematode (PCN) treatment.

Figure S8. Concentration of total P (plant and AM fungal-acquired) in plant shoots for each potato cyst nematode (PCN) treatment.

Table S1. Summary of statistics from linear mixed-effects models showing the effect of the potato cyst nematode (PCN) infection treatment of a plant and/or the effect of the PCN infection treatment of the neighbouring plants on the PCN reproductive success, root colonisation and plant growth parameters.

How to cite this article: Magkourilou, E., Durant, E. K., Bell, C. A., Daniell, T. J., Urwin, P. E., & Field, K. J. (2024). Plant pests influence the movement of plant-fixed carbon and fungal-acquired nutrients through arbuscular mycorrhizal networks. *Functional Ecology*, *00*, 1–11. https://doi.org/10.1111/1365-2435.14693