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REGULAR ARTICLE

Mycorrhizosphere mediated Mayweed Chamomile invasion in the Kashmir Himalaya, India

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Abstract Recent studies have established the controlling influence of rhizospheric biota, especially arbuscular mycorrhizal fungi (AMF), on colonization and spread of some alien plants in their introduced range. But how AMF from different geographical sources influence traits that contribute to invasiveness, particularly in presence of neighbouring plants of other species, has been rarely investigated. Thus, we compared the influence of some local (Kashmir Himalayan isolates) and non-local (isolates from Rajasthan, India) AMF isolates of *Glomus moseae*, *G. fasciculatum* and *Gigaspora margarita* on vegetative and reproductive attributes of Mayweed Chamomile (*Anthemis cotula* L.), a highly invasive species in the Kashmir Himalaya, India. We also examined whether or not the neighbouring plant species, namely *Daucus carota* L. (Apiaceae) alters the mutualistic interaction between the AMF and *A. cotula*. Pot experiments revealed greater positive impact of the local than the non-local AMF on vegetative as well as reproductive attributes of *A. cotula*. Experimental field studies showed that the incidence of highly prevalent *Arum*-type mycorrhizal colonization in natural populations of *A. cotula* was reduced in presence of *D. carota*. Besides, the local AMF significantly promoted growth of *A. cotula* more than *D. carota* under mixed-culture conditions. These results suggest that the facilitation of some alien plant invasions by AMF needs to be considered together with plant–plant interactions and invasion-induced changes in the soil microbial community.

Keywords *Anthemis cotula* · Arbuscular mycorrhizas · Chamomile invasion · India · Kashmir Himalaya · Mycorrhizosphere

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Introduction

Biological invasion, a major component of current global environmental change, leads to habitat deprivation, reduced biodiversity, alteration of ecosystem services and functions (Simberloff and von Holle 1999). These modifications bring about significant harmful ecological and economic impacts (Perrings et al. 2005; Pimentel et al. 2005). Many invasive plants are known to successfully establish mutualistic associations with AMF and the facilitative role of arbuscular mycorrhizas in plant invasions is largely through enhanced nutrient acquisition and transfer

(Marler et al. 1999; Zabinski et al. 2002; Carey et al. 2004; Burns 2004), improved drought tolerance (e.g. Ruiz-Lozano et al. 1995), enhanced herbivore avoidance (Abigail et al. 2005), evasion of native enemies (Shah and Reshi 2007), and alteration of competitive interactions of invasive plants with native species (Shah et al. 2006; Casper and Castelli 2007). Degree of plant growth promotion by AMF, however, is context specific and depends on habitat conditions, identity of the alien plant species, and nature of AMF symbiont (Streitwolf-Engel et al. 1997; Eom et al. 2000; Stampe and Daehler 2003). For example, AMF inocula from different sources are known to have a differential effect on growth and performance of host species (Bever 1994), and also on the outcome of competitive interactions between invasive and native plant species (Scheublin et al. 2007). While considerable progress has been achieved in understanding the ecological role of mycorrhizal mutualisms in invasiveness of certain alien plant species (Reinhart and Callaway 2006; Fumanal et al. 2006), the underlying mechanisms that govern such novel interaction have not been fully explained and thus merit further research through robust field and experimental studies (Shah and Reshi 2007). Hence we studied the role of AMF isolates of different geographical origins in promotion of invasiveness of *Anthemis cotula* L. (Mayweed chamomile, Stinking mayweed), an annual, herbaceous member of sunflower family (Asteraceae), native to southern Europe–west Siberia (Erneberg 1999). It grows as a common weed of arable lands and farmyards in Scottish lowlands, Ireland, England and Wales (Kay 1971). Its success in disturbed habitats has been attributed to a protracted recruitment pattern, high population size even after seedling mortality (Allaie et al. 2005), allelopathic activity of its aqueous leaf leachate (Allaie et al. 2006), herbivore induced overcompensatory growth (Rashid et al. 2006), profuse production of achenes and synchrony between their germination and favourable environmental conditions (Rashid et al. 2007) and mutualistic facilitation by AMF (Shah and Reshi 2007). We also examined the influence of neighbouring plant species, *Daucus carota*, on the mutualistic interaction between the AMF and *A. cotula*. *Daucus carota* (Apiaceae) is one of the common co-associates of *A. cotula* in Kashmir Himalaya.

Materials and methods

Field studies

We carried out field studies at five study sites (Table 1) located in different parts of the Kashmir Himalaya (32° 20′ to 34° 50′ North latitude and 73° 55′ to 75° 35′ East longitude). All the study sites experienced sub-Mediterranean type of climate and average temperature during the study period (April to September, 2006) ranged from 7.2°C to 30.9°C. Total annual rainfall at each of the study sites was about 1,000 mm. At each site, we established replicate monospecific patches of *A. cotula* by continuously removing the individuals of its co-associates. We also established replicate heterospecific patches wherein individuals of *A. cotula* and *D. carota* were allowed to grow together. We regularly eliminated any species other than the study species that tended to grow in these patches throughout the course of the experiment and maintained constant density of plants across different study sites. We studied three patches per site and patch area was maintained uniformly at 5 m^2. Average distance between patches in a study site was about 2 m. Each patch was divided into a central zone of 2.5 m^2 and a surrounding buffer zone to reduce edge effects from surrounding vegetation. We collect-

Table 1 Brief description of sampling sites and percent mycorrhizal root length colonization (%RLC) of *Anthemis cotula* in different Kashmir Himalayan habitats in monocultures (A) and in combination with *Daucus carota* (A + D)

Site	Habitat type	Latitude	Longitude	Altitude (m.a.s.l.)	%RLC (A)	%RLC (A + D)
Zakura	Dry, exposed, moderately disturbed	34°–5′	74°–50′	1,587	84.6 ± 2.4	71.0 ± 1.6
Shikarghat	Dry, exposed, highly disturbed	34°–7′	74°–39′	1,584	80.6 ± 0.7	64.2 ± 1.5
Nagbal	Dry, protected, undisturbed	34°–18′	74°–56′	1,586	67.5 ± 0.8	43.0 ± 1.3
Narbal	Partly moist, moderately disturbed	34°–8′	74°–40′	1,584	64.5 ± 1.4	51.0 ± 0.3

Values of %RLC are means (±SD) at the seedling stage of the plants ed 15 plants from the central zone of each patch by excavating the whole root systems which were pooled together for assessment of mycorrhizal colonization. Randomly selected 100 root pieces (1 cm long) were cleared in 15% KOH, acidified in 1 N HCl and stained with trypan blue followed by destaining in 50% Lactic acid in accordance with the modified procedure of Phillips and Hayman (1970). We used the modified line intersection method (McGonigle et al. 1990) and frequency distribution method of Bierman and Linderman (1981) to determine the percentage of root length colonized by AMF.

Pot trial

We established a pot trial in a randomized block design with three replications per treatment in the Botanical Garden of the University of Kashmir, Srinagar, J&K, India, to test the effect of AMF source (local vs. non-local), and neighbour (monoculture vs. mixed culture) in invasiveness of *A. cotula*. We transferred seedlings of the test species to earthen pots (22 cm × 28 cm) filled with sterilized garden soil (clay = 28%, silt = 50%, sand = 22%, pH = 7.5 and organic carbon = 1.6%) mixed with sand in a ratio of 2:1. The soil was sterilized by autoclaving three times at 85°C for 90 min with a 12 h interval between each autoclaving. The non-local AMF isolates, originally collected from Rajasthan—a region more than 600 km away from the Kashmir Himalaya, were obtained from School of Life Sciences, Jawahar Lal Nehru University, New Delhi, India. The native AMF were generated from the soils invaded by *A. cotula* using trap cultures. We used spore size, colour, and ornamentation for identification of AMF isolates using original descriptions of Schenck and Perez (1990) and the INVAM (http://invam.caf.wvu.edu). We placed a mixed mycorrhizal inoculum (50 g) of *Glomus moseae*, *G. fasciculatum* and *Gigaspora margarita* 3 cm below the surface of soil so as to ensure contact of seedling roots with the inoculum. The AMF inoculants were chosen on the basis of their abundant association with natural populations of *A. cotula* (Shah and Reshi 2007). Two seedlings per pot both in case of mono- and mixed cultures were maintained under natural light conditions (12 to 14 h), relative humidity (58.5–79.3) and temperature (7.2–30.9°C) and the pots were watered to field capacity on alternate days.

Plant growth analyses

We harvested the pot grown individuals of *A. cotula* from each of the above mentioned treatments at maturity and recorded the shoot and root length, dry mass, number of branches and capitula per plant. Shoot and root length were measured with the help of a standard measuring tape. Root and shoot dry mass was determined after drying the above- and below-ground plant parts at 80°C for 48 h to constant weight. Since we were interested only in elucidating the effect of AMF on invasive attributes of *A. cotula* in mono- and mixed cultures, the data on growth characteristics of *D. carota* are not given.

We calculated AMF dependency of the target plant species in monoculture or in mixed-culture following Van'der Heijden (2002):

$$\text{AMF dependency} = 1 - (b/\mathrm{a}), \mathrm{a} \geq b$$
$$- 1 + (\mathrm{a}/b), \mathrm{a} < b$$

where '*a*' is the average dry mass of AMF treated plants and '*b*' is the dry mass of the untreated plants. Basic statistics, such as trait means and variances were obtained using SPSS 10. Multiple analysis of variance (MANOVA) was used to study the response of attributes, including dry mass of shoots and roots (g), shoot length and root length (cm) and number of branches and number of capitula per plant by to different treatments of AMF (local vs. non-local), and neighbour (monospecific vs. heterospecific). We performed univariate analyses of variance and compared each treatment to the control by Tukey HSD.

Results

A. cotula, in monospecific patches at Zukura and Shikarghat, had more than 80% *Arum*-type root length colonization (RLC) and more than 60% RLC in other two study sites at Nagbal and Narbal (Table 1). This *Arum*-type AMF colonization was characterized by extensive intercellular hyphae and terminal arbuscles in root cortical cells of *A. cotula*. However, degree of root colonization of *A. cotula* was reduced in the neighbourhood of *D. carota* (Table 1) at all the study sites and highest reduction (24.5%) was recorded at Nagbal.

Effect of mycorrhizal inoculation on different attributes of *A. cotula* in mono- and mixed cultures using local and non-native AMF in comparison with control (no AMF used) is presented in Fig. 1. Perusal of results reveals that local AMF more than doubled its shoot length (Fig. 1b) and improved shoot dry mass by more than four times in comparison to uninoculated plants (Fig. 1d). However, both these attributes were only slightly improved in response to inoculation with non-local AMF. Even when *A. cotula* was grown in association with *D. carota*, local AMF had more positive influence on length and dry mass of shoot than non-native AMF (Fig. 1b, d). Root length of *A. cotula* did not show any significant change in response to inoculation either with local or non-local AMF (Fig. 1a), irrespective of whether grown under monoculture or mixed culture conditions, but roots were thicker and the dry mass was enhanced more by local than non-native AMF (Fig. 1c). Number of branches per plant in *A. cotula* was also improved more by local than non-local AMF (Fig. 1e). In comparison with untreated control plants, number of capitula in *A. cotula* grown in monoculture was over three times more in plants inoculated with local AMF and two times more in plants treated with non-local AMF. Under mixed-culture conditions, local and non-local AMF increased number of capitula in *A. cotula* by about three and two times, respectively, in

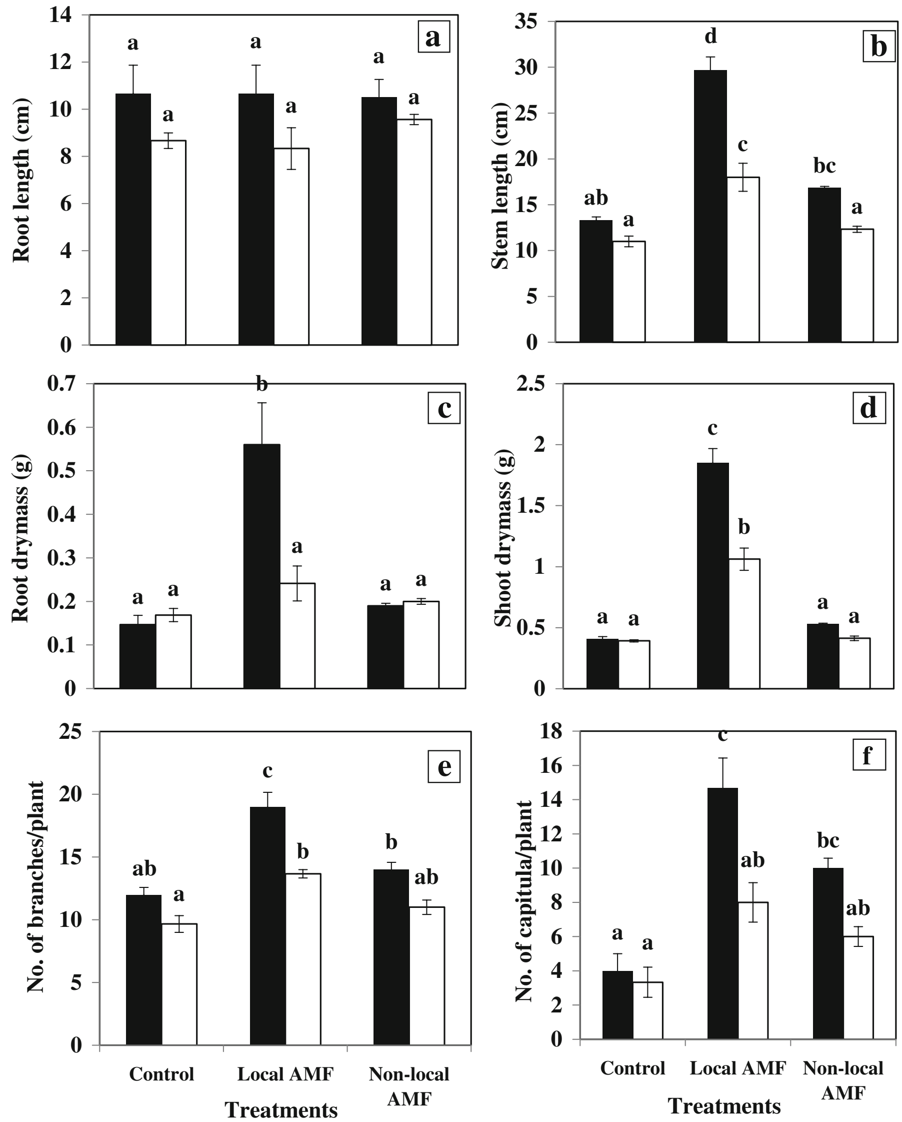

Fig. 1 Means (±standard error) of various growth and fitness attributes of *Anthemis cotula* in monoculture (■) and in association with *Daucus carota* (□) under no (control), local, and non-local AMF treatments. Means that do not share a lower-case letter are significantly different following Tukey's post hoc test

Table 2 Statistical results of MANOVA (control included and excluded) examining the effects of mycorrhizas, neighbour and their interaction on invasiveness of *Anthemis cotula*

Effect	MANOVA Pillai	*df*	*F*	*P*
MANOVA with control included				
Mycorrhizae	1.483	12	5.260	0.000
Neighbour	0.777	6	6.389	0.004
Mycorrhizae × neighbour	2.637	30	2.046	0.011
MANOVA with control excluded				
Mycorrhizae	0.927	6	10.531	0.010
Neighbour	0.941	6	13.295	0.006
Mycorrhizae × neighbour	1.997	18	1.659	0.163

'*Pillai*' is Pillai's Trace test statistic for MANOVA

comparison with uninoculated control treatment (Fig. 1f). The MANOVA (Table 2) showed that mycorrhizal inoculation significantly influenced the traits that contribute to invasiveness of *A. cotula*. However, the local and non-local AMF isolates differed significantly in their influence on various attributes of *A. cotula*. Irrespective of the geographical source of AMF, co-occurrence of *D. carota* also had a significant influence on the extent of growth promotion by AMF (Table 2). Analysis of variance revealed that AMF inoculation significantly ($P < 0.001$) influenced various vegetative and reproductive attributes of *A. cotula* both in mono- as well as in mixed-culture. All the investigated attributes, except length and dry mass of roots, were significantly influenced by the co-occurrence of *D. carota* with *A. cotula*. Mycorrhization, particularly with local AMF, positively influenced all the attributes of *A. cotula,* except root length and dry mass.

Irrespective of whether or not growing in association with *D. carota*, inoculation of *A. cotula* with local AMF decreased root: shoot ratio (Fig. 2) in comparison with non-local AMF. Mycorrhizal Inoculation Effect (MIE) in *A. cotula* due to local and non-native AMF in the absence of *D. carota* was 75.26 and 22.7, respectively and the same in presence of *D. carota* was reduced to 56.98 and 8.64, respectively upon inoculation with local and non-local AMF.

Discussion

Significant AMF colonization of *A. cotula* across different spatially separated populations (Table 1) together with improvement in its growth and fitness attributes upon AMF inoculation points towards possible contributory role of arbuscular mycorrhizal fungi in promoting the invasion of various habitats by this species in the Kashmir Himalaya, India. Higher incidence of AMF association with roots of some alien plant species have also been reported by Read et al. (1976) and Fumanal et al. (2006). Our study further

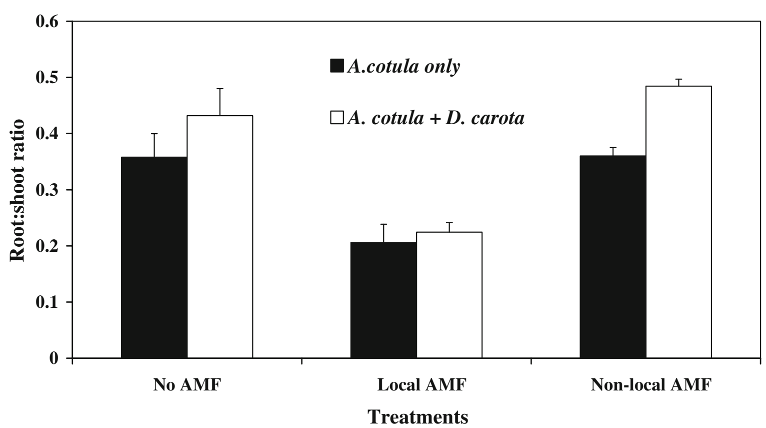

Fig. 2 Root: shoot ratio of *Anthemis cotula* with and without local or non-local AMF in presence and absence of *Daucus carota*. Values are means ± standard error at final harvest

established that mere presence of AMF mutualists does not necessarily confer advantage on the host; instead the source of AMF determines the extent of benefit. The present study demonstrated that local AMF had more positive influence on various traits of *A. cotula* than non-local AMF. However, the benefits derived by *A. cotula* from AMF association were significantly influenced by the co-occurring *D. carota*, as has also been observed by Callaway et al. (2003) while studying the effects of soil fungi on interactions between *Centaurea melitensis*, an exotic invasive weed in central California, and two co-occurring grasses, *Nassella pulchra* and *Avena barbata*. Mummey et al. (2005) also reported that the AMF community colonizing the roots of *Dactylis glomerata* was strongly controlled by neighbouring roots of an invasive forb, *Centaurea maculosa*. More recently, Hawkes et al. (2006) and Mummey and Rillig (2006) also demonstrated change in AMF assemblages in native plant roots in presence of invasive species. Instances of neighbouring plants significantly influencing invasive plants and *vice-versa* are also known (Stampe and Daehler 2003; Hallett 2006).

A positive effect of AMF inoculation on vegetative and reproductive attributes with consequent increases in fitness of *A*. *cotula* in the absence of co-occurring *D. carota* is similar to previous findings (Shah et al. 2006; Shah and Reshi 2007). We observed a more positive feedback from local than non-local AMF, both in mono- and mixed cultures. Despite favourable influences on root and shoot dry mass of *A. cotula* by local AMF inoculation, declines in root: shoot ratio (Fig. 2) is suggestive of mycorrhizal facilitation in uptake of mineral nutrients with possible implications for resource allocation. The trend in root: shoot ratio under different treatments, however, needs allometric analysis to validate whether or not the differences in the ratios are due to decreased growth and delayed development or reallocation in response to varying resources. The observed differences in growth and reproductive attributes of *A. cotula* in presence of *D. carota* could possibly be because of the interference of the latter with the belowground AMF mutualistic interactions. Similar inference has also been drawn by Stinson et al. (2006) who demonstrated that invasive plants can suppress growth of the native plants by disrupting their mutualistic associations with belowground AMF.

Positive Mycorrhizal Inoculation Effect (MIE) on *A. cotula*, especially by local AMF, points towards greater dependency of this alien invasive species on the mycorrhizal mutualism. Reduction in MIE in presence of *D. carota* could be due to alteration of the feedback between AMF and *A. cotula*. While plant species with more mycorrhizal dependency also exhibit greater mycorrhizal species sensitivity (Van'der Heijden 2002), such AMF specificity of *A. cotula* requires further investigation for its confirmation. Even being an inhabitant of ruderal habitats where disturbance impairs the mycorrhization incidence (Reeves et al. 1979), *A. cotula* appears to draw belowground AMF community to its advantage in the Kashmir Himalaya.

The present study allows us to conclude that local AMF have a more positive effect on almost all attributes that contribute to fitness and invasiveness of *A. cotula* as compared to non-local AMF. However, the extent and intensity of benefits accrued from AMF association with *A. cotula* are significantly influenced by the presence of neighbouring plant species, such as *D. carota*. We suggest future studies to further examine the tripartite (host–AMF–neighbour) interactive feedback in relation to alien plant invasions which would facilitate better understanding of factors promoting invasions.

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