



Original article

Arbuscular mycorrhizal colonization, plant chemistry, and aboveground herbivory on *Senecio jacobaea*Stefan Reidinger^{a,*}, René Eschen^{a,1}, Alan C. Gange^a, Paul Finch^a, T. Martijn Bezemer^b^aSchool of Biological Sciences, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK^bNetherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB Wageningen, The Netherlands

ARTICLE INFO

Article history:

Received 7 June 2011

Accepted 11 August 2011

Available online 27 August 2011

Keywords:

Arbuscular mycorrhizal fungi

Insect herbivores

Plant chemistry

Senecio jacobaea

Plant diversity

ABSTRACT

Arbuscular mycorrhizal fungi (AMF) can affect insect herbivores by changing plant growth and chemistry. However, many factors can influence the symbiotic relationship between plant and fungus, potentially obscuring experimental treatments and ecosystem impacts.

In a field experiment, we assessed AMF colonization levels of individual ragwort (*Senecio jacobaea*) plants growing in grassland plots that were originally sown with 15 or 4 plant species, or were unsown. We measured the concentrations of carbon, nitrogen and pyrrolizidine alkaloids (PAs), and assessed the presence of aboveground insect herbivores on the sampled plants.

Total AMF colonization and colonization by arbuscules was lower in plots sown with 15 species than in plots sown with 4 species and unsown plots. AMF colonization was positively related to the cover of oxeye daisy (*Leucanthemum vulgare*) and a positive relationship between colonization by arbuscules and the occurrence of a specialist seed-feeding fly (*Pegohylemyia seneciella*) was found. The occurrence of stem-boring, leaf-mining and sap-sucking insects was not affected by AMF colonization. Total PA concentrations were negatively related to colonization levels by vesicles, but did not differ among the sowing treatments.

No single factor explained the observed differences in AMF colonization among the sowing treatments or insect herbivore occurrence on *S. jacobaea*. However, correlations across the treatments suggest that some of the variation was due to the abundance of one plant species, which is known to stimulate AMF colonization of neighbouring plants, while AMF colonization was related to the occurrence of a specialist insect herbivore. Our results thus illustrate that in natural systems, the ecosystem impact of AMF through their influence on the occurrence of specialist insects can be recognised, but they also highlight the confounding effect of neighbouring plant species identity. Hence, our results emphasise the importance of field studies to elucidate interactions between AMF and organisms of different trophic levels.

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1. Introduction

Understanding the mechanisms that determine the abundance of species in ecosystems is one of the most important issues in ecology. While changes in abiotic factors are good predictors of plant community development over large spatial and temporal scales

Abbreviations: AMF, arbuscular mycorrhizal fungi; C, carbon; N, nitrogen; P, phosphorous; PAs, pyrrolizidine alkaloids.

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(Wardle et al., 2004), soil organisms can be important drivers of more local and short-term changes (Gange et al., 1990; Van der Putten et al., 1993; De Deyn et al., 2003; Kardol et al., 2006). One of the best-studied groups of soil organisms are the arbuscular mycorrhizal fungi (AMF), which form symbiotic associations with the majority of land plant species (Newman and Reddell, 1987; Smith and Read, 1997). AMF rely on photosynthetically fixed carbon provided by their host plant and in return supply the plant with nutrients that have been taken up from the soil. Due to an increased nutrient uptake, plants forming mycorrhizal associations are often bigger than non-mycorrhizal plants (Smith and Read, 1997). However, plants do not always benefit from AMF and negative plant growth responses to AMF colonization can occur when the net costs of the symbiosis exceed the net benefits (Johnson et al., 1997; Gange and Ayres, 1999). Further, AMF species differ in their effects on plant growth, depending on the identity of both the

fungus and the plant (Streitwolf-Engel et al., 1997; Van der Heijden et al., 1998).

Individuals of the same plant species frequently vary in AMF colonization levels and in the composition of AMF communities (e.g. Eason et al., 2001; Šmilauer, 2001; Carey et al., 2004; Opik et al., 2006, 2009; Wilson et al., 2006; Ishii et al., 2007; Meding and Zasoski, 2008; Uibopuu et al., 2009; Van de Voorde et al., 2010), and the relationship between AMF colonization levels and plant growth responses can range from positive to negative (Gange and Ayres, 1999; Hart and Reader, 2002; Bennett and Bever, 2009; Powell et al., 2009; Garrido et al., 2010; Zaller et al., 2011). Moreover, Garrido et al. (2010) showed that plant biomass allocation can be affected by AMF colonization levels, resulting in increased or decreased biomass allocation to different plant parts. The benefit plants derive from the association with AMF can further depend on the abiotic soil environment (Zaller et al., 2011). Interestingly, plant species typical of disturbed, open habitats often do not form mycorrhizal associations (Janos, 1980), or respond negatively to AMF colonization (Francis and Read, 1995; Rinaudo et al., 2010).

Besides influencing plant size, AMF colonization can alter the resistance of plants to insect herbivores. In the majority of manipulative studies investigating the interaction between AMF colonization and insect herbivores, AMF colonization decreased the performance of generalist chewing insects (Koricheva et al., 2009), which may be because of an increase in the production of plant defence compounds (Pozo and Azcón-Aguilar, 2007), to which generalist insects often respond negatively (Manninen, 1999). In contrast, the performance of specialist and generalist sucking insects and specialist chewing insects is usually higher on mycorrhizal than on non-mycorrhizal plants (Koricheva et al., 2009), though the mechanism is currently unknown (Gange, 2007). Most AMF–insect herbivore studies have been conducted by comparing growth of insect herbivores on mycorrhizal and non-mycorrhizal plants under controlled conditions. However, under natural conditions, non-mycorrhizal individuals of plant species capable of forming mycorrhizal associations are hardly ever found (Harley and Harley, 1987).

There is a paucity of field studies assessing the complex relationships among naturally occurring variations in AMF colonization levels, plant growth and herbivory, and a lack of consensus as to whether effects observed in the laboratory translate into changes in insect growth and population dynamics in the field (Gehring and Bennett, 2009; Hartley and Gange, 2009). The main reason for the low number of field studies with different levels of AMF colonization is that the abundance of AMF in the field is notoriously difficult to manipulate. For instance, reducing AMF colonization levels through fungicide application also affects soil fungi other than AMF, potentially influencing the abundance of plant pathogens and soil nutrient cycling. Furthermore, soil fungicides can exhibit direct toxic effects on insect herbivores when taken up by the plant (Laird and Addicott, 2008). Therefore, only a few studies have attempted to study AMF–plant–herbivore interactions in the field and it remains unclear whether the effects of AMF on herbivores in controlled greenhouse studies can also be observed under natural, more complex settings. Even though data from non-manipulative field studies are of a correlative nature and do not demonstrate causality, a comparison between AMF–plant–herbivore data obtained from correlative field studies and causal data obtained from manipulative, controlled experiments may unveil whether interactions between AMF and herbivores can also be observed in the field.

We studied whether differences in AMF colonization levels of *Senecio jacobaea* L. (ragwort; Asteraceae) are related to variation in plant size and the number and community structure of insect herbivores feeding on it. *S. jacobaea* is a biennial plant, spending its first year as a rosette and flowering the following summer. Since it requires gaps in the vegetation for successful establishment,

S. jacobaea is most commonly found in disturbed habitats (Harper and Wood, 1957). The plant can contain high levels of pyrrolizidine alkaloids (PAs), which pose a severe threat to grazing livestock and which can influence growth and the community structure of saprophytic soil fungi (Hol and Van Veen, 2002; Kowalchuk et al., 2006). Despite the high toxicity of *S. jacobaea*, both specialist and generalist insects feed on this plant species (Harper and Wood, 1957). *S. jacobaea* has previously been described as a facultative mycorrhizal species (Bower, 1997), and soil fungicide application in the field has been found to decrease AMF colonization levels and to increase plant size and it has been suggested that AMF are parasitic in this plant species (Gange et al., 2002). However, it is unknown whether the effect of AMF colonization on *S. jacobaea* is always negative, or whether it depends on the biotic and abiotic environment of the plant.

This study was part of an ongoing field experiment in The Netherlands, with experimental plots that were unsown, or were sown with either 4 or 15 plant species (Bezemer et al., 2006). After sowing, new plant species were allowed to colonize the plots from the soil seed bank and the surrounding vegetation. *S. jacobaea*, which was not included in any of the seed mixtures, started to establish in the plots soon after the start of the experiment, and initially the cover and biomass of *S. jacobaea* were highest in the unsown plots, but *S. jacobaea* cover in these plots sharply declined five years later (Bezemer et al., 2006). The sowing treatments had distinct effects on the community composition of insect herbivores feeding on *S. jacobaea*: plants in unsown plots were less likely to be infested with leaf miners, seed feeders and stem borers than plants in sown plots, and there was a strong positive relationship between plant size and the occurrence of insect herbivores (Bezemer et al., 2006).

The aim of this study was to determine the effects of the sowing treatments on AMF colonization levels of *S. jacobaea* and on the associated insect herbivore fauna. We hypothesized that AMF colonization of *S. jacobaea* plants growing in plots with high *S. jacobaea* cover (unsown plots) would be higher than that in plots with low cover (sown plots), due to accumulations of *S. jacobaea*-specific AMF communities, which can reduce the mutualistic benefit received by the plant (Bever, 2002). We further hypothesized that *S. jacobaea* biomass would be negatively related to AMF colonization levels, because AMF have previously been suggested to negatively affect growth of this plant species (Bower, 1997; Gange et al., 2002), and because species of disturbed habitats often respond negatively to AMF (Francis and Read, 1995; Rinaudo et al., 2010). We tested whether differences in AMF colonization among the sowing treatments were related to the abundance and the community structure of insect herbivores feeding on *S. jacobaea*. We measured leaf nitrogen and carbon concentrations and the concentration of pyrrolizidine alkaloids (PAs), which are main defence compounds in *S. jacobaea* (Rice, 1984), in an attempt to elucidate the underlying mechanisms of how AMF and insect herbivores may interact with each other.

2. Materials and methods

2.1. Field experiment

The experiment was set up in 1996 on a former arable field of 15 ha that was cultivated until 1995. An area of 0.5 ha was fenced, ploughed and three different sowing treatments were applied to plots of 10 × 10 m: sowing with 15 plant species, sowing with a subset of 4 species, or not sowing. There were five replicate blocks, with each block containing one plot of each sowing treatment. The five replicate plots of the 4 species treatment were sown with different combinations of plant species (Appendix 1). This

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