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Effect of soil volume and plant density on mycorrhizal infection and growth response

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Summary The effect of soil volume and plant density on mycorrhizal infection and growth response was studied with onion. There was a significant negative correlation between percentage vesicular-arbuscular mycorrhizal infection and root density. The growth response due to mycorrhiza decreased when less soil was available for the plant. The root : shoot ratio decreased with increasing plant density in both mycorrhizal and non-mycorrhizal plants. Pot size did not affect the root : shoot ratio.

Introduction

The extent to which a plant benefits from mycorrhiza, which is expressed mainly as increased phosphate uptake and growth, can be different when it is grown alone than when another plant species is present. This occurs when both species are host plants for vesicular-arbuscular (VA) mycorrhizal fungi[3,4], and when one of the species is a non-host[6,7,11]. In addition, the amount of VA mycorrhizal infection that develops in a given plant is affected by adjacent species[2,3,4,9,11]. The reasons for these observations are not fully understood, but inhibitory effects could result from toxic chemicals in the exudates or seed coats of certain species[10], for example, or from physical competition by the roots of each species for a limited supply of soil nutrients. That root competition may influence mycorrhizal activity is likely because it has been shown that, for plants grown in pots, the volume of soil available to a plant affects its uptake of phosphate[1,8]. To investigate this aspect further, and to avoid the complication of interspecific interactions, a study on the effect of different soil volumes (*i.e.* pot size) and different plant densities on a single plant species, with and without mycorrhiza, was therefore undertaken.

Materials and methods

Three-week-old onion seedlings, *Allium cepa* L., cv. Ailsa Craig, were transplanted to a sand : soil mixture consisting of 40% autoclaved sand, 10% autoclaved grit, and 50% γ-irradiated (1.1 Mrad) soil from Sawyers field at Rothamsted (the soil contained 10 mg kg^{-1} $NaHCO_3$-soluble P). The mixture was supplemented with 0.55 g KNO_3, 0.087 g $MgSO_4 . 7H_2O$, 0.056 g K_2HPO_4 and 0.58 g lime per Kg which raised the pH to about 6.5.

Three factors were studied, namely pot size (diameter 7.5 cm, 10.0 cm and 12.5 cm, contaning 200 cm^3, 450 cm^3 and 900 cm^3 of soil:sand mixture, respectively), plant density (1,

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Table 1. Volume of soil:sand mixture available per plant (cm^3 soil/plant) in the different treatments. 12 volumes, ± mycorrhizal inoculation, giving 24 treatments in total. Symbols match those in Figs. 1 and 2

No plants/pot	cm^3 soil/pot		
	●	■	▲
	200	450	900
1	200	450	900
3	67	150	300
6	33	75	150
12	17	38	75

3, 6 and 12 seedlings per pot) and mycorrhizal status (with and without VA mycorrhiza). This gives a total of 24 treatments (Table 1). The mycorrhizal inoculum consisted of a mixture of spores, mycelium and roots infected with *Glomus mosseae* (Nicol and Gerd.) Gerd. and Trappe and *Glomus caledonium* (Nicol. and Gerd.) Trappe and Gerd. About 0.5 g of inoculum was placed in the soil beneath each seedling. Some inoculum was washed on filter paper and the filtrate given to all pots to ensure that the controls received the normal microflora associated with the inoculum. Each treatment was replicated four times.

Plants were harvested after 11 weeks. Dry weights of roots and shoots were determined after drying at 80°C. Part of each root system was used to estimate total root length and mycorrhizal infection after clearing and staining[12]. The results were analyzed with a 2-factor analysis of variance for mycorrhizal and non-mycorrhizal plants separately.

Results and discussion

Usually less infection was found per seedling when smaller pots or higher planting densities were used. There was a significant negative correlation ($p < 0.05$) between percentage VA mycorrhizal infection and root density (Fig. 1). VA mycorrhizal infection decreased from about 65% at the lowest root density to 55% at the highest root density. These findings suggest that root density may also be an important factor in certain interspecific interactions resulting in less infection, *e.g.* in normally strongly mycorrhizal plants like onion growing with other VA mycorrhizal hosts such as lettuce[11].

It has been reported[13] that the rate of spread of VA mycorrhizal infections between plants is much affected by root density. However, in the present study, any differences in rate of spread of VA fungi in the soil cannot explain the differences in % VAM infection because each seedling was inoculated individually. Possibly changed soil P levels affected infection, because plants can take up P more effectively from small pots than from large ones[1,8].

The root:shoot ratio was always smaller in mycorrhizal plants (mean 0.56) than in non-mycorrhizal plants (0.87). Pot size did not affect the root:shoot ratio. However, increasing plant density significantly ($p < 0.01$) decreased the root:shoot ratio in the mycorrhizal plants from 0.60 with 1 plant per pot to 0.47 with 12 plants per pot. The corresponding values for non-mycorrhizal plants were 1.0 to 0.71. A similar decrease was found by Fitter[4] when *Lolium perenne* was grown together with *Holcus lanatus.*

No statistically significant interactions between pot size and plant density were found for dry weight of shoot, dry weight of root or root: shoot ratio. Thus these values were constant per given volume of soil per plant, whether the volume was changed by pot size or by planting density.

The average shoot dry weight of a mycorrhizal plant was 130 mg (range = 38 to 243 mg) and of a non-mycorrhizal one 16 mg (range = 14 to 18 mg). The dry weight ratio of mycorrhizal to non-mycorrhizal plants, *i.e.* the growth response due to VA mycorrhiza, changed

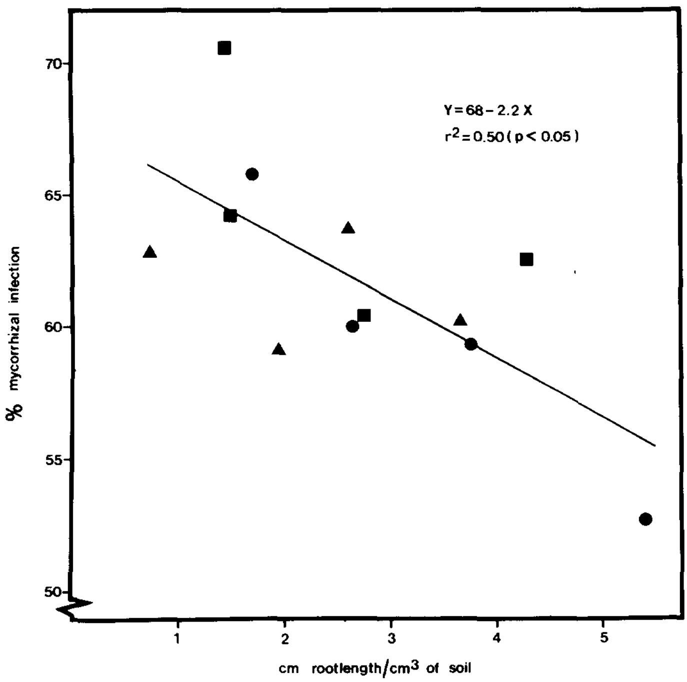

Fig. 1. The influence of root density on percentage mycorrhizal infection. ● = 7.5 cm pot, ■ = 10 cm pot and ▲ = 12.5 cm pot.

considerably between treatments. Ratios ranged from 2.4 to 17.2 for shoot dry weights and from 1.9 to 9.6 for root dry weights.

The ratio of mycorrhizal to non-mycorrhizal shoot dry weights appeared to increase with available soil volume up to about 400 cm^3 soil per plant and then to level off to a constant value (Fig. 2). The interpretation from these data that the maximum mycorrhizal effect was reached below 900 cm^3 soil mixture per plant is also based on other observations with onions grown under similar conditions. This effect was irrespective of whether the available soil volume was changed by plant density or by pot size. The same trend was found for root dry weights. Hence, although a significant mycorrhizal response was found in all treatments, the actual growth increment due to VA mycorrhiza was highly dependent on the size of the pot and on the number of plants growing in each pot. This confirms earlier observations[5] that mycorrhizal benefits disappeared when several plants were grown together in a pot such that the P-depletion zones around their roots overlapped.

These results on mycorrhizal growth effects have two important implications. Firstly, they point to the difficulties intrinsic to making comparisons between pot trials from different studies, because the size of a reported mycorrhizal response tells us little beyond showing that a mycorrhizal response is possible under the growing conditions used. Secondly, the volume of soil available to a plant under field conditions is quite different to that available to a plant growing in a pot, which could be one reason for the different results often obtained in glasshouse and field experiments on inoculation with VA mycorrhizal fungi.

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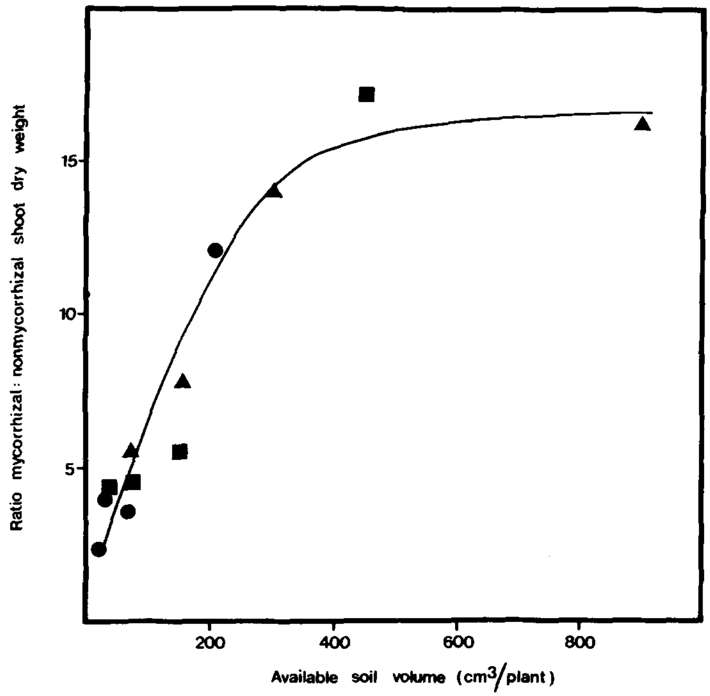

Fig. 2. Effect of available soil volume per plant on the mycorrhizal : non-mycorrhizal shoot ratio of onions in Sawyers soil. Graph fitted by hand. ● = 7.5 cm pot, ■ = 10 cm pot and ▲ = 12.5 cm pot.

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