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Plant invasions induce a shift in Glomalean spore diversity

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Abstract: Very little has hitherto been known about the response of structurally and functionally diverse arbuscular mycorrhizal fungi (AMF) to plant invasions. We investigated the impact of two alien invasive species, namely *Anthemis cotula* and *Conyza canadensis,* on rhizospheric AMF at different sites in the Kashmir Himalaya, India. We compared AMF species composition, and density of their spores in the rhizospheric soils of *A. cotula* and *C. canadensis* with comparable nearby un-invaded sites. Whilst 9 and 7 AMF species were recovered from the rhizospheres of *A. cotula* and *C. canadensis*, respectively, the corresponding un-invaded sites yielded 17 and 10 AMF species. Only 3 AMF species were common between the rhizospheres of the two invasive species. The spore density of AMF, unlike species richness, was higher in the rhizospheres of both the invasive species compared with the un-invaded sites nearby. This study brings to light alien invasive species-specific shifts in AMF diversity.

Resumen: Al día de hoy se sabe muy poco sobre la respuesta de los hongos micorrizógenos arbusculares (HMA), diversos estructural y funcionalmente, a las invasiones de plantas. Nosotros investigamos el impacto de dos especies invasoras exóticas*, Anthemis cotula* y *Conyza canadensis*, sobre los HMA rizosféricos en diferentes sitios de los Himalaya de Cachemira, India. Comparamos la composición de especies de HMA y la densidad de sus esporas en los suelos rizosféricos de *A. cotula* y *C. canadensis*, con sitios no invadidos cercanos y comparables. Mientras que se recuperaron 9 y 7 especies de HMA de las rizosferas de *A. cotula* y *C. canadensis*, respectivamente, los sitios no invadidos arrojaron 17 y 10 especies de HMA. Sólo tres especies de HMA fueron comunes a las rizosferas de las dos especies invasoras. La densidad de esporas de HMA, a diferencia de la riqueza de especies, fue mayor en las rizosferas de ambas especies invasoras que en los sitios no invadidos cercanos. Este estudio revela cambios en la diversidad de HMA que son específicos de la especies invasora exótica.

Resumo: Muito pouco tem sido conhecido, até agora, sobre a resposta estrutural e funcional dos diversos fungos arbusculares micorrízicos (AMF) à invasão de plantas. Investigámos o impacte de duas espécies invasivas, nomeadamente a *Anthemis cotula* e a *Conyza canadensis*, na rizosfera dos AMF em diferentes locais na Cashemira no Himalaia, Índia. Comparámos a composição específica dos AMF, e a densidade dos seus esporos nos solos da camada rizosférica de *A. cotula* e *C. canadensis*, com locais comparáveis próximos e não invadidos. Enquanto 9 a 7 espécies AMF foram recuperadas das rizosferas de *A. cotula* e *C. canadensis*, respectivamente, os correspondentes locais não invadidos apresentaram 17 a 10 AMF espécies. Só 3 espécies AMF eram comuns entre as rizosferas das duas espécies invasoras. A densidade dos esporos dos AMF, ao contrário da riqueza específica, era mais elevada nas rizosferas das duas espécies invasivas quando confrontadas com os locais próximos não invadidos. Este estudo põe a nu as mudanças específicas na diversidade das AMF.

Key words: Arbuscular mycorrhizae, *Anthemis cotula, Conyza canadensis,* Kashmir Himalaya, plant invasion.

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Introduction

Arbuscular mycorrhizal fungi (AMF) form mutualistic associations with a majority of vascular plants and contribute to increased nutrient uptake (Smith & Read 1997), resistance against heavy metals and pathogens (Galli *et al.* 1994; Hardie 1985), and improved water relations (Augé *et al.* 2001) of the host plants. Besides being an important component of belowground biodiversity, AMF are also important determinants of above-ground plant diversity and productivity (van Der Heijden *et al.* 1998).

Many biotic and abiotic factors, such as farming practice (Boddington & Dodd 2000), weed control and crop management (Baumgartner *et al.* 2005), soil tillage (Jansa *et al.* 2002), moisture content (Anderson *et al.* 1983), identity of host species (Bever *et al.* 1996), organic matter (Ryan *et al.* 1994), nutrient status (Douds & Millner 1999), pH (van Aarle *et al.* 2002), and temperature (Koske 1987), can influence diversity and distribution of AM fungi. Invasive plants are also reported to significantly affect diversity of soil microbiota, with accompanying influences on pools and fluxes of soil resources (Ehrenfeld 2004). Alien plants may alter the ecology of invaded soils (Duda *et al.* 2003) or disrupt mutualistic associations between native plants (Stinson *et al.* 2006) and pave the way for their further invasion at the cost of native species, thereby leading to an invasion meltdown. Invasions by alien species, mediated by AMF, have attracted some attention recently (Callaway *et al.* 2004; Fumanal *et al.* 2006; Klironomos 2002; Shah & Reshi 2007; Shah *et al.* 2008a, 2008b), and the need for assessment of the impact of invasive plants on the structure of AMF communities is also increasingly being stressed.

The role of AMF in facilitation or inhibition of alien plant invasion may vary with host species, plant life history stage, neighbour identity, resource availability, and abiotic conditions (Hartnett *et al.* 1994; Johnson *et al.* 1997; Shah *et al.* 2008a, 2008b). Given the variability in the degree to which host plants influence specific AM fungi (Sanders & Fitter 1992), we especially need to know how alien plant species influence AMF communities in invaded soils. We conducted the present study on the species-specific impacts of two aggressive alien invasive species (*Anthemis cotula* L. and *Conyza canadensis* Cronquist) on the structure and composition of AMF communities in natural habitats in the Kashmir Himalaya.

Materials and methods

Study area and host plant species

The study was conducted at different sites in the Kashmir Himalaya (32° 20'-34° 50' N latitude and 73° 55'-75° 35' E longitude). This biogeographically distinct region is a world famous tourist destination, owing to its sub-Mediterranean type of eco-climatic conditions, topographic heterogeneity, and floristically rich landscapes. The growing tourism, trade, and transport contribute significantly to the introduction of alien species with large scale habitat disturbances also contributing to alien plant invasions.

Although alien flora of the region is represented by 571 plant species (Khuroo *et al.* 2007), for the present study we selected two highly invasive herbaceous species, *Anthemis cotula* and *Conyza canadensis*. *A. cotula* (mayweed chamomile, stinking mayweed), a member of the sunflower family (Asteraceae), is native from southern Europe to west Siberia (Erneberg 1999), where it grows in both natural habitats and agricultural fields. In the Kashmir Himalayan region *A. cotula* is a highly invasive species of disturbed sites, and its large-scale invasion has been attributed to its protracted recruitment pattern, large population size even after seedling mortality (Allaie *et al.* 2005), and allelopathy (Allaie *et al.* 2006). Besides, invasion by *A. cotula* has been shown to be facilitated by AMF mutualists, both in the field and under controlled pot conditions (Shah & Reshi 2007; Shah *et al.* 2008a, 2008b). Herbivore-induced over-compensatory growth (Rashid *et al.* 2006), and profuse production and synchrony between germination of achenes and favourable environmental conditions (Rashid *et al.* 2007) also facilitate invasion by *A. cotula*.

C. canadensis (butterweed), also a member of the Asteraceae, is native to North America. It grows abundantly in many disturbed sites and pastures, and has a strong potential to encroach pristine landscapes in the Kashmir Himalaya. Large-scale invasion by these species could potentially endanger native species of the region.

Soil sampling and mycorrhizal studies

We collected soil samples from the rhizospheres of the two invasive species at seedling, pre-flowering, and post-flowering stages at three locations (University Campus, Nagbal and Bandipore) from March 2006 to November 2006, to assess the diversity and abundance of AM fungal spores. From each site soil samples were also collected from nearby comparable un-invaded habitats to serve as controls. While the University Campus site (34° 5′ N latitude, 74° 50′ E longitude; altitude 1584 m) was dry, protected, and undisturbed, the Bandipore site (34° 25′ N latitude, 74° 5′ E longitude; 1716 m) was relatively moist and moderately disturbed. The Nagbal site (34° 18′ N latitude, 74° 56′ E longitude; altitude 1586 m), was exposed and highly disturbed.

For the present study, only those sites were selected where both the study species occurred in near-monocultures. Three patches per site were studied and patch area was maintained uniformly at 5 m^2. Each patch was separated from the others by 2-m spacing and was divided into a central zone of 2.5 m^2 and a surrounding buffer zone to reduce edge effects from surrounding vegetation. Approximately 2 kg of soil was collected from each patch using a 2.5 cm wide soil corer to a depth of 25 cm from 15 individuals of the invasive species. Subsamples from each site were thoroughly mixed to form composite samples. Field-collected soil samples were placed in polythene bags for transportation to the laboratory for subsequent spore analysis. The spores and sporocarps were isolated from 50 g of soil from each sample using the wet sieving and decanting method (Gerdemann & Nicolson 1963). Samples were centrifuged in a sucrose gradient (Walker *et al.* 1982). Quantification was carried out in Petri dishes with a gridline of 1 cm per side under a compound microscope (Lugo & Cabello 2002). Ten divisions were counted and related to the total number of spores by using the method modified by McKenney & Lindsey (1987).

AMF species were identified on the basis of spore size, colour, ornamentation, and wall characteristics. The specimens were matched with the original descriptions (Schenck & Perez 1990) and with those provided by the INVAM (http://invam.caf.wvu.edu). Only intact, cytoplasm-filled spores were counted and spore density was expressed per g dry soil. Sporocarps and spore clusters were counted as one unit. Spores of each morphotype were mounted in polyvinyl alcohol-lactic acid-glycerol (PVLG) and PVLG mixed with Melzer's reagent (1:1, v:v).

Mean spore density in soils invaded by *A. cotula* and *C. canadensis* and in the soils of nearby corresponding un-invaded habitats, were subjected to analysis of variance using SPSS 10.

Results

Our survey of arbuscular mycorrhizal fungi (AMF) at different invaded and un-invaded sites in the Kashmir Himalaya resulted in the identification of a total of 28 AMF species representing 7 genera and 5 families (Table 1). Ten AMF species belonged each to Glomaceae and Gigasporaceae, six to Acaulosporaceae and one each to Archaeosporaceae and Paraglomaceae. The results, however, showed significant differences in AMF associated with the two invasive plant species, *Anthemis cotula* and *Conyza canadensis*. While *A. cotula* and *C. canadensis* were associated with 4 and 2 members of Glomaceae and Acaulosporaceae, respectively, no species of Archaeosporaceae was found in their rhizospheres. There were 3 species of Gigasporaceae associated with *A. cotula* and none with *C. canadensis. C. canadensis,* however, had one species of Paraglomaceae associated with it, but this species did not occur in conjunction with *A. cotula*.

Nine AMF species were recovered from the rhizosphere of *A. cotula* and seven from that of *C. canadensis*. In contrast, the un-invaded sites near *A. cotula* and *C. canadensis* yielded 17 and 11 AMF species, respectively (Table 1). Of the 9 AMF species detected from the rhizosphere of *A. cotula* only three were common to the rhizosphere of *C. canadensis*. Density of AMF spores differed significantly across sites and between the two invasive host plant species (Figs. 1 & 2). Unlike species richness, the density of AMF spores was higher in the invaded rhizospheric soils than in nearby un-invaded soils.

The number of AMF spores per gram of soil in the rhizosphere of *A. cotula* was highest at Bandipore, the relatively moist and moderately disturbed site, and lowest at Nagbal, the highly disturbed site. In the case of sites invaded by *C. canadensis,* AMF spore density was highest at the undisturbed site on the University Campus and lowest at the highly disturbed Nagbal site. There were significant differences ($p < 0.001$) in the spore density between invaded and un-invaded sites with respect to both *A. cotula* and *C. canadensis* (Table 2). However, the variations in AM spore density amongst the sites were relatively less significant ($p < 0.01$) for both the species.

Discussion

Whilst the influence of host plants on AMF

Table 1. Species of arbuscular mycorrhizal fungi found in soils invaded by *Anthemis cotula* {I(*Ac*)} and *Conyza canadensis* {I(*Cc*)} and in soils of nearby un-invaded habitats (UI). X denotes the presence of a species.

AMF taxa	UI	I(*Ac*)	UI	I(*Cc*)
Glomaceae				
Glomus caledonium (Nicol. & Gerd.) Trappe & Gerd.	X		X	
G. lamellosum Dalpe, Koske & Tews	X			
G. etunicatum Becker & Gerd.	X			
G. intraradices Schenck & Smith				
G. mosseae (Nicol. & Gerd.) Gerd. & Trappe	X	X		
G. claroideum Schenck & Smith	X			
G. dimorphicum Boyetchko & Tewari		X		X
G. fasciculatum (Thaxter) Walker & Koske			X	X
G. diaphanum Morton & Walker		X		
G. luteum Kennedy, Stutz & Morton		X		X
Gigasporaceae				
Gigaspora decipiens Hall & Abbott	X			
G. margarita Becker & Hall		X	X	
Scutellospora erythropa (Koske & Walker) Walker & Sanders	X			
S. verrucosa (Koske & Walker) Walker & Sanders		X		
S. heterogama (Nicol. & Gerd.) Walker & Sanders	X	X		
S. dipurpurascens Morton & Koske	X			
S. calospora (Nicol. & Gerd.) Walker & Sanders	X			
S. pellucida (Nicol. & Schenck) Walker & Sanders	X			
S. sp.			X	
S. sp.			X	
Acaulosporaceae				
Acaulospora spinosa Walker & Trappe	X	X		
A. laevis Gerd. & Trappe	X	X		
A. foveata Trappe & Janos				X
A. paulineae Blaszkowski	X			
A. sp.	X		X	
Entrophospora infrequens (Hall) Ames & Schneider	X			
Archaeosporaceae				
Archaeospora trappei Morton & Redecker			X	
Paraglomaceae				
Paraglomus occultum (Walker) Morton & Redecker	X			X

Table 2. Results of a two-way ANOVA on the impact of invasion (I^2) on spore density in soils invaded by *Anthemis cotula* and *Conyza canadensis* with invasion and invaded sites as fixed factors.

Source	df	MS		F	
		A. cotula	*C. canadensis*	*A. cotula*	*C. canadensis*
Invasion impact (I^2)	1	72.00	40.50	34.11***	20.25***
Sites	2	12.17	6.00	5.76*	3.00*
I^2*Sites	2	8.17	0.00	3.87*	0.00NS
Error	12	2.11	2.00		
Total	17				

P< .001***; P< .01*; NS= non significant species composition is discernible from previous studies (Bever *et al.* 1996; Johnson *et al.* 1991), our results more specifically focused on the impact of invasive plants on AMF communities. The present study indicated changes in structure and composition of AMF communities in the rhizospheres of *Anthemis cotula* and *Conyza canadensis* relative to nearby un-invaded habitats (Table 1). Our findings also revealed species-specific impacts of the investigated invasive plants on rhizospheric AMF spore density and diversity (Table 1, Figs. 1 & 2).

Other studies have also shown a greater number of AMF species in un-invaded sites compared with neighbouring invaded sites (Burrows & Pfleger 2002; Mummey & Rillig 2006). However, a greater AMF spore density in invaded soils relative to nearby un-invaded soils may possibly be due to allelochemicals that induce AMF sporulation (Akiyama *et al.* 2005). There is evidence to suggest that both *A. cotula* and *C. canadensis* are allelopathic (Allaie *et al.* 2006; Shaukat *et al.* 2003). Experimental pot culture studies supported by biochemical and molecular analyses are needed to confirm the precise mechanism of their influence on AMF spore density and diversity.

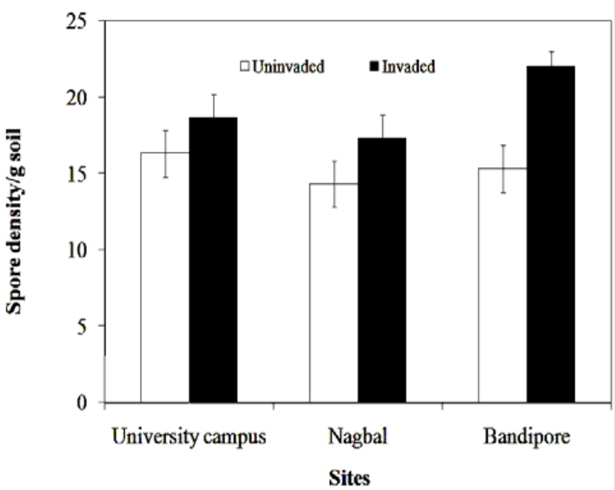

Fig. 1. Number of AMF spores (±SD) per gram of rhizospheric soil at three sites invaded by *Anthemis cotula* in comparison to nearby un-invaded sites.

While invasion by some alien species are mediated by soil biota, including AMF (Callaway *et al.* 2004; Fumanal *et al.* 2006), some invaders can potentially disrupt belowground connectivity of native plants through AMF (Stinson *et al.* 2006). Though AMF play a significant role in establishment and spread of the alien *A. cotula* in its introduced range (Shah *et al.* 2008a, 2008b), this species, in turn, negatively influences the community structure and composition of these mutualists. On the one hand, invasion by *A. cotula* and *C. canadensis* reduced AMF diversity, while on the other hand, it increased spore abundance significantly. Such shifts in Glomalean species diversity and distribution may be attributed to invasion-induced alteration of the soil microenvironment (Douds & Millner 1999) and the resulting changes in soil microbial activity (Belnap *et al.* 2005) or a combination of a suite of host-plant traits. Working out such factors may improve our understanding of the mechanism of plant invasion and the impact of invaders on native soil communities.

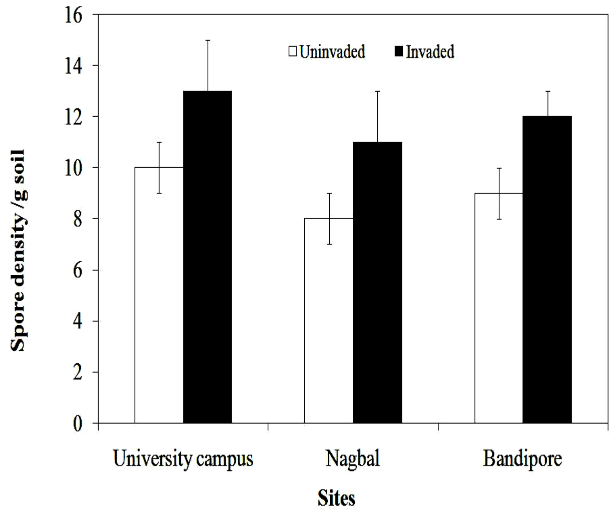

Fig. 2. Number of AMF spores (±SD) per gram of rhizospheric soil at three sites invaded by *Conyza canadensis* in comparison to nearby un-invaded sites.

The present preliminary study suggests that alien invasive plants may affect abundance and diversity of AMF species. The implications of a decrease in AMF diversity on plant biodiversity remains an open question and merits consideration in the context of possible biotic homogenization of diverse belowground soil communities due to plant invasions.

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