

## VESICULAR-ARBUSCULAR MYCORRHIZAL INFECTION OF "HOST" AND "NON-HOST" PLANTS: EFFECT ON THE GROWTH RESPONSES OF THE PLANTS AND COMPETITION BETWEEN THEM

J. A. OCAMPO

Soil Microbiology Department, Estación Experimental del Zaidin, Professor Albareda 1,  
18008 Granada, Spain

(Accepted 1 June 1986)

**Summary**—The effect of host plant infection on the mycorrhizal response of non-host plants was examined in a double pot system. The absence of nutrient transfer from a mature host (sorghum) to a young non-host (cabbage) indicates the inability of the atypical infection of non-host plants to take up nutrients. However, nutrient transfer between mature and young sorghum plants, possibly through mycelial connections, was observed. The direction of this nutrient transfer seemed to depend on the nutrient status of the nurse plant. Because the nurse plants were grown in P-deficient soil, mature sorghum competed with young sorghum plants. Sorghum infected with vesicular-arbuscular (VA) mycorrhiza was better equipped than non-infected sorghum to compete with young cabbage for soil nutrients.

### INTRODUCTION

Vesicular-arbuscular (VA) mycelial connections have been observed between plants of the same species (Hirrel and Gerdemann, 1979; Whittingham and Read, 1982) and between plants of different species (Heap and Newman, 1980). Such connections permit measurable nutrient transfer from well-developed mature nurse plants to young sink plants (Whittingham and Read, 1982). In addition, slight mycorrhizal infections have been reported to develop in non-host plants when a mycorrhizal host plant was present (Hirrel *et al.*, 1978; Ocampo *et al.*, 1980). Cortical mycelium and vesicles (but not arbuscules) developed in the non-host plants and there were many clumps of endophyte mycelium on the root surfaces, usually attached to entry points (Ocampo *et al.*, 1980). This suggests that non-host plants may be responsive to mycorrhizal infection; an effect mediated through nutrient transfer from host plants by mycelial connections. However, if plants are interconnected in this way, competition for mineral nutrients, especially phosphorus, may be more dependant upon the ability of each plant to extract nutrients from the fungus rather than from the soil (Newman, 1978). In fact, when two species grew together, VA mycorrhiza favoured one species more than the other; this effect was enhanced by plant competition for nutrients, especially P (Crush, 1974; Fitter, 1977; Hall, 1978). We have examined the possibility of nutrient transfer between "host" and "non-host" plants via mycorrhizal hyphae and considered the importance of mycorrhizal infection on plant competition.

### MATERIALS AND METHODS

The experiments were carried out in open pots of P-deficient soil (Barea *et al.*, 1980). The soil was steam-sterilized, mixed with 25% (w/w) of sterile

sand. Sorghum (*Sorghum vulgare* L.) and cabbage (*Brassica oleraceae* L.) were the test plants. They were inoculated with soil from stock plant cultures of *Glomus mosseae* which contained spores, mycelium and infected root fragments. Five-g of such inoculum were added per pot. There were also VA uninoculated controls which received the filtrate from the inoculum.

Seedlings were transplanted into pots containing 250 g of the soil-sand mixture and grown in a glasshouse at 19–25°C for 3 months, during which time the inoculated plants became infected by mycorrhizal fungi. Inoculated and uninoculated plants were then transferred to specially designed pots.

#### Experiment 1

Leonard jars (Vincent, 1970) with 250 g of sterilized sand-vermiculite mixture (1:1, v/v) in the top section were used to form a double-pot system (Fig. 1a) (Menge *et al.*, 1978). The 3 month-old mycorrhizal and non-mycorrhizal sorghum plants were placed in each pot in such a way that approximately half of their root system was situated on each side (inner and outer pots). The pots were kept in a glasshouse for 2 weeks while plants became established. Then, 2-week-old cabbage seedlings were planted in the outer pot. There were three treatments: (1) mycorrhizal source plant supplied with a diluted (1/2) Hewitt's nutrient solution from the bottom of the Leonard jars (M); (2) non-mycorrhizal source plants supplied in the same way (NM), and (3) mycorrhizal source plant supplied with distilled water (M-DW) in outer jars. All sink plants (cabbage) received distilled water. Twenty weeks after transplanting, plants were harvested and the shoot dry weights, recorded.

#### Experiment 2

Three-month-old sorghum plants (VA inoculated and uninoculated) were planted in a double-pot

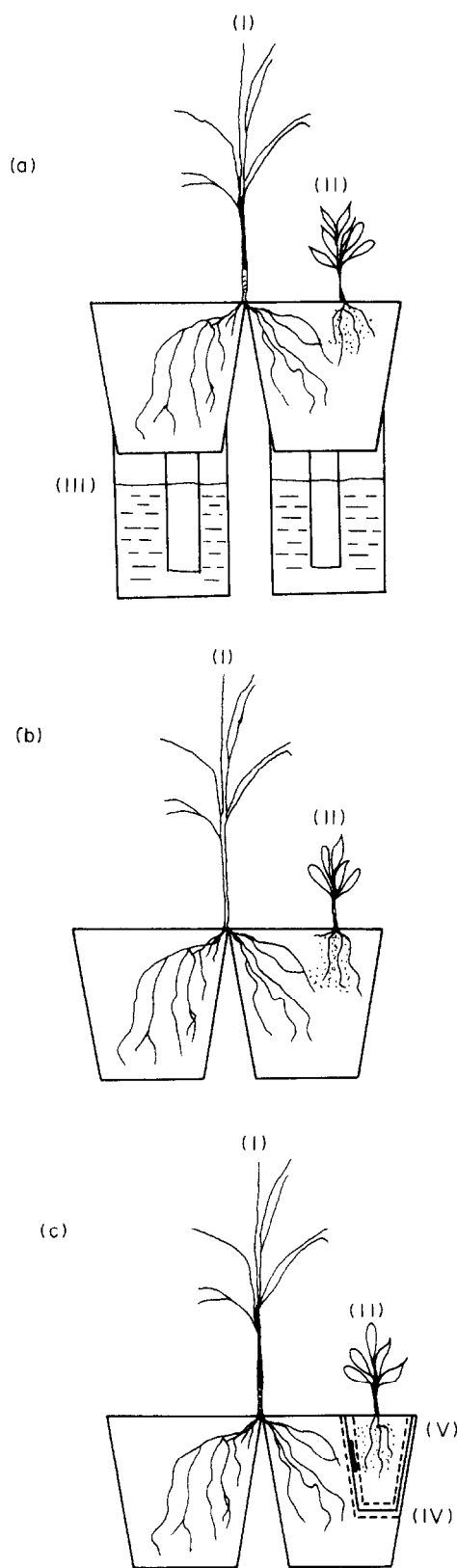


Fig. 1. Pot systems: (a) double Leonard jars; (b) double pot system; (c) double pot system with mature and young roots separated; (I) mature plant; (II) young plant; (III) nutrient solution or distilled water; (IV) nylon mesh; (V) Millipore filter.

Table 1. Experiment 1. Shoot dry wt (mg) of nurse sorghum and sink cabbage plants grown in a double Leonard jar system

Treatments	Sorghum	Cabbage
M + DW	533a	250a
NM + NS	12622b	285a
M + NS	12866b	240a

M + DW = mycorrhizal plants supplied with distilled water. NM + NS = minus mycorrhiza plus nutrient solution incl. P; M + NS = with inoculum of VA mycorrhizas plus nutrient solution incl. P. Numbers in same column followed by same letter are not significantly different at  $P = 0.05$  using Duncan's multiple-range test.

system (Menge *et al.*, 1978) in which both inner and outer sections were filled with 500 g of the sterilized soil:sand mixture described above (Fig. 1b). One mature sorghum plant was placed in each pot, so that approximately half its root system was in each pot. These pots were kept in a glasshouse for 2 weeks while plants became established, after which a 2-week-old cabbage or sorghum seedling was planted in the outer pot.

Once a fortnight during the following 16 weeks plants in the inner pots received 10 ml of a nutrient solution (Hewitt's) lacking P.

The treatments tested were as follows: mature sorghum plus young cabbage (H + nh); mature sorghum plus young sorghum (H + h); mature sorghum (H) grown alone in a double pot system; young sorghum (h) and cabbage (nh) grown alone in single 250 g pots. In a third system (Fig. 1c) young plants were separated from mature plants by a pot with a lateral hole in which was placed a Millipore filter (3  $\mu$ m pore dia) protected by a sandwich of nylon mesh (50  $\mu$ m mesh) to prevent contact between plant roots but allow passage of nutrients. There were two treatments: mature sorghum plant plus young sorghum plant (H/h) and mature sorghum plant plus

Table 2. Experiment 2. Shoot dry wt (mg) of VA inoculated and uninoculated sorghum and cabbage plants in the double-pot system

Plant combination	Shoot dry wt (mg)	
	NM not inoculated	M inoculated
(1) H <sup>1</sup> (mat. sorghum) + nh (cabbage)	1233a 800b	2432a 235b
(2) H (mat. sorghum) + h (young sorghum)	1600c 632d	2364a 736c
(3) H <sup>2</sup> (mat. sorghum) — nh (cabbage)	1100a 830b	2366a 665e
(4) H <sup>2</sup> (mat. sorghum) — h (young sorghum)	1460c 732e	2413a 1010d
(5) H (mat. sorghum)	1700c	2402a
(6) h (young sorghum)	863e	1163d
(7) nh (cabbage)	937b	738e

NM = minus mycorrhiza; M = with inoculum of VA mycorrhizas; Numbers in same column followed by same letter are not significantly different at  $P = 0.05$  using Duncan's multiple-range test. <sup>1</sup>For notation, see Material and Methods. <sup>2</sup>Plants were separated by a Millipore filter.

Table 3. Experiment 2. Shoot N, P, K, Ca and Mg contents (% dry matter) of VA inoculated and uninoculated sorghum and cabbage plants grown in double pot system

	Plant combination	Content (% dry matter)									
		NM not inoculated					M inoculated				
		N	P	K	Ca	Mg	N	P	K	Ca	Mg
(1)	H (mat. sorghum)	0.91a	0.08a	3.5a	0.60a	0.25a	2.72a	0.22a	6.5a	3.55a	1.47a
	+ (cabbage)	1.91e	0.18e	4.3e	1.70e	0.34e	0.63d	0.05d	1.4d	0.40d	0.10d
(2)	H (mat. sorghum)	1.26b	0.11b	4.5b	1.14b	0.58b	2.74a	0.23a	6.2a	3.50a	1.36a
	+ (young sorghum)	0.70c	0.06c	3.4a	0.45c	0.14c	0.90b	0.08b	4.1b	0.61b	0.32b
(3)	H (mat. sorghum)	0.97a	0.08a	3.5a	0.65a	0.27a	2.71a	0.22a	6.3a	3.52a	1.12a
	— (cabbage)	1.80e	0.17e	4.1e	1.61e	0.30e	1.89e	0.19e	4.4e	1.65e	0.35e
(4)	H (mat. sorghum)	1.16b	0.10b	4.4b	1.10b	0.50b	2.70a	0.22a	6.1a	3.48a	1.37a
	— (young sorghum)	0.71c	0.07cd	3.4a	0.51c	0.16cd	1.33c	0.15c	5.2c	1.16c	0.32c
(5)	H (mat. sorghum)	1.36b	0.12b	4.7b	1.18b	0.57b	2.75a	0.23a	6.7a	3.62a	1.50a
(6)	h (young sorghum)	0.80c	0.07d	3.6a	0.58c	0.20cd	1.35c	0.16c	5.1c	1.19c	0.37c
(7)	nh (cabbage)	1.95e	0.19e	4.3e	1.72e	0.32e	1.90e	0.18e	4.5e	1.70e	0.36e

Legend as for Table 2.

young cabbage plant (H/nh), with five replicate pots per treatment.

After 16 weeks, plants were harvested and shoot dry matter recorded. Root samples of each replicate were cleared and stained (Phillips and Hayman, 1970) and mycorrhizal infection assessed on 30 random 1 cm root segments per replicate at  $\times 160$  magnification (Ocampo *et al.*, 1980).

## RESULTS

### Experiment 1

Table 1 shows that differences in yields of the young cabbage plants between treatments were not significant.

### Experiment 2

A significant decrease in the yields (Table 2) and nutrient concentrations (Table 3) of the young non-host cabbage (nh) plants when grown with VA infected mature sorghum (H) plants. There was no significant decrease in the shoot dry wt and nutrient concentrations of the young non-host (nh) plants either when the mature host (H) plant was uninoculated or when there was no root contact between both plants (H/nh).

The young sorghum (h) plants showed a significant decrease when grown with a mature host (H), but this decrease was not significant when there was no root contact (H/h). The concentration of nutrients, especially P, in shoot tissues was higher for the non-host (nh) than for the uninoculated host plants (H and h) (Table 3).

There were no significant differences in the VA mycorrhizal infection of the young host (h) plants ( $46.4 \pm 4.4$ ) in any of the treatments tested. However, there was slight mycorrhizal infection in the young non-host (nh) plants, but only when grown together with host plants ( $3.8 \pm 1.2$ ).

## DISCUSSION

Mycorrhizal infection in non-host plants when grown near infected host plants has been observed

(Hirrel *et al.*, 1978; Ocampo *et al.*, 1980), but no nutrient transfer from mature host plants to young non-host plants has been detected (Tables 1 and 3). The low level of infection and the absence of arbuscules within the non-host plants suggest that this type of infection may not be active in nutrient transfer. However, the presence of many clumps of endophyte mycelium (possibly originating from the infected host plants) on their root surfaces could have increased the nutrient depletion zone (mainly with respect to P) around the non-host root (Hayman, 1983) thereby decreasing the growth of these plants more than when the external mycelium was not in contact with the non-host plant rhizosphere (Table 2).

My results indicate that mycelial linkage between plants may be an important mechanism of nutrient transfer between plants which is in agreement with the findings of Whittingham and Read (1982). However, nutrient transfer between plants might be different when the nurse plants differ markedly in nutrient status, because as the nurse plants were grown in soil with nutrient solution lacking P, mature infected plants competed with young plants for nutrients; this competition would have been less when there was no contact between roots of both plants. It is known that VA mycorrhizas could influence the balance between species in a community by favouring the species dependent on mycorrhizal infection when growing in low P soils (Reeves *et al.*, 1979; Janos, 1980). In that way VA mycorrhizal mature sorghum was better equipped than non-VA infected mature sorghum to compete with young cabbage for soil nutrients. VA mycorrhizas induced a depression of growth in cabbage by increasing the growth of sorghum and its ability to compete with cabbage. However, when plant species grow together in the absence of mycorrhizal fungi, species that do not respond to mycorrhizal infection or are normally not infected are likely to dominate plant communities on poor soils (Janos, 1980). In the present study, young cabbage plants competed successfully with sorghum when the

latter were not VA infected. This may be related to their superior ability to take up P from soil in the absence of fungal symbionts (Schwab *et al.*, 1984).

*Acknowledgements*—I thank Dr D. S. Hayman, Rothamsted Experimental Station, England and Dr J. M. Barea, Estación Experimental del Zaidín, Spain, for helpful advice, criticism and for grammatical correction of the manuscript. Financial support for this study has been obtained from Comisión Asesora de Investigación Científica y Técnica.

#### REFERENCES

- Barea J. M., Escudero J. L. and Azcon-Aguilar C. (1980) Effects of introduced and indigenous VA mycorrhizal fungi on nodulation, growth and nutrition of *Medicago sativa* in phosphate-fixing soils as affected by P fertilizers. *Plant and Soil* **54**, 283–296.
- Crush J. R. (1974) Plant growth responses to vesicular-arbuscular mycorrhiza. VII Growth and nodulation of some herbaceous legumes. *New Phytologist* **73**, 743–752.
- Fitter A. H. (1977) Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. *New Phytologist* **79**, 119–125.
- Hall I. R. (1978) Effects of endomycorrhizas on the competitive ability of white clover. *The New Zealand Journal of Agricultural Research* **25**, 509–515.
- Hayman D. S. (1983) The physiology of vesicular-arbuscular endomycorrhizal symbiosis. *Canadian Journal of Botany* **61**, 944–963.
- Heap A. J. and Newman E. I. (1980) Links between roots by hyphae of vesicular-arbuscular mycorrhizas. *New Phytologist* **85**, 169–171.
- Hirrell M. C. and Gerdemann J. W. (1979) Enhanced carbon transfer between onions infected with a vesicular-arbuscular mycorrhizal fungus. *New Phytologist* **83**, 731–738.
- Hirrell M. C., Mehravaran H. and Gerdemann J. W. (1978) Vesicular-arbuscular mycorrhizae in Chenopodiaceae and Cruciferae: Do they occur? *Canadian Journal of Botany* **56**, 2813–2817.
- Janos D. P. (1980) Mycorrhizae influence tropical succession. *Biotropica* **12**, 56–64.
- Newman E. I. (1978) Root microorganisms: their significance in the ecosystem. *Biological Reviews* **53**, 511–554.
- Ocampo J. A., Martin J. and Hayman D. S. (1980) Influence of plant interactions on vesicular-arbuscular mycorrhizal infections. I. Host and non-host plants grown together. *New Phytologist* **84**, 27–35.
- Phillips J. M. and Hayman D. S. (1970) Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Transaction of the British Mycological Society* **55**, 158–161.
- Reeves F. B., Wagner D., Moorman T. and Kiel S. (1979) The role of endomycorrhizas in the revegetation practices in the semi-arid west. I. Comparison of incidence of mycorrhizae in severely disturbed VS natural environments. *American Journal of Botany* **66**, 6–13.
- Schwab S. M., Leonard R. T. and Menge J. A. (1984) Quantitative and qualitative comparison of root exudates of mycorrhizal and mycorrhizal plant species. *Canadian Journal of Botany* **62**, 1227–1231.
- Vincent J. M. (1970) *A Manual for the Practical Study of the Root-Nodule Bacteria*. IBP Handbook No. 15. Blackwell, Oxford.
- Whittingham J. and Read D. J. (1982) Vesicular-arbuscular mycorrhiza in natural vegetation systems. III. Nutrient transfer between plants with mycorrhizal interconnections. *New Phytologist* **90**, 277–284.