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REGULAR ARTICLE

Arbuscular mycorrhizal fungi shift competitive relationships among crop and weed species

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Abstract
Aims Arbuscular mycorrhizal (AM) symbioses affect plant competitive relationships within and among species and may be involved in the interactions among agricultural weed species and crops, depending on their mycorrhizal status. In this work, the impact of native AM fungi (AMF) on maize-weed(s) and weed–weed competitive relationships was assessed, using *Solanum nigrum* and *Chenopodium album* as model host and non-host weeds, respectively.
Methods Growth performance, nutrient use and competitive ability of crop and weed species were assessed in the pure stand and in different model plant communities of host and non-host species.
Results Results showed that maize performance decrease was more severe when grown with *C. album* than with *S. nigrum*. Differential responses to AMF occurred in the two weed species tested: mycorrhizal *S. nigrum* showed reduced biomass and N uptake when grown in competition with *C. album*. The negative performances observed when mycorrhizal *S. nigrum* grew in competition with *C. album* corresponded to *C. album* larger biomass production and N uptake.
Conclusions Results showed that AMF are able to alter the competitive relationships between co-occurring plant species differing in their mycorrhizal status (host/non-host), thus representing key soil organisms to be taken into account in sustainable weed management strategies.

Keywords Arbuscular mycorrhizal fungi · *Zea mays* · *Chenopodium album* · *Solanum nigrum* · Sustainable weed management · Non-host plants

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Introduction

Co-occurring plant species interact with each other and compete for growth limiting resources such as sunlight, water and nutrients. The outcome of these complex interactions may be affected by soil microbes, in particular when involved in pathogenic and mutualistic associations (Van der Putten and

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Peters 1997; Smith and Read 2008). Arbuscular mycorrhizal (AM) fungi (AMF) are beneficial soil borne symbionts (phylum Glomeromycota) living in the roots of about 80% of land plant species, including most agricultural crops and weeds (Schussler et al. 2001). AMF play a major role in plant nutrition, absorbing and translocating mineral nutrients, such as P, N, Zn and Cu, to the host cells (Smith and Read 2008) by means of large extraradical mycelial networks spreading from mycorrhizal roots into the soil (Giovannetti et al. 2001, 2004).

Different studies have shown that AMF colonisation may affect plant performance and competitive relationships within and among co-occurring plant species (Eissenstat and Newman 1990; Hamel et al. 1992; Hartnett et al. 1993; Moora and Zobel 1996; Rejon et al. 1997; Scheublin et al. 2007; Schroeder-Moreno and Janos 2008). AMF effects on plant competitive relationships varied depending on the responsiveness of plant species to fungal colonization (Watkinson and Freckleton 1997). Accordingly, plant benefits were largest in the most responsive plants (Hartnett et al. 1993; West 1996; Scheublin et al. 2007), although they were reduced at high P availability and high plant density (Johnson 1998; Schroeder-Moreno and Janos 2008).

Agricultural weed species, including either mycorrhizal and non- or weakly mycorrhizal plants, varied in their responses to AMF, since mycorrhizal symbioses induced plant growth responses in the majority of host plant–fungus combinations, whereas no responses or negative performances were reported when non-host plants were challenged with AMF (Vatovec et al. 2005). In studies involving individual plant species, i.e. in the absence of competition, AMF reduced growth of non-host weeds (Francis and Read 1995; Muthukumar et al. 1997; Johnson 1998) while produced positive growth responses in host weeds (Koide and Lu 1992, 1995; Heppell et al. 1998; Vatovec et al. 2005; Ayres et al. 2006). Interestingly, in mixed cultures of a host crop and non-host weeds, Rinaudo et al. (2009) reported a reduction of total weed biomass in the presence of AMF.

Since most studies investigating AMF impact on plant competition analysed only host plants, poor knowledge is available on the competitive relationships among non-host plant species or between host and non-host plants. Furthermore, inclusion of crop plants in competitive studies could be very important, considering that weeds can severely affect crop productivity. In agroecosystems, crops and weeds of different mycorrhizal status are likely to co-exist, thus the role of AMF in crop–weed or weed–weed competition might be significant, especially in sustainable, low-input agriculture. Accordingly, knowledge on AMF/weeds relationships may provide important basic information to design innovative, ecologically-based weed management systems relying on reduced use of external inputs.

This work investigated the impact of AMF on maize–weed(s) and weed–weed competitive relationships under controlled conditions, by using *Solanum nigrum* and *Chenopodium album* as model host and non-host weeds, respectively. In particular, we assessed growth performance, nutrient use, mycorrhizal benefits and competitive ability both in the pure stand and in different model plant communities of host and non-host species.

Materials and methods

Plant material

Zea mays L. (cv. Arzano) was used as mycorrhizal crop. *Chenopodium album* L. and *Solanum nigrum* L. were used as AMF non-host and host plant species, respectively, since they are two of the most problematic weeds often associated with maize (Bárberi and Mazzoncini 2001; Davis et al. 2005). Seeds of each weed species were purchased from the Herbiseed company (www.herbiseed.com).

Experimental design

A glasshouse pot experiment was laid out according to a randomised complete block design with two AMF treatments (mycorrhizal presence, AMF^+ and mycorrhizal absence, AMF^-) and seven plant competition treatments, including any mono-, bi- or tri-specific combinations for each AMF treatment: (1) *Z. mays* L. alone (M); (2) *C. album* L. alone (C); (3) *S. nigrum* L. alone (S); (4) *Z. mays* + *C. album* (M + C); (5) *Z. mays* + *S. nigrum* (M + S); (6) *Z. mays* + *C. album* + *S. nigrum* (M + C + S); (7) *C. album* + *S.*

nigrum (C + S). There were four replicates of each treatment resulting in a total of 56 pots (Fig. 1).

Experimental set-up

This study was carried out in a non heated glasshouse with open flanks at the Department of Agronomy and Agro-Ecosystem Management, University of Pisa (lat. 43°40′ N, long. 10°19′ E) from May to July 2007. Pots of 30 cm diameter and 30 cm height were filled with 10 kg of autoclaved (80°C for 2 h) soil for the AMF^- treatment (control). Control pots received 100 ml of a filtrate, obtained by sieving natural soil through a 50 μm pore diameter sieve and through Whatman N. 1 paper, to ensure a common microflora for all treatments. Unsterilised natural soil was used in the AMF^+ treatment to provide indigenous field AMF populations. All soil was collected at 0–50 cm depth in a long-term maize cropping systems experiment carried out at the Interdepartmental Centre for Agri-environmental Research E. Avanzi (CIRAA) of the University of Pisa, Italy since 1989. Soil chemical analysis showed a pH of 8.0, 1.70% organic matter, 0.12% total nitrogen and 16.8 mg kg^{-1} available P. Sand, silt and clay content was 49.4, 39.3 and 11.3% respectively (USDA classification).

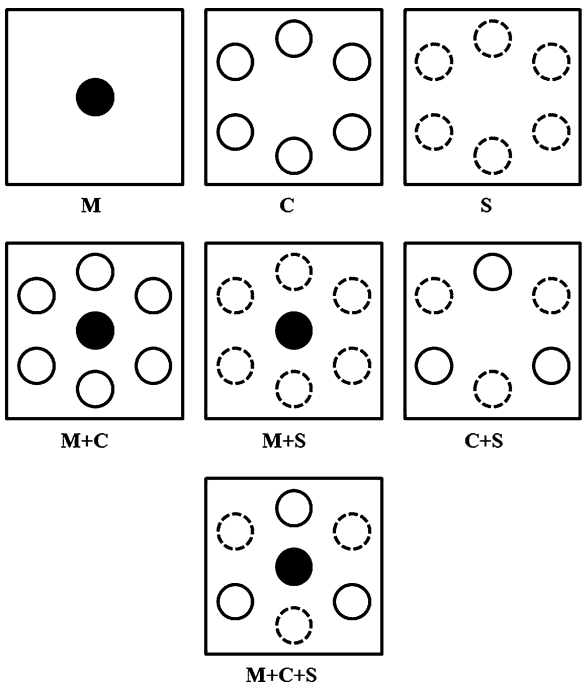

Fig. 1 Schematic representation of experimental pots, showing plant arrangement around each maize plant (where present) in the different competition treatments. *Filled circle = Zea mays* (*M*); *open continuous circle = Chenopodium album* (*C*); *open dotted circle = Solanum nigrum* (*S*). Each combination was repeated three times in each pot

Seeds were directly sown into the pots, where crop and weed seedlings thinning was carried out 3 days and 6 days after emergence, respectively, to obtain the planned number of plants pot^{-1}. Three maize plants pot^{-1} were left either in monoculture or in mixture with weeds. Maize plants were arranged in such a way that they were equally distant from each other. In maize plus one weed species combinations, 6 weed seedlings surrounding each maize plant were left, thus resulting in 18 weed plants pot^{-1}. For the maize plus two weed species combinations, the same final weed density was maintained, thus resulting in three seedlings $species^{-1}$ around each maize plant, in alternate arrangements. The same plant arrangement and density was used for the pots with one weed species or with the two weed species combined, without maize in the centre of the weeds (Fig. 1). Pots were watered regularly to maintain a moisture content between 20% and 25% of the soil dry weight. During the whole period of the experiment, random sample pots were weighed prior to water addition to estimate the amount of water lost by evapotranspiration, which was reintegrated through watering until the desired level was reached. Unwanted plant species emerging in the pots were immediately removed. No fertilisation was applied to the pots (Fig. 2).

Data collection and processing

All parameters were gathered 56 days after sowing. *Z. mays* was in the stem elongation stage, before inflorescence emergence (stage 34–35 of the extended BBCH scale; Lancashire et al. 1991), while *C. album* (flowering stage; stage 81 of the extended BBCH scale; Hess et al. 1997) and *S. nigrum* (fruiting stage; stage 65 of the extended BBCH scale; Hess et al. 1997) already reached the reproductive stage. Total aboveground biomass for each plant species was determined by cutting plants at the base and oven drying the aboveground biomass for three days at 60°C until constant weight. After dry weight determination, plant samples were ground and analysed for total N with the Kjeldahl method (Jones 1991) and for total P with the molybdate blue ascorbic acid method

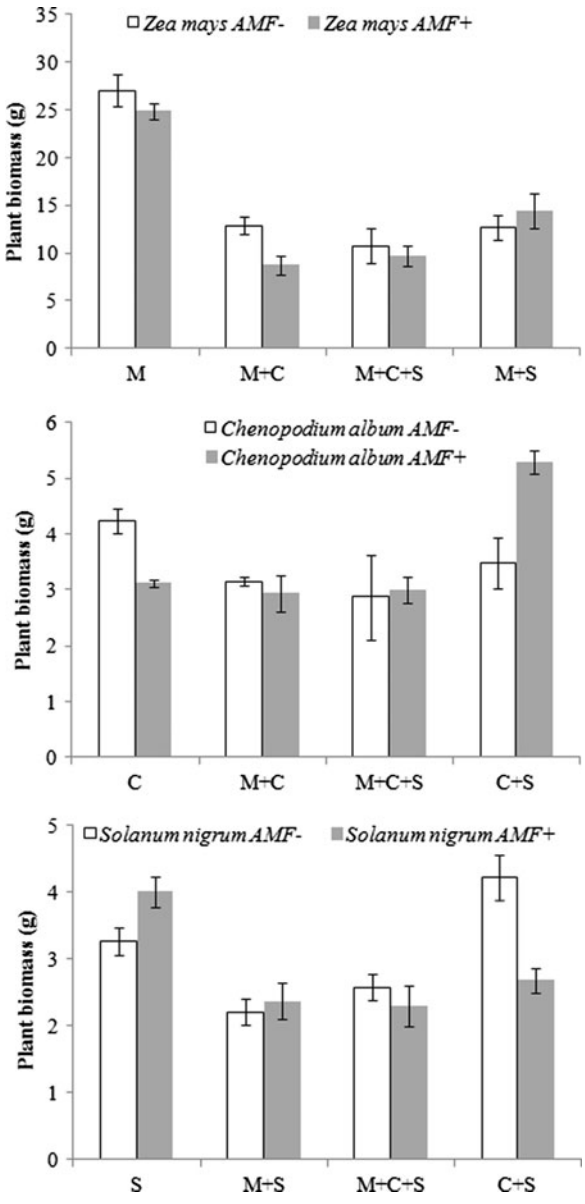

Fig. 2 Above-ground biomass of mycorrhizal (AMF^+) and nonmycorrhizal (AMF^-) *Zea mays*, *Chenopodium album* and *Solanum nigrum*, grown alone or in competition with one or two of the other species

(Watanabe and Olsen 1965). Total N and P per plant were calculated multiplying P and N concentrations by dry weight per plant. Total N and P per plant were used to calculate phosphorus (PUE) and nitrogen (NUE) use efficiency, i.e. the biomass produced for each unit of N or P uptake (ratio of dry weight/plant P or N content). Number of inflorescences for *C. album* and number of fruits for *S. nigrum* were determined on three randomly collected plants pot^{-1}. A subsample of known fresh weight was taken from three roots of each plant species, which were washed and analysed for mycorrhizal colonisation following the clearing and staining method, using lactic acid instead of lacto-phenol (Phillips and Hayman 1970) and the gridline intersect method (Giovannetti and Mosse 1980).

Mycorrhizal benefit (MB), percent change in biomass or nutrient content in AM plants (calculated as $MB = (Q_{AMF}{}^{+} - Q_{AMF}^{-})/Q_{AMF}{}^{-}$; Smith and Read 2008) was used to estimate plant species benefit induced by AMF presence in terms of nutrient uptake (nitrogen and phosphorus) and biomass, with or without competition. $Q_{AMF}{}^{+}$ is the value of parameter Q in the presence of AMF and $Q_{AMF}{}^{-}$ is the value of the same parameter in the absence of AMF. MB was calculated only on data showing significant differences between AMF^+ and AMF^- values. A zero value of MB indicates no benefit, while a value >0 indicates a benefit from the symbiosis for a given species.

The competitive balance index (C_b; Wilson 1988) was used to determine maize competitive ability against *C. album* or *S. nigrum* or both and the competitive ability of *C. album* against *S. nigrum* in presence or absence of AMF. In the case of interactions among three species, three different C_b values were computed for maize: one *vs* both weed species, one *vs C. album* alone (in the presence of *S. nigrum*) and one *vs S. nigrum* alone (in the presence of *C. album*). C_b was computed using the formula:

$$C_b = \log_e[(W_{ab}/W_{ba})/(W_{aa}/W_{bb})]$$

where:

- W_{aa} weight *per plant* of species 'a' grown in monoculture
- W_{bb} weight *per plant* of species 'b' grown in monoculture
- W_{ab} weight *per plant* of species 'a' grown in competition with species 'b'
- W_{ba} weight *per plant* of species 'b' grown in competition with species 'a'

Positive C_b values indicate that species 'a' has higher competitive ability than species 'b' in the presence (AMF^+) or absence (AMF^-) of AMF, whereas negative values indicate the opposite. Maize was set as species 'a' in all treatments whereas *C.*

album was set as species 'a' when grown in association with *S. nigrum*.

Statistical analysis

Analysis of variance (F test) for two-way randomised complete block design was used to evaluate the effects of AMF presence/absence on maize/weed and weed/weed competitive interactions on plant above-ground biomass, total N and P uptake plant^{-1}, number of inflorescences plant^{-1} of *C. album* and number of fruits plant^{-1} of *S. nigrum.* One way ANOVA was performed to compare, within the same plant species, percent AM fungal colonisation among the different competition treatments, after arcsine transformation of data. One way ANOVA was also performed, when significant *P* values for factors or their interaction were obtained from two-way ANOVA, to compare AMF treatment effect on biomass, N and P uptake, number of inflorescences and competitive ability (C_b), within the same species and competition treatment, and to compare the same parameters among the different competition treatments, within the same AMF treatment. Among MB data, only those calculated for maize P uptake, which showed significant differences between AMF^+ and AMF^- in all competition treatments, were submitted to one-way ANOVA.

Results

Mycorrhizal colonization

As expected, no AMF root colonization was observed in roots of the three plant species in the AMF^- treatments. Plant competition influenced AMF colonisation only in the non-host species *C. album*, which showed negligible AMF colonisation in the pure stand and 17–26% colonised root length in the mixed stands (df=3; $P<0.001$). Though, mycorrhizal colonization of *C. album* consisted only of intercellular hyphae and vesicles, while arbuscules were never detected (Fig. 3). No significant differences in AMF colonisation among competition

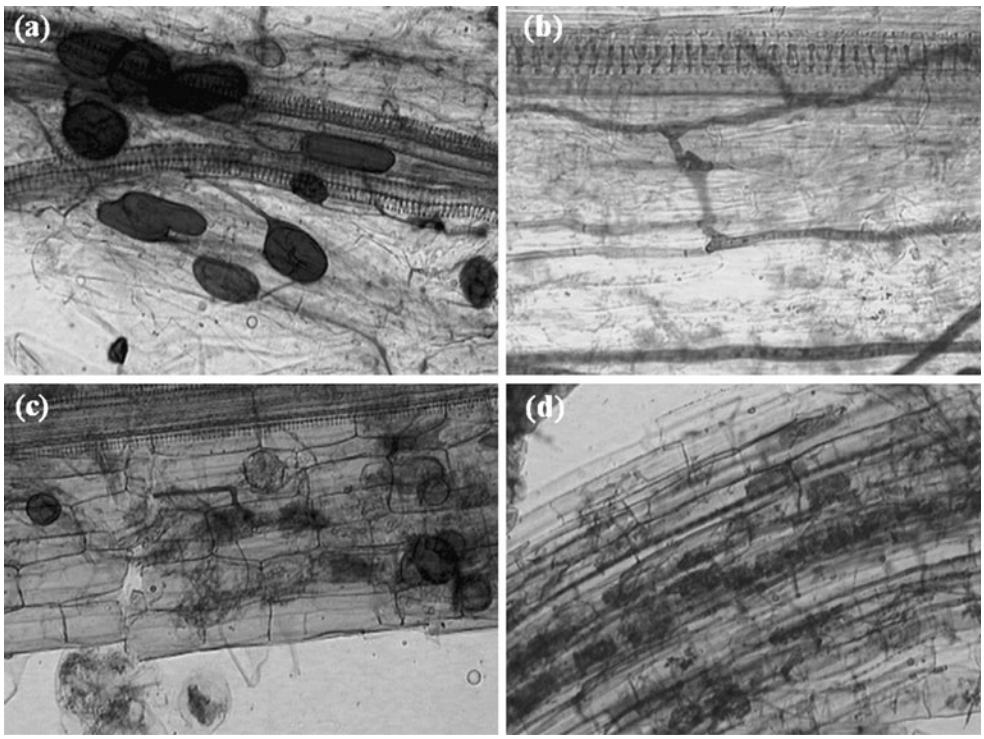

Fig. 3 Representative light micrographs (images) of colonisation patterns by indigenous arbuscular mycorrhizal fungi in trypan blue stained roots of: **a**, **b** *Chenopodium album*, showing vesicles and intercellular hyphae; **c** *Solanum nigrum* and **d** *Zea mays* showing intercellular hyphae and arbuscules

treatments were observed in maize and *S. nigrum*. However, maize root colonisation was always high, ranging from 56.5% in the pure stand to 70.2% in M+C, whereas colonisation in *S. nigrum* ranged from 12.6% in M+S to 22.6% in the pure stand (Table 1).

Above-ground plant biomass and weed fecundity

Two-way ANOVA showed a significant effect of competition treatments only on above-ground biomass of *Z. mays* and significant interactive effects of competition and mycorrhizal treatment in *C. album* and *S. nigrum* (Table 2).

Analysis performed on all eight replicates for each competition treatment, independently on AMF treatment, showed that maize biomass significantly decreased in the presence of competing plant species (by 47.9–60.6%) (Table 3).

In the pure stand, the AMF^+ *C. album* above-ground biomass was lower (−26%) than the AMF^- *C. album* one, while it increased by 50% with respect to AMF^- when *C. album* and *S. nigrum* were grown together (Table 3, Fig. 2). *C. album* biomass did not significantly vary among remaining competitionxAMF treatments (Table 3).

S. nigrum biomass increased in the presence of AMF in the pure stand (+21%), while it was reduced by 36% in C+S (Table 3). In AMF^+ treatments, the presence of competing species always resulted in significantly lower *S. nigrum* biomass, with 40%, 32% and 42% reduction in M+S, C+S and M+C+S, respectively, as compared to the pure stand. In AMF^- treatments, biomass of *S. nigrum* in C+S was significantly higher than that obtained in the other competition treatments, whereas biomass recorded in the pure stand was not significantly different from the other competitionxAMF treatments (Table 3).

Number of *C. album* inflorescences was not affected by competition treatments, while it was significantly reduced by AMF presence (df=1; P= 0.002) (Table 4). Neither AMF nor competition affected *S. nigrum* fruit number (data not shown).

Table 1 Percentage of root length colonised by AMF in *Zea mays* (M), *Chenopodium album* (C) and *Solanum nigrum* (S) grown alone or in competition with one or two of the other plant species

Treatment	*Zea mays*[a]	*Chenopodium album*	*Solanum nigrum*
M	56.5±6.7		
C		0.5±0.4 b	
S			22.6±5.3
M+C	70.2±10.5	25.8±2.7 a	
M+S	67.2±4.1		12.6±3.3
M+C+S	67.5±5.2	24.3±4.5 a	15.3±4.6
C+S		17.3±4.4 a	13.1±1.9

[a] Values are means of four replicates ± SE of the mean. In each column, values followed by different letters are significantly different (P<0.001)

P and N uptake

AMF and competition treatments influenced plant P and N uptake in the different species. Results of two-way ANOVA showed that AMF treatments significantly affected P uptake in maize and *C. album*, while it had no effect on their N uptake. Competition significantly affected P and N uptake in all species excepted for P uptake of *C. album* (Table 2). *S. nigrum* also showed a significant AMF x competition interaction for N uptake.

Maize P uptake was significantly higher in AMF^+ than in AMF^- (from 2.1- to 3.4-fold), across all competition treatments. Furthermore, it was significantly reduced (between 85% and 127%) by the presence of weeds in all competition treatments, except in the binary mixture with *S. nigrum* in the presence of AMF (Table 5). P uptake of *C. album* was significantly decreased by AMF presence (Table 5). By contrast, P uptake of *S. nigrum,* which was unaffected by AMF presence, was significantly higher (on average +72%) in the pure stand and in the binary mixture with *C. album* than in both combinations with maize (Table 5).

The presence of competing species reduced maize N uptake independently of AMF treatments, and values obtained in all the competition treatments were significantly lower than the values in the pure stand (Table 6). Although AMF as factor did not significantly affect N uptake in both weed species (Table 2), a significant interaction between AMF and competition treatments occurred. *C. album* N uptake was reduced in the presence of AMF in the pure stand (−46.5%) with respect to AMF^- values, and increased in the binary mixture with *S. nigrum* (Table 6),

Table 2 Two-way ANOVA *P* values for above-ground biomass, P and N uptake responses of *Zea mays*, *Chenopodium album* and *Solanum nigrum* to mycorrhizal inoculation (AMF) and plant competition (COMP)

Species	Source of variation	Df	Biomass[a]	P uptake	N uptake
Z. mays	AMF	1	0.201	0.004	0.481
	COMP	3	0.000	0.005	0.000
	BLOCK	3	0.868	0.310	0.325
	AMFxCOMP	3	0.196	0.094	0.263
	AMFxBLOCK	3	0.454	0.325	0.460
	COMPxBLOCK	9	0.236	0.249	0.303
C. album	AMF	1	0.229	0.023	0.076
	COMP	3	0.008	0.552	0.030
	BLOCK	3	0.960	0.796	0.877
	AMFxCOMP	3	0.019	0.065	0.057
	AMFxBLOCK	3	0.930	0.669	0.854
	COMPxBLOCK	9	0.563	0.196	0.599
S. nigrum	AMF	1	0.067	0.322	0.777
	COMP	3	0.000	0.001	0.000
	BLOCK	3	0.227	0.323	0.202
	AMFxCOMP	3	0.000	0.194	0.006
	AMFxBLOCK	3	0.691	0.184	0.190
	COMPxBLOCK	9	0.527	0.512	0.597

[a]Factors with significant effect and/or significant interaction were used for oneway/pairwise comparisons

showing the largest value among competition treatments (on average +104.4%). On the contrary, AMF^+ *S. nigrum* grown with *C. album* showed lower N uptake (−30%) with respect to AMF^-. *S. nigrum* N uptake was affected by competing plants, and values recorded in the AMF^+ pure stand were significantly higher than in all competition treatments (on average +90.9%). Interestingly, *S. nigrum* N uptake in the AMF^- pure stand and in C+S were significantly higher (on average +80.0%) than in the combinations which included maize (Table 6).

Mycorrhizal benefit

Mycorrhizal colonisation provided a benefit to maize in terms of P uptake, regardless of competition treatment, whereas negative MB values were observed for above-ground biomass in M+C (−0.32±0.07, mean±SE of the mean). No MBs were consistently observed for all parameters in the *C. album* pure stand, whereas a MB of 0.60±0.23 (mean±SE of the mean) was obtained for biomass when *C. album* was grown in competition with *S. nigrum*. In contrast to *C. album*, *S. nigrum* was benefited by mycorrhizal colonisation in terms of above-ground biomass in the pure stand, and negative values were recorded for *S. nigrum* biomass and N uptake when grown with *C. album*.

Competitive balance index (C_b)

Generally, maize was less competitive than either *C. album* or *S. nigrum* in all plant stands, regardless of AMF treatments, as shown by its consistently negative C_b values (Table 7). However, AMF colonisation reduced maize competitive ability against *C. album* in the binary mixtures, whilst it significantly increased its competitive ability against *S. nigrum*.

The competitive relationships between the two weed species were completely reversed by AMF presence: *C. album* was more competitive than *S. nigrum* in the presence of AMF whilst the opposite was observed in the AMF^- treatment (Table 7).

PUE and NUE

PUE and NUE can be considered as the efficiency with which P and N are used to produce plant biomass (dry weight). Both in the absence and in the presence of competitors, mycorrhizal inoculation significantly decreased PUE of *Z. mays*, since the

Table 3 Above-ground biomass (g plant^{-1}) of mycorrhizal (AMF$^+$) and nonmycorrhizal (AMF$^-$) *Zea mays* (M), *Chenopodium album* (C) and *Solanum nigrum* (S), grown alone or in competition with one or two of the other species

Treatment	*Zea mays*		
	AMF$^+$	AMF$^-$	All data
M	24.9±0.8	27.0±1.7	25.95±0.95 a
M+C	8.7±1.0	12.9±0.9	10.81±1.00 b
M+S	14.4±1.8	12.7±1.3	13.52±1.06 b
M+C+S	9.7±1.1	10.8±1.9	10.21±1.02 b
P value[a]			<0.001
Treatment	*Chenopodium album*		*Solanum nigrum*
C AMF$^-$	4.2±0.2 ab		
C AMF$^+$	3.1±0.1 b		
M+C AMF$^-$	3.2±0.1 b		
M+C AMF$^+$	2.9±0.3 b		
C+S AMF$^-$	3.5±0.5 b		4.2±0.3 a
C+S AMF$^+$	5.3±0.2 a		2.7±0.1 b
M+C+S AMF$^-$	2.9±0.8 b		2.6±0.2 b
M+C+S AMF$^+$	3.0±0.2 b		2.3±0.3 b
S AMF$^-$			3.3±0.2 ab
S AMF$^+$			4.0±0.2 a
M+S AMF$^-$			2.2±0.2 b
M+S AMF$^+$			2.4±0.3 b
P value	0.001		< 0.001

For *Zea mays*, means of four replicates ± SE of the mean (AMF$^+$ and AMF$^-$) and means of all eight replicates ± SE of the mean are reported

[a] *P* values refer to results of one way ANOVA comparing the different treatments. In the columns, values followed by different letters are significantly different ($P \leq 0.05$)

increase in P content of mycorrhizal plants was not followed by a similar increase in biomass (Table 8). *S. nigrum* PUE was not affected by mycorrhizal colonisation, except when the host weed grew in the presence of *C. album*: in such a treatment a significant reduction in AMF$^+$ *S. nigrum* biomass with respect to AMF$^-$, without differences in P content, significantly decreased PUE. The opposite behaviour was observed for the non-host weed *C. album*, in which PUE was significantly enhanced by AMF in the presence of *S. nigrum*, since the same P content resulted in an increase of *C. album* biomass of 127.1%, compared with non inoculated plants (Table 8). No significant differences in PUE were observed among competition treatments, both in AMF$^+$ and AMF$^-$ plants, for *Z. mays* and *S. nigrum*, whereas AMF$^+$ *C. album* showed significant differences between plants grown with *Z. mays* (M+C) or with both competitors (M+C+S) and those grown with *S. nigrum* (C+S) (Table 8).

Values of NUE (data not shown) were never significantly affected by competition or by mycorrhizal inoculation, except for AMF$^+$ and AMF$^-$ *C. album* grown alone (df=1; F=31.36; P=0.021).

Discussion

In this work, plant growth responses and competitive interactions were studied in an experimental system, where an AMF host crop (maize) and two weeds, one host (*S. nigrum*) and one non-host (*C. album*) were grown together in the presence or absence of a natural AMF community. Results showed that AMF altered the competitive relationships between co-occurring plant species with different mycorrhizal status (host/non-host).

Mycorrhizal colonization

Colonized root length of maize and *S. nigrum* was unaltered by competition treatments while that of *C. album* was negligible in the pure stand, and increased significantly when grown with the host plants maize or *S. nigrum*. It is interesting to note that *C. album,* belonging to a family known as non-host, showed intraradical colonization with hyphae and vesicles, but without any arbuscule. Colonization of non-host

Table 4 Number of inflorescences plant^{-1} produced by mycorrhizal (AMF$^+$) and nonmycorrhizal (AMF$^-$) *Chenopodium album* (C) grown alone or in competition with *Zea mays* (M) or *Solanum nigrum* (S) or both

Treatment	AMF$^+$[a]	AMF$^-$
C	18.0±8.5	71.8±10.9
C+S	43.5±8.7	82.5±7.0
M+C	36.8±14.4	69.0±26.2
M+C+S	33.5±9.8	40.3±9.1
All data[b]	32.94±5.3[c]	65.88±7.9

[a] Values are means of four replicates ± SE of the mean

[b] Values are means of 16 replicates ± SE of the mean

[c] Values significantly different (P=0.002) between AMF$^+$ and AMF$^-$

Table 5 Phosphorus uptake (mg plant^{-1}) in mycorrhizal (AMF$^+$) and non mycorrhizal (AMF$^-$) *Zea mays* (M), *Chenopodium album* (C) and *Solanum nigrum* (S), grown alone or in competition with one or two of the other species

Treatment	*Zea mays*[a]		*Chenopodium album*		*Solanum nigrum*		
	AMF$^+$	AMF$^-$	AMF$^+$	AMF$^-$	AMF$^+$	AMF$^-$	All data[c]
M	34.9±3.9 b[b]	15.2±3.1 b					
C			4.2±0.6	9.7±0.5			
S					6.1±1.1	4.1±0.2	5.1±0.6 a
M+C	15.6±2.3 a[b]	7.5±0.7 a	5.3±0.8	6.4±0.3			
M+S	27.5±5.7 ab[b]	8.2±1.3 a			3.0±0.3	2.4±0.2	2.7±0.2 b
M+C+S	18.9±1.1 a[b]	6.7±1.3 a	5.2±0.6	6.6±2.1	3.2±0.5	3.6±0.2	3.4±0.3 b
C+S			7.4±1.0	7.2±0.9	5.7±1.1	5.3±0.6	5.4±1.0 a
All data[c]			5.5±0.4 [b]	7.5±0.6			
P value	0.01	0.03	0.01				<0.001

[a] Values are means of four replicates ± SE of the mean

[b] Values are significantly different ($P \leq 0.05$) between AMF$^+$ and AMF$^-$ within the same plant species. *P* values refer to results of one way ANOVA comparing the different competition treatments or (*C. album*) mycorrhizal treatments on all data

[c] Values are means of eight (*S. nigrum*) and 16 (*C. album*) replicates ± SE of the mean. In columns, values followed by different letters are significantly different ($P \leq 0.05$) among competition treatments

plants belonging to *Chenopodioideae*, *Brassicaceae* and *Amaranthaceae* was previously reported (Miller 1979; Allen et al. 1989; Giovannetti et al. 1994; DeMars 1996; Rydlova and Vosatka 2001; Orlowska et al. 2002; Regvar et al. 2003), although data on the occurrence of arbuscules and on AMF effects on plant growth were inconsistent (Williams et al. 1974; Lovera and Cuenca 1996; Regvar et al. 2003; Vatovec et al. 2005). Ocampo (1980) and Stejskalova (1990) observed mycorrhizal colonization of *C. album* when grown together with maize and onion (both AMF hosts), a phenomenon described as the 'nurse-plant effect'. In this work, established extraradical mycelial networks originating from host roots (maize or *S. nigrum*) might have spread in the soil and colonized the root system of nearby *C. album* plants (Malcova et al. 2001; Sykorova et al. 2003; Enkhtuya et al. 2005). Accordingly, Puschel et al. (2007) showed colonization of non-host plants when grown in the presence of pre-existing extraradical mycelial networks, while no colonization was observed when only spores were used as inoculum. It is of interest to note that tomato mutants unable to establish AMF symbioses when inoculated with germinated spores, where colonised in the presence of symbiotic mycelium originating from mycorrhizal roots of a host plant growing nearby (David-Schwartz et al. 2003).

Plant responses in the pure stand

Mycorrhizal symbiosis enhanced maize P uptake with no related increase in biomass or N uptake, which turned out in reduced PUE. These results are consistent with AMF role in enhanced P uptake by host plants even if overall biomass or N uptake remain unaffected (Landis et al. 2005; Reynolds et al. 2005; Smith and Read 2008; Smith and Smith 2011). In the literature, the absence of mycorrhizal plant benefits has been commonly attributed to large C drain by the fungal symbionts (Fitter 1991). Furthermore, whole field soil inoculum without any N fertilization, utilised in our experiment, could have caused nitrogen immobilization, resulting in no growth response in AMF$^+$ maize. Nevertheless, important non-nutritional mycorrhizal benefits, due to changes in water relations, phytohormone levels and carbon assimilation have been reported (Smith and Read 2008). Interestingly, AMF mediated P uptake was also active in those plants, known as 'nonresponsive hosts', where no increases in P content and biomass were observed (Li et al. 2008; Grace et al. 2009).

In the pure stand, significantly larger plant biomass was detected in AMF$^+$ *S. nigrum*, whereas AMF$^+$ *C. album* showed decreased P content and biomass, as compared to AMF$^-$, consistently with previous data

Table 6 Nitrogen uptake (mg plant^{-1}) in mycorrhizal (AMF$^+$) and non mycorrhizal (AMF$^-$) *Zea mays* (M), *Chenopodium album* (C) and *Solanum nigrum* (S), grown alone or in competition with one or two of the other species

Treatment	*Zea mays*		
	AMF$^+$	AMF$^-$	All data
M	15.3±0.5	17.2±2.4	16.31±1.19 b
M+C	5.5±0.5	7.0±0.4	6.28±0.43 a
M+S	8.6±1.3	6.8±0.5	7.72±0.72 a
M+C+S	6.1±0.8	6.5±0.6	6.32±0.44 a
P value			<0.001
Treatment	*Chenopodium album*		*Solanum nigrum*
C AMF$^-$	4.3±0.3 ab		
C AMF$^+$	2.3±0.4 bc		
M+C AMF$^-$	2.7±0.1 abc		
M+C AMF$^+$	2.5±0.3 abc		
C+S AMF$^-$	3.4±0.4 abc		3.7±0.3 ab
C+S AMF$^+$	4.6±0.3 a		2.5±0.2 bc
M+C+S AMF$^-$	2.9±0.9 abc		2.1±0.2 c
M+C+S AMF$^+$	2.0±0.6 c		2.1±0.2 c
S AMF$^-$			3.5±0.2 ab
S AMF$^+$			4.2±0.3 a
M+S AMF$^-$			1.9±0.1 c
M+S AMF$^+$			2.0±0.3 c
P value[a]	0.003		<0.001

For *Zea mays*, means of four replicates ± SE of the mean (AMF$^+$ and AMF$^-$) and means of all eight replicates ± SE of the mean are reported

[a] *P* values refer to results of one way ANOVA comparing the different treatments. In the columns, values followed by different letters are significantly different ($P \leq 0.05$)

on non-host plants (Grime et al. 1987; van der Heijden et al. 1998; Ruotsalainen and Aikio 2004). Interestingly, Jordan et al. (2000) reported that AMF inoculation reduced *C. album* growth rate by 80%. So far, the actual mechanism underlying such a phenomenon is still unclear: production of allelopathic metabolites by AMF, reducing root hair production and possibly affecting non-host plant direct nutrient uptake, has been hypothesized (Francis and Read 1994; Cameron 2010; Facelli et al. 2010). Other authors suggested that AMF colonisation of non-host plant roots may lead to parasitic interactions involving plant defence responses and root cell and/or plant death (Allen et al. 1989; Giovannetti and Lioi 1990).

AMF significantly reduced *C. album* inflorescence production in the pure stand, compared to the AMF$^-$ treatment, consistently with previous data (Sanders and Koide 1994). Our results suggest that low P and N uptake by AMF$^+$ *C. album* might be involved in the reduced production of inflorescences.

Maize–weed and weed–weed competitive interactions

Competition with weeds significantly decreased maize N and P uptake and biomass accumulation, although AMF$^+$ maize consistently showed larger P uptake in all competitive treatments, with respect to AMF$^-$. Both in the absence and in the presence of competitors, PUE of AMF$^+$ maize decreased as compared to AMF$^-$ plants, since P content enhancement was not paralleled by plant biomass increase. Growth reduction in the presence of competing plants was often observed in mycorrhizal plants (Hartnett et al. 1993; Kytoviita et al. 2003; Schroeder-Moreno and Janos 2008; Hausmann and Hawkes 2009), possibly due to physiological changes induced by AMF in host roots, affecting their ability to acquire nutrients via the direct pathway, independently from AMF (Facelli et al. 2010). In our work the addition of N could have changed the outcome of competition, allowing mycorrhizal maize plants to positively respond to AMF inoculation, possibly enhancing their competitivity towards weeds. Our data suggest that *S. nigrum* low P uptake in M+S treatment may facilitate maize, which is better able to

Table 7 Competitive balance index (C_b) for *Zea mays* (M) against each of the weed species in the binary or tertiary competition treatments, and for *Chenopodium album* (C) against *Solanum nigrum* (S) in the binary or tertiary species mixtures in the presence (AMF$^+$) or absence (AMF$^-$) of mycorrhizae, and corresponding *P* values

Competition treatment	AMF$^+$	AMF$^-$
M vs C	−0.98 (P= 0.07)	−0.45
M vs C [+ S][a]	−0.91 (P=0.35)	−0.48
M vs S	−0.02 (P=0.05)	−0.37
M vs S [+ C][b]	−0.39 (P=0.26)	−0.72
M vs C+S	−0.55 (P=0.89)	−0.59
C vs S	0.93 (P=0.01)	−0.47
C vs S [+ M][c]	0.52 (P=0.04)	−0.24

[a] *Z. mays* vs *C. album* (in the presence of *S. nigrum*)

[b] *Z. mays* vs *S. nigrum* (in the presence of *C. album*)

[c] *C. album* vs *S. nigrum* (in the presence of *Z. mays*)

Table 8 Phosphorus use efficiency (PUE, mg aboveground biomass/mg P taken up) in *Zea mays* (M), *Chenopodium album* (C) and *Solanum nigrum* (S) in the different competition treatments, in the presence (AMF^+) or absence (AMF^-) of mycorrhizae

Treatment	*Zea mays*[a]		*Chenopodium album*		*Solanum nigrum*	
	AMF^+	AMF^-	AMF^+	AMF^-	AMF^+	AMF^-
M	745.04±100.21	2058.79±458.93				
C			2547.27±507.98ab	1843,32±137.06		
S					731,84±147.78	799,16±67.73
M+C	578.06±63.03	1773.96±196.86	1691.11±279.63b	1566,48±92.26a		
M+S	552.79±54.16	1590.38±106.64			786,36±59.30	938,54±149.76
M+C+S	513.65±57.46	1650.34±137.82	1716.37±146.50b	1257,16±283.54a	744,31±56.23	706,96±27.48
C+S			4015.95±509.69a[b]	1768,21±446.52a	506,41±58.07	818,78±73.13
All data	597.38±39.1[b]	1768.37±127.1				
P			0.001			

[a] In columns, values followed by different letters are significantly different ($P \leq 0.05$) among competition treatments. *P* value refer to results of one way ANOVA comparing the different competition treatments

[b] Values significantly different between AMF^+ and AMF^- within the same plant species

benefit from mycorrhiza-mediated P uptake, as compared to the other competition treatments, whereas maize plant benefit, competitivity and P uptake data were the lowest in mycorrhizal treatments when maize grew together with the non-host weed *C. album*. Such findings indicate that AMF are able to affect the competitive ability of maize, depending on the mycorrhizal status of the competing weeds.

The two weed species tested showed differential responses to AMF: AMF^+ and AMF^- *S. nigrum* showed similarly reduced biomass and N uptake when grown in competition treatments, although its performances with *C. album* (C+S) significantly declined in the presence of AMF. Interestingly, negative performances of AMF^+ *S. nigrum* in the presence of the non-host *C. album* were concurrent with *C. album* larger N uptake and biomass production, confirming AMF ability to shift competitive relationships between host and non-host plants. Accordingly, N capture by *Brassica napus*, a non-host species, was found to increase in the presence of AMF, particularly when grown in competition with the host *Plantago lanceolata* (Hodge 2003).

In the presence of AMF, the non-host weed *C. album* appeared not to change its ability to acquire P, according to its inability to host intracellular fungal structures involved in P transfer to host roots. Nevertheless, it was shown that P translocation to plants by AMF occurred in plant mutants where only intercellular fungal structures were developed (Manjarrez et al. 2011).

Unravelling the mechanisms by which mycorrhizal fungi may alter plant performance in interspecific competition is extremely difficult, due to the differences in nutrient acquisition and growth strategies of the competing plants (Smith and Read 2008; Facelli et al. 2010). The results obtained in this work with *S. nigrum* and *C. album* mixture may depend on the relative mycotrophy of competitors, consistently with data from mixed communities: negative effects were detected on dominating plants grown with low mycotrophic competitors, whose competitive ability was enhanced by AMF (Grime et al. 1987). Accordingly, the detrimental effects of AMF on nutrient uptake and productivity of non-hosts occurring in the pure stand are not necessarily shown when the same species are grown in competitive conditions. Moreover, the establishment of non-mycorrhizal controls in sterilised soil plus natural soil filtrate, although widely used (Smith and Smith 1981; Ceccarelli et al. 2010; Asghari and Cavagnaro 2011), may cause indirect effects on plant growth, as compared to mycorrhizal treatments set up in unsterile soil (Koide and Li 1989). Such difficulty reduces the possibility of drawing conclusions predictive of plant behaviour in field conditions.

The potential role of AMF as agroecosystem engineers has only recently been tackled (Jordan et al. 2000; Rinaudo et al. 2009; Cameron 2010), despite the obvious importance of AMF in plant competitive relationships. AMF role in crop–weed and weed–weed interactions, involving plants with different competitive abilities and mycorrhizal status, is still not well understood. Experiments with a limited number of interacting plant species are necessary to unravel step by step (and case by case) the mechanisms underlying AMF effects in crop–weed and weed–weed competitive relationships.

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