



# Negative influence of non-host plants on the colonization of *Pisum sativum* by the arbuscular mycorrhizal fungus *Glomus mosseae*

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## Abstract

We studied the influence of the arbuscular mycorrhizal (AM) non-host plants *Stellaria media* (Caryophyllaceae), *Chenopodium album* and *Spinacea oleracea* (Chenopodiaceae), *Brassica campestris*, *B. nigra*, *Capsella bursa-pastoris* and *Sisymbrium altissimum* (Brassicaceae), *Juncus balticus* (Juncaceae), *Urtica dioica* (Urticaceae) and of the AM host plant *Taraxacum officinale* (Asteraceae) on the colonization of *Pisum sativum* by the AM fungus *Glomus mosseae*. None of the non-host plants tested were colonized by *Glomus mosseae*. Older non-host plants competed with *P. sativum*. No inhibition of AM colonization was observed in host plants that were grown in the same pot and at the same time as non-host plants. However, when non-host plants were grown for 30 d before *P. sativum*, they inhibited mycorrhizal colonization of the latter. In a split pot system the presence of *U. dioica* on the left-side decreased AM colonization of *P. sativum* roots on the left-side, but not on the right-side. Non-host plants decreased the inoculum potential of *G. mosseae* and in some cases the percentage AM colonization of host plants cultivated after non-host plants. These results indicate that roots of non-host species have factors that seem to affect the AM fungus before it establishes in the root of host plants. © 1999 Elsevier Science Ltd. All rights reserved.

**Keywords:** Arbuscular mycorrhiza; *Glomus mosseae*; Non-host plants; *Pisum sativum*; *Taraxacum officinale*

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## 1. Introduction

Arbuscular mycorrhizal (AM) symbioses are absent from plants belonging to families such as Brassicaceae, Chenopodiaceae, Juncaceae, Cyperaceae and Urticaceae (Brundrett, 1991; Vierheilig et al., 1996). The mechanisms behind this constitutive lack of colonization of non-host plants remain unclear. An early hypothesis was that roots of non-hosts secreted compounds into the rhizosphere that inhibited AM colonization in plants that are normally mycorrhizal (Hayman et al., 1975; Peterson and Bradbury, 1995; Vierheilig et al., 1995a,b). However, alternative expla-

nations for the lack of AM colonization of non-host plants have been proposed. The observation that AM fungal hyphae are able to grow around and on the roots of many non-host species without penetrating root tissues indicated that the absence of AM colonization from non-hosts plants does not result from the exudation of toxic substances (Ocampo et al., 1980; Hayman, 1983; Schmidt and Reeves, 1984). These findings suggested that non-host plants fail to produce the signals required by AM fungi for successful colonization, or that barriers to mycorrhizal colonization in non-host plants are intrinsic and related to physiological characteristics of the root cortex or epidermis (Ocampo et al., 1980).

The previous growth of non-mycorrhizal plants has a detrimental effect on the spread of AM fungi in soil, on the inoculum potential of soils, and on the subsequent infectivity of AM fungi (Harinikumar and Bagyaraj, 1988; Koide and Schreiner, 1992; Vierheilig

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and Piche, 1995). The roots of non-mycorrhizal plants may contain chemical factors that inhibit mycorrhizal fungi (Brundrett, 1991). Several non-host plants secrete inhibitory compounds from their roots (Vierheilig and Piche, 1995). Volatile compounds from roots of Brassicaceae can inhibit AM spore germination and hyphal development, whereas compounds from Chenopodiaceae plants roots do not (Vierheilig and Ocampo, 1990; Schreiner and Koide, 1993; Vierheilig et al., 1995a,b).

The medium in which plants are grown also influences the negative effects of non-host plants on AM fungi. For example, Powell (1982) observed that previous kale cropping decreased clover yield in two soils but not in another, and El-Atrach et al. (1989) found that non-host cabbage inhibited the AM colonization of alfalfa roots inoculated with spores of *G. mosseae* when the host plant was grown in sand-vermiculite, but not when it was grown in soil. The age of the roots may also influence interactions with AM fungi (Hayman, 1983; Brundrett, 1991). Studies with three crucifers showed some AM colonization and a direct correlation between AM development and plant age or developmental stage possibly due to loss of defensive capabilities in senescent tissues (DeMars and Boerner, 1995).

Our aim was to further explore how non-host plants from different families influence AM colonization of the host plant *Pisum sativum*.

## 2. Materials and methods

Four experiments were done in 500 ml open pots of sterilized soil-sand and one experiment in 500 ml open pots of sterilized sand-vermiculite (1:1 v/v) under the same experimental conditions. The soil pots were filled with a gray loam soil obtained from the garden of the Estacion Experimental del Zaidín (Granada, Spain). The soil (pH 8.1, 1:1, soil:water method), contained ( $\text{mg kg}^{-1}$ ): 6.2 P ( $\text{NaHCO}_3$ -extractable), 0.3 N and 132 K, and consisted of (%): 35.8 sand, 43.6 silt, 20.5 clay, and 1.8 organic matter. It was mixed with quartz sand (2:3, v/v) and steam-sterilized ( $100^\circ\text{C}$ , 3 h) prior to use. The plant species that were believed to be non-mycorrhizal (non-host plants) were: *Stellaria media* L. (Caryophyllaceae), *Chenopodium album* L. and *Spinacea oleracea* L. (Chenopodiaceae), *Brassica campestris* L., *B. nigra* L., *Capsella bursa-pastoris* L. and *Sisymbrium altissimum* L. (Brassicaceae), *Juncus balticus* Willenow (Juncaceae), and *Urtica dioica* L. (Urticaceae). The mycorrhizal host plants were *Taraxacum officinale* Weber (Asteraceae) and *Pisum sativum* L. var. Lincoln (Fabaceae). Seeds were sown in moist vermiculite after soaking for 2 h in water. One-week-old seedlings were transplanted to pots and

grown under greenhouse conditions (*J. balticus* seedlings were transplanted after 4 months). Natural light was supplemented with Sylvania incandescent and cool-white fluorescent lamps ( $400 \text{ nmol m}^{-2} \text{ s}^{-1}$ , 400–700 nm photosynthetically active radiation), providing a 16 h photoperiod. Air temperatures were automatically maintained between 25 to  $19^\circ\text{C}$ , and relative humidity averaged 50%. Plants were watered from below as needed to keep the soil moist to the surface level. Watering was supplemented ( $10 \text{ ml week}^{-1} \text{ pot}^{-1}$ ) with a Long Ashton nutrient solution (Hewitt, 1952) lacking phosphate.

The AM inoculum consisted of rhizosphere soil (10 g) containing spores and root fragments (*Sorghum vulgare* L) of the AM fungus *Glomus mosseae* (BEG No. 12). The inoculum was mixed throughout each soil pot. Uninoculated controls received the soil filtrate (through Whatman No. 1 filter paper) from the AM inoculum to provide soil microorganisms that were associated with the AM inoculum. After the periods detailed below for each experiment, shoot dry matter was recorded. Root samples of each replicate were cleared and stained (Phillips and Hayman, 1970) and the percentage of root length colonization by AM fungi was determined by the gridline intersect method (Giovannetti and Mosse, 1980). To avoid confusing host and non-host roots when both plants were grown together, the roots from each pot were carefully washed to separate the two species and only roots clearly attached to the main root system were examined.

### 2.1. Experiment 1. Effect of non-host plants of different ages on the percentage of AM colonization of host plants

In this experiment the non-hosts *U. dioica* and *S. oleracea* were grown for 0, 10, 20 and 30 d before *P. sativum* was transplanted to pots. The non-host *B. nigra*, *C. album* or *J. balticus* were grown 0 or 30 d before *P. sativum* was transplanted to pots. In each treatment host and non-host plants were grown together for an additional 30 d prior to harvest. Two *P. sativum* seedlings were grown without non-host plants for 30 d as controls. After harvest shoot dry weight and the percentage of AM root colonization were recorded in each of the three replicates per treatment.

### 2.2. Experiment 2. Interaction between host and non-host plants grown together

In this experiment the non-host plants *S. media*, *B. campestris*, *C. bursa-pastoris*, *S. altissimum*, *C. album*, *S. oleracea*, *B. nigra* and *U. dioica* or host plants *P. sativum* and *T. officinale* were grown for 30 d before

*P. sativum* was transplanted to pots and grown for another 60 d. Pots with two *P. sativum* seedlings were used as controls. After harvest, percentage AM colonization of roots was recorded.

2.3. Experiment 3. Interaction between host and non-host plants a in double-pot system

Thirty-day-old *U. dioica* plants were planted on the left-side of a double-pot system (Ocampo, 1986) in which both the left and right sides pots were inoculated with *G. mosseae*. One 13 day-old *P. sativum* plant was placed in the double-pot system such that approximately half its root system was in each side. Treatments with *P. sativum* without *U. dioica* were also set up. Host and non-host plants were then grown together in this double-pot system for 30 d. After harvest shoot dry weight and percentage of AM colonization of roots were recorded.

2.4. Experiment 4. Influence of host and non-host plants on AM inoculum potential

The hosts *P. sativum*, *Anagallis arvensis*, *T. officinale* and the non-hosts *B. campestris*, *B. nigra*, *C. bursa-pastoris* and *S. altissimum* were cultivated in pots with 500 ml (200 g) of sand-vermiculite inoculated with 10 g of *G. mosseae*. Pots inoculated with *G. mosseae* but without plants were used as controls. Plants were grown for 10 weeks in a greenhouse under the conditions described above. Every week 5 ml of 1/2 strength Long Ashton nutrient solution plus 50 mg phosphate l<sup>-1</sup> (Hewitt, 1952) were added to each pot. After 10 weeks the plants (shoot and roots) were removed from the five replicate pots per plant and two assays were done: (1) *Medicago sativa* plants were grown for 6 weeks in sand-vermiculite pots in which the host and non-host plants were grown. At harvest we recorded the percentage of root length colonization of the five replicate pots per plant. (2) The number of effective propagules of the AM fungus *G. mosseae* was estimated by the most probable number (MPN) method (Porter, 1979) using *M. sativa* as the test plant. To determine MPN, samples of 10 ml of sand-vermiculite from each of the five pots per host and non-host plants were used. From each sample 5 dilutions (10<sup>-1</sup>–10<sup>-5</sup>) were prepared and each dilution was tested in 5 plant pots (100 ml pots). The *M. sativa* seedlings were harvested after 6 weeks to record the presence or absence of mycorrhizal colonization.

2.5. Statistical treatments

The experiments were repeated three times, each data point in the average of replicates samples from one representative experiment. The percentage values

Table 1  
Shoot dry weight per plant of *Pisum sativum* and per non-host plants when *P. sativum* was transplanted to non-host pots after different periods of non-host plant growth<sup>a</sup>

<i>P. sativum</i> transplanted to non-host pots after (d)	Alone	Shoot dry weight (mg) of <i>P. sativum</i> grown with					Shoot dry weight (mg) of non-host plants grown with <i>P. sativum</i>				
		<i>S. oleraceae</i>	<i>U. dioica</i>	<i>B. nigra</i>	<i>C. album</i>	<i>J. balticus</i>	<i>S. oleraceae</i>	<i>U. dioica</i>	<i>B. nigra</i>	<i>C. album</i>	<i>J. balticus</i>
0	240ab 1,2	270b 2,3	171a 1	350b 4	204a 1,2	180a	20a	190a	50a	50a	
10	290b 2	170a 1	nd	nd	nd	290a	40ab	nd	nd	nd	
20	250ab 2	140a 1	210b 1,2	nd	nd	470b	60b	nd	nd	nd	
30	200a 1	130a 1	120a 1	140a 1	123a 1,2	500b	160c	350b	530b	142b	

<sup>a</sup> Mean values followed by the same letter in columns or by same number in rows are not significantly different ( $P \leq 0.05$ ). nd = not determined.

Table 2

Percentage arbuscular mycorrhizal root length colonization of *Pisum sativum* planted to non-host pots after different periods of growth of non-host plants<sup>a</sup>

<i>P. sativum</i> transplanted to non-host pots after (d)	Alone	Percent root length colonization grown with				
		<i>S. oleraceae</i>	<i>U. dioica</i>	<i>B. nigra</i>	<i>C. album</i>	<i>J. balticus</i>
0	30a 1	72c 3	42d 2	29b 1	32b 1	30b 1
10	23a 1,2	16b 1	27c 2	nd	nd	nd
20	23a 2	12ab 1	11b 1	nd	nd	nd
30	27a 2	2 a 1	3a 1	3a 1	10a 1	8a 1

<sup>a</sup> Column means followed by the same letter or row means followed by the same number are not significantly different ( $P \leq 0.05$ ). nd = not determined.

of AM root length colonization were arcsine transformed for statistical analysis. In Experiment 1 the data for *P. sativum* (host plant) were subjected to a two-way analysis of variance. One factor was the plants species and the other factor was the period for which the non-host plants was grown alone before *P. sativum* was transplanted. The least square means test ( $P \leq 0.05$ ) was used to identify significant groups. The data for the non-host plants in experiment 1 and for all plants in the other experiments were analyzed by one-way analysis of variance and the Duncan's multiple range test ( $P \leq 0.05$ ).

### 3. Results

Non-significant differences were found between shoot dry weight of *P. sativum* grown alone and grown together with *S. oleraceae*, *B. nigra* or *J. balticus* (Table 1). However, shoot dry weight of *P. sativum* was significantly greater when the host was cultivated together with *U. dioica* or with *C. album* (Table 1). Shoot dry weight of *P. sativum* grown together with *S. oleraceae*, *U. dioica* or *C. album* was lower when the host was transplanted after 10, 20 and 30 d with *S. oleraceae* and *U. dioica* and after 30 d with *C. album*. There were no significant differences when *P. sativum* was grown with *B. nigra* or *J. balticus* after any period (Table 1). The dry weight of non-host plants cultivated together with *P. sativum* increased significantly when *P. sativum* plants were planted with 20- and 30-d-old non-host plants (Table 1).

As Table 2 shows, percentage AM root length colonization in *P. sativum* was significantly lower when the host plants were transplanted to pots in which the non-host had been grown for 10, 20 or 30 d. The percentage of AM root length colonization in *P. sativum* grown alone was similar to that of the host plant transplanted to pots at the same time as *C. album*, *B. nigra* or *J. balticus*, and higher when it was cultivated at the same time as *U. dioica* or *S. oleraceae* (Table 2). The reduction in percentage AM root colonization in

*P. sativum* increased with the age of the non-host plant at the moment when the host was transplanted (Table 2).

Normal AM colonization, with the presence of hyphae, arbuscules and vesicles in *P. sativum* root, was observed in all treatments in which non-host roots were present. No mycorrhizal colonization was observed in the roots of any non-host plants tested; however, more external hyphae and fewer aborted entry points were observed when host and non-host plants were transplanted at the same time than when long periods elapsed until the transplantation of *P. sativum* to the non-host pot (data not shown).

The percentage of AM root length colonization in *P. sativum* transplanted 30 d after non-host plants and then grown for 60 d with the non-host decreased significantly in the presence of all non-host plants (Table 3). The presence of *T. officinale* increased the percentage of AM root length colonization in *P. sativum*, but *P. sativum* did not affect the percentage of root length colonization in *T. officinale* (Table 3).

Table 3

Percentage arbuscular mycorrhizal colonization of *Pisum sativum* transplanted 30 d after the host *Taraxacum officinale* and the non-host plants (Companion plants). Both plants in each pot were then grown together for 60 d<sup>a</sup>

Plant combination	Percent root length colonization	
	<i>P. sativum</i>	companion plant
<i>P. sativum</i>	65c	73a
<i>T. officinale</i>	81d	76a
<i>S. media</i>	30b	0
<i>B. campestris</i>	47b	0
<i>C. bursa-pastoris</i>	11a	0
<i>S. altissimum</i>	32b	0
<i>C. album</i>	8a	0
<i>S. oleraceae</i>	45b	0
<i>B. nigra</i>	9a	0
<i>U. dioica</i>	7a	0

<sup>a</sup> Column values followed by same letter are not significantly different according to Duncan's multiple range test ( $P \leq 0.05$ ).

Table 4

Shoot dry weight and percentage of arbuscular mycorrhizal root length colonization of *Pisum sativum* grown with half of its root on each side of the split pot for 30 d after *Urtica dioica* and *S. oleraceae* in a double pot system<sup>a</sup>

Plant combination	Shoot dry weight	Percent root colonization	
		right pot	left pot
<i>P. sativum</i> with <i>U. dioica</i> in left pot	410a	32b	6a
<i>P. sativum</i> with <i>S. oleraceae</i> in left pot	370a	35b	4a
<i>P. sativum</i> without non-host plant in left pot	480a	40b	50b

<sup>a</sup> For each non-host combination column values followed by the same letter are not significantly different according to Duncan's multiple range test ( $P \leq 0.05$ ).

Non-significant differences were found in shoot dry weight of *P. sativum* grown in the double pot system in the presence and in the absence of *U. dioica* (Table 4). A significant decrease in the percentage of AM colonization in the left-side root of *P. sativum* was observed in the presence of *U. dioica*. However, the differences in the percentage of AM colonization in the right-side root of *P. sativum* were not significant when the left-side root was in the presence or in the absence of *U. dioica* roots (Table 4).

The number of propagules of *G. mosseae* inoculated to sand-vermiculite pots increased significantly after harvest of the host *P. sativum*, *A. arvensis* and *T. officinale* and decreased after harvest of the non-hosts *C. bursa-pastoris*, *B. campestris*, *B. nigra* and *S. altissimum* (Table 5). The percentage of root length colonization of *M. sativa* plants was lower when plants were grown in pots in which the non-hosts *B. campestris* (inoculum potential 0.21 propagules ml<sup>-1</sup> of sand-vermiculite) and *B. nigra* (inoculum potential 0.19 propagules ml<sup>-1</sup> of sand-vermiculite) were grown. Prior culture of *A. arvensis* increased the inoculum potential of *G. mosseae* and the percentage of root colonization of *M. sativa*; however, no difference was found in the percentage of root length colonization between *M. sativa* plants grown in pots with inoculum potentials of 15.8 to 0.43 propagules ml<sup>-1</sup> sand-vermiculite (Table 5).

#### 4. Discussion

All of the non-host plant families used in our study have been described as non-mycorrhizal (Harley and Harley, 1987; Koide and Schreiner, 1992; Vierheilig et al., 1996). Although some AM colonization has been described in some Caryophyllaceae, Chenopodiaceae and Polygonaceae, in *C. bursa-pastoris*, and in several *Sisymbrium* species of the Brassicaceae family (DeMars and Boerner, 1994; Francis and Read, 1994), in our study none of the non-host plants inoculated with *G. mosseae* and cultivated under our experimental conditions showed mycorrhizal colonization.

The competitive effect of non-hosts on the dry weight of *P. sativum* increased with the age of the non-host plants, and with their negative effect on the AM colonization of host plant roots. The capacity of hosts to compete against non-host plants was reported to be influenced by the mycorrhizal status of the host plants (Ocampo, 1986).

The roots of non-host plants that were grown together with host plants at same time, showed some internal hyphae and aborted entry points as was observed in other Brassicaceae and Chenopodiaceae plants cultivated together with host plants (Ocampo et al., 1980). When host plants were grown together with non-host plants, mycorrhizal colonization of host plants was not inhibited and in some cases was

Table 5

The most probable number (MPN) of infective propagules of *Glomus mosseae* after host and non-host plant culture and percentage of root length colonization of *Medicago sativa* grown in sand-vermiculite pots with different inoculum potentials<sup>a</sup>

Plants	MPN of propagules ml <sup>-1</sup> of sand-vermiculite	Percent root length colonization
Control	1.84d	20b
<i>P. sativum</i>	15.12e	27bc
<i>A. arvensis</i>	18.41e	32c
<i>T. officinalis</i>	15.82e	18b
<i>C. bursa-pastoris</i>	0.91c	28bc
<i>B. campestris</i>	0.21a	2a
<i>B. nigra</i>	0.19a	2a
<i>S. altissimum</i>	0.43b	20c

<sup>a</sup> Columns values sharing the same letter are not significantly different according to the new Duncan's multiple range test ( $P \leq 0.05$ ).

increased (Ocampo et al., 1980); in fact, AM colonization of the host *P. sativum* was greater when this plant was grown at the same time as the non-hosts *S. oleraceae* and *U. dioica*. The absence of AM colonization of the non-host plants may be due to intrinsic inhibitory factors (Ocampo et al., 1986). However, when non-host plants were grown for 30 d before *P. sativum*, all non-host plants inhibited mycorrhizal colonization in *P. sativum*. The inhibition of AM colonization of host plants by non-host plants has been documented under certain field and greenhouse conditions (Hayman et al., 1975; El-Atrach et al., 1989; Vierheilig et al., 1995a,b). Non-host roots can compete with the host plant root, thus reducing the root system of the host to degree a that can limit the chance for contact between fungus and root. However, plants of the same family, such as *B. campestris* and *B. nigra*, have different degrees of inhibition of AM colonization of *P. sativum*. Inhibition by volatile substances produced by non-host plants has also been described; however, these inhibitory substances are present in several plants of the Brassicaceae family but not in the non-host Chenopodiaceae (Vierheilig and Ocampo, 1990). These findings therefore cannot fully explain the nature of the inhibitory substances produced by all the non-host plants tested in our experiments.

Although we do not know the nature of the inhibitory substances produced by the non-host plants we tested, the null effect on mycorrhizal colonization on the non-exposed root side of *P. sativum* when the other root side was exposed to the non-host plant in split pot experiments suggest that these substances are non-systemic. The finding that non-host plants were able to decrease the inoculum potential of soils indicates that the substances produced by non-host roots may have a negative effect on AM fungi in soils (Wulff, personal communication). Different non-host plants decreased the inoculum potential of *G. mosseae* inoculated into sand-vermiculite pots to different degrees; in some cases the decrease was sufficient to decrease the percentage AM colonization of host plants cultivated after the non-host plants. We have also noted that the host *A. arvensis* increased the inoculum potential in different soils, whereas the non-hosts *C. bursa-pastoris* decreased the potential under different plant growth conditions (data not shown; Wulff, personal communication). The previous growth of non-mycorrhizal plants in soil can have a detrimental effect on the subsequent infectivity of AM fungi in some cases but not in others (Brundrett, 1991). However, although the non-hosts *C. bursa-pastoris* and *S. altissimum* decreased inoculum potential, they did not decrease the percentage AM colonization of alfalfa plants. The decrease in inoculum potential caused by non-host plants therefore does not entirely explain the decrease in AM colonization of *P. sativum* roots when

host plants were grown in the presence of mature non-host plants. One study has found evidence in the rhizosphere of some non-host plants of AM inhibitory compounds that appear to affect the spread of mycorrhizal fungi in soil (Vierheilig et al., 1995).

The results of our coculture experiments support the hypothesis that the roots of non-host species produce substances that, depending on the amount that reaches the rhizosphere, can stimulate or inhibit the establishment of AM fungi in host roots. These compounds appear to affect the AM fungi before they become established in the root and are apparently non-systemic in nature. Future studies should help to elucidate the characteristics of these substances.

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