



Arbuscular mycorrhizal fungal hyphae enhance transport of the allelochemical juglone in the field

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ABSTRACT

Allelopathy is a biological phenomenon where plants have harmful effects on growth of surrounding plants through the production of chemical substances. Here we focus on allelochemical processes which operate belowground, can influence plant interactions and therefore potentially affect plant community structure. Soil hyphae of arbuscular mycorrhizal fungi (AMF) may enhance transport processes in the soil matrix by providing direct connections between plants facilitating infochemical exchange.

In a two-component field study we showed that soil hyphae likely play a crucial role in movement of allelochemicals in natural soils and greatly expand bioactive zones by providing effective transport pathways for chemical compounds. First, we tested the effects of *Juglans regia* leaf litter extract addition in intact or disrupted hyphal networks and simultaneously determined growth reducing effects on sensitive *Lycopersicon lycopersicum* plants. Second, we analyzed the effect of juglone on tomato by directly adding leaf litter. In both approaches we found an increase of juglone transport if a hyphal network was present, resulting in reduced growth of target plants.

Our results, together with previous work, add to the body of evidence for hyphae of soil fungi playing an important role in the transfer of allelochemicals and effectively acting as transport highways in the field. We suggest that hyphal connections, mostly formed by AMF, increase the effectiveness of allelochemicals in natural systems and can play a crucial role in chemical interaction processes in the soil.

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1. Introduction

Allelopathy is an often controversially discussed topic of great interest to plant and soil ecologists. The biological phenomenon in its broader sense is understood as the direct or indirect harmful effect of one plant on another through the production of chemical compounds that are released into the environment (Rice, 1974). These allelochemicals must accumulate to phytotoxic levels and reach a target plant to be of ecological relevance (Choesin and Boerner, 1991). The allelopathic influence ranges from affecting germination, growth, development, reproduction and distribution of a number of plant species to plant–plant interactions and eventually might play an important role in determining plant community structure (Bais et al., 2003; Blair et al., 2005; Inderjit and Duke, 2005). Allelochemical compounds are found in many types of plants releasing them by a variety of mechanisms into the

rhizosphere, including decomposition of residues, volatilization and root exudation (Bertin et al., 2003).

Growth inhibition caused by the presence of walnut trees in the landscape is one of the classical examples of allelopathy. American black walnut (*Juglans nigra* L.) is the most commonly studied species (Willis, 2000), but harmful influences on the environment were also observed in other members of the family Juglandaceae including *J. regia* (Daglish, 1950; Ponder and Tadros, 1985; Prataviera et al., 1983), the plant used in our study. Walnut toxicity is related to the aromatic phytotoxic compound juglone (5-hydroxy-1, 4 naphthoquinone) (Rice, 1974), and occurs in all plant parts, but especially in leaves and roots (Segura-Aguilar et al., 1992). In living tissues juglone is mostly found in a reduced and nontoxic form, the so-called hydrojuglone, which is transformed in the soil after cleavage of the glycosidic bond and oxidation of the aglycone to the toxic juglone (Bertin et al., 2003). The effects of juglone on woody and herbaceous plants are mostly negative (but see Whittaker and Feeny, 1971), plants responding with stunting, wilting and necrosis caused by growth inhibition at micromolar concentrations (Hejl et al., 1993; Jose and Gillespie, 1998),

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disruption of photosynthesis and respiration (Jose and Gillespie, 1998) and interference with water uptake (Hejl and Koster, 2004). Numerous ornamental and agricultural plants including tomato, which we use here as target plant, are quite sensitive to juglone (Crist and Sherf, 1973). Both rhizodeposition and leaching of juglone and its precursor out of decomposing leaves and other plant parts are important mechanisms by which the allelochemical arrives in the soil and can hence influencing adjacent plants (Rietveld, 1983).

Factors which shape soil complexity like soil composition and structure (Inderjit, 2001; Schmidt and Ley, 1999), soil moisture (Blair et al., 2006) and the content and composition of organic matter (Schmidt and Ley, 1999), as well as the presence and dynamics of microbial communities (Blum, 2004; Cipollini et al., 2012) can influence the extent to which allelopathy contributes to plant community dynamics. Furthermore diffusion rates, sorption of chemical compounds to mineral and organic matter and chemical as well as microbial degradation can affect the functioning of allelochemicals in the soil (Kaur et al., 2009; Rettenmaier et al., 1983; Schmidt and Ley, 1999). Microbial degradation is probably critical for allelopathic effectiveness because high rates of degradation in the rhizosphere and beyond decreases the amount of allelochemicals in the soil and thus shrinks the bioactive zone of the respective compound.

Most studies of allelopathy have not taken into account the existence of soil hyphal networks, mostly formed by arbuscular mycorrhizal fungi (AMF) (Barto et al., 2012). These fungi colonize the roots of the vast majority of plant species, but also form a mycelial network in the soil, potentially linking root systems of multiple plant species in a community (Giovannetti et al., 2001; Mikkelsen et al., 2008; Voets et al., 2006). These hyphal links, potentially forming common mycelial networks (CMNs), may act as “superhighways” connecting different plants belowground (Barto et al., 2012) and could enlarge bioactive zones of allelopathic compounds in natural soils, described in the Network Enhanced Bioactive Zone model (NEBaZ; Barto et al., 2012). Several transport functions of CMNs have been studied, such as the movement of water (Egerton-Warburton et al., 2007; Querejeta et al., 2003) and nutrients (He et al., 2003; Mikkelsen et al., 2008; Walder et al., 2012) as well as metals (Meding and Zasoski, 2008), but very few studies have examined the potential transport of infochemicals via CMNs. Studies have addressed signal-induced intraspecific plant communication (Song et al., 2010), underground signals warning neighboring plants of aphid attack (Babikova et al., 2013) or allelochemicals in soil (Barto et al., 2011; Achatz et al., 2014). Recently it was shown that transport via hyphae could also be beneficial to the hyphae themselves by potentially protecting them from fungivores (Duhamel et al., 2013).

CMNs or parts of a CMN could mediate an accelerated movement of the allelochemical out of the rhizosphere of the producing plant, the place with highest microbial activity, thus reducing vulnerability to microbial degradation. While it is not clear if substances move within or along the hyphae of such networks (Barto et al., 2012), which is beyond the scope of our study to disentangle, the presence of hyphae appears to favor the movement of allelochemicals compared to diffusing through the soil matrix. As a consequence of these higher flow rates, allelochemicals may reach levels that induce growth inhibition in the target plant.

The aim of our study was to experimentally test the hypothesis that AMF-mycelium enhances juglone effects under field conditions, when adding either juglone-containing extract or leaf litter. Recently, Achatz et al. (2014) have provided first evidence, using a combination of controlled pot experiments (using mycorrhizal fungal inoculation) and field observations under walnut trees, that juglone bioactive zones in soil can be increased by the presence of

an AMF mycelium. Our intention here was to complement these results by employing a different experimental design: creating continuous and interrupted hyphal networks in the field using root exclusion compartments (RECs), combined fully factorially with addition of juglone in the form of leaf litter and litter extract. We thus avoided using fungal inoculation as the method providing mycorrhizal hyphae in the study, but instead used the resident mycelium; and on the other hand we experimentally added juglone-containing material, rather than relying on production of this substance by trees *in situ*. Our experiment had two parts, one with addition of *J. regia* L. leaf litter outside RECs, one with addition of an aqueous extract of walnut leaves outside the RECs.

2. Materials and methods

2.1. General study design

The study was carried out in a semi-natural grassland field plot (Institute of Biology of Freie Universität Berlin, 10 m × 1.8 m), mainly consisting of *Lolium perenne* and *Poa annua* (AM fungal colonization of 5 random root samples: 42.2 ± 4%), to take advantage of a pre-existing hyphal network of AMF and the resident microbial community. We used a modified in-growth core design (Johnson et al., 2001) consisting of root exclusion compartments (RECs) which were either static, to permit a connection to the surrounding mycelium or rotated, to interrupt the mycelium connection (Fig. 1). Then RECs were prepared by covering the sides and the bottom of small plastic baskets (Poeppelmann Teku[®] 5 × 5 cm, G, 0.07 l, Poeppelmann, Germany) with 30 µm mesh (Sefar Nitex 03-30/18, Sefar GmbH, Edling, Germany) to exclude roots but permit hyphae to grow in (Fig. 1a). The RECs were filled with well-mixed, sieved (1 mm), sandy soil (sand = 74%, silt = 18%, clay = 8%; pH = 7.1; organic C = 1.87%, N = 0.12%) from an experimental field of the Institute of Biology of Freie Universität Berlin. To avoid differences in AMF inoculum potential or other soil properties between treatments (which may have been present in the field plot) all RECs contained the same soil.

Tomato seeds were pre-germinated in glass beads for 1 week before planting them into the field. Tomato seedlings of the same age were then planted into the RECs ($n = 8$) just before inserting them into the field plot. We chose tomato because it is known to be sensitive to juglone (Crist and Sherf, 1973).

After placing the RECs in the soil, the whole experimental area was covered with a mesh (mesh size: 5 mm) on wooden sticks (ca. 50 cm above soil) in an attempt to prevent disturbance through nutrient input by birds or small mammals or feeding on tomato plants by snails. The experimental plot area was divided in two halves, one for each experiment (litter and leachate addition, respectively; see description below); these two experiments were statistically analyzed separately. Both experiments had a 2 × 2 factorial design (RECs rotated or not, juglone-containing material added or not), arranged in blocks (treated as a random effect, see below) each containing all 4 treatment combinations. Experimental units were separated by 20 cm. Initially we started with a high number of replicates ($n = 20$) because we expected a potentially high seedling loss through external conditions in the semi-natural field plot. Despite using a protection mesh, several seedlings had to be excluded from statistical analysis because they were damaged or eaten and we thus ended up with $n = 8$ in experiment 1 and $n = 6$ in experiment 2.

To permit a connection to the existing mycorrhizal fungal network in the field plot, half of the RECs were kept static after placing them in the soil (to a depth of 5 cm), the others were rotated three times a week by 1–2 mm to ensure severing of hyphae attempting to cross into the RECs. This movement of half of the

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