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Growth responses of several plant species to mycorrhizae in a soil of moderate P-fertility

I. Mycorrhizal dependency under field conditions*

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Summary The growth of twenty plant species was compared under field conditions in a methyl bromide fumigated and non-fumigated soil. The non-fumigated soil had a wild endomycorrhizal flora and contained 100 µg/g of available phosphorus. No phosphorus was added to the soil but both fumigated and non-fumigated plots received a basal fertilization of 100 kg/ha N–NH_4NO_3 and 100 kg/ha K–KCl. Based on plant growth responses, three groups of plants were distinguishable. Plants from group I were mycorrhizal and had better growth in non-fumigated than in the fumigated soil. This group was the most important, including sixteen plant species. Stunting of plants from group I following soil fumigation was mainly attribuable to the destruction of mycorrhizae. Plants from group II (oat and wheat) grew equally well in non-fumigated and fumigated soils. For these plants which were mycorrhizal in the non-fumigated plots, the P-content of the soil was sufficient for growth and therefore no stunting was observed in the absence of mycorrhizae. Plants from group III (cabbage and garden beet) grew better in fumigated than in non-fumigated soil. Their better growth in fumigated soil was tentatively attributed to the destruction of soil-borne pathogens. They did not form mycorrhizae in non-fumigated soil.

A new method of calculating mycorrhizal dependency is proposed, and the value calculated was named relative field mycorrhizal dependency (RFMD) index. It is also proposed that the acronym RFMD receive a superscript representing in µg/g the quantity of available P in the soil. Carrot with its characteristic root systems had the highest $RFMD^{100}$ index (99.2%), but other plants with high phosphorus requirements for normal growth had a wide range of $RFMD^{100}$ index values.

Introduction

According to Gerdemann [8], in nature the mycorrhizal condition is the rule and the non-mycorrhizal condition the exception. Even though about 90% of plant species form endomycorrhizae, there is a wide range of plant responses to

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vesicular arbuscular (VA) mycorrhiza. It has been shown consistently that different plant species differ in their nutrient requirement and that VA mycorrhizal plants have better phosphorus nutrition than non-mycorrhizal plants[23,36]. Hence it can be expected that plants requiring higher P-fertilization would benefit from the VA mycorrhizal symbiosis more than plants having low phosphorus requirements.

Baylis[1] suggested that mycorrhizae control the evolution of roots and this explains why plants with magnolioid root systems are more dependent upon mycorrhizae for phosphorus uptake than plants with graminoid root systems. The same author reported that cultivated tomato that does not show phosphorus deficiency symptoms has about twice the P-concentration of wild unselected species. Consequently, selection of crop plants could result in plants that are dependent upon high P fertilization and require mycorrhizae to meet their P requirements in low P soils. The mycorrhizal dependency of a plant is certainly related to the soil fertility, and we think that if in general plants are known to be dependent on mycorrhizae according to the morphology of their root systems, the determination of the dependency value must be considered in relation to the ecological conditions. According to Gerdemann[9], mycorrhizal dependency is the degree to which a plant relies upon the mycorrhizal condition to produce its maximum growth or yield at a given level of soil fertility. Menge *et al.*[21] defined this parameter numerically as the ratio of dry mass of a mycorrhizal plant to a non-mycorrhizal plant expressed as a percentage. Plants in the Chenopodiaceae and Cruciferae do not normally form mycorrhizae[12] and would not be classified as mycorrhiza dependent, but other plants such as *Leptospermum scoparium* are highly mycorrhiza dependent having a growth increase up to 13000% when mycorrhizal.

In some nurseries soil fumigation is an important method of controlling fungal pathogens, nematodes and weeds. For several years, nursery men have observed stunting of seedlings planted in fumigated soil[15,30,32]. Stunting of seedlings was attributed to the destruction of mycorrhiza by fumigation and its correction was possible by mycorrhizal inoculation of plants[3,19,20,34]. However, some citrus species are more tolerant of the absence of mycorrhiza than others[17,21,24,37] indicating that species within one genus can differ in mycorrhizal dependency.

Menge *et al.*[21] have demonstrated the mycorrhizal dependency of several citrus cultivars in low P-soil. Since the use of fertilizer is widely spread in agriculture, it is unusual to find an agricultural soil with a very low P-fertility. The purpose of this study was to determine the degree of mycorrhizal dependency of several plants species in a soil of moderate P-fertility under field conditions.

Materials and methods

The experiment was conducted in a nursery located at Pont-Rouge, 50 km northeast of Québec City, Canada, on a non-previously fumigated sandy loam. According to the System of Soil

Table 1. List of plant species studied and description of some corresponding experimental details

Plant species	Propagation	Experimental unit	Number of plants per row or seeding rate	Number of plants sampled per unit	Plant part harvested
Cabbage (*Brassica oleracea* L. var. Copenhagen Market)	B	plot (2 m × 2 m) with 2 rows	7	6	head
Carrot (*Daucus carota* L. var. Nantaise)	A	plot (2 m × 2 m) with 4 rows	D	4 × 0.25 m row section	root
Common Ninebark (*Physocarpus opulifolius* L. Maxim)	C	1 row (2 m)	9	3	shoot
Current (*Ribes alpinum* L. var. Smithii)	C	1 row (2 m)	9	3	shoot
Fababean (*Vicia faba* L.)	A	plot (2 m × 2 m) with 4 rows	D	12	shoot
Garden Beet (*Beta vulgaris* L. var. Dark Red)	A	plot (2 m × 2 m) with 4 rows	D	6	root
Garden Pea (*Pisum sativum* L.)	A	plot (2 m × 2 m) with 4 rows	D	6	shoot
Kidney Bean (*Phaseolus vulgaris* L. var. Brittle Wax)	A	plot (2 m × 2 m) with 4 rows	D	12	shoot
Leek (*Allium porrum* L. var. American Flag)	B	plot (2 m × 2 m) with 3 rows	19	12	shoot
Marigold (*Tagetes patulus* L. var. Golden Boy)	B	1 row (2 m)	9	3	shoot
Oat (*Avena sativa* L. var. Alma)	A	plot (2 m × 2 m) with 12 rows	90 kg/ha	4 × 0.50 m row section	shoot
Pepper (*Capsicum frutescens* L. var. Bell Boy)	B	plot (2 m × 2 m) with 2 rows	5	6	fruit
Potato	A	plot (2 m × 2 m)	11	1 m row	tuber

(*Solanum tuberosum* L. var. Belleisle)		with 3 rows		section	
Purple Leaf Sand Cherry	C	1 row (2 m)	9	3	shoot
(*Prunus cistena* M. E. Hansen)					
Slender Purple – Osier Willow	C	1 row (2 m)	9	3	shoot
(*Salix purpurea* L. var. Gracilis)					
Spirea	C	1 row (2 m)	9	3	shoot
(*Spiraea bumalda* L. var. Gold Flame)					
Sweet Corn	A	plot (2 m × 2 m)	D	6	shoot
(*Zea mays* L. var. Span Cross)		with 4 rows			
Tartarian Honeysuckle	C	1 row (2 m)	9	3	shoot
(*Lonicera tatarica* L. var. Hack's Red)					
Tomato	B	plot (2 m × 2 m)	2	4	fruit
(*Lycopersicum esculentum* Mill. var. Springset)		with 2 rows			
Wheat	A	plot (2 m × 2 m)	120 kg/ha	4 × 0.50 m	shoot
(*Triticum aestivum* L. var. Glenlea)		with 12 rows		row section	

A	Seeded in the field.
B	Seeded in sterilized topsoil in the greenhouse and transplanted to the field.
C	Cuttings rooted in vermiculite in the growth chamber and transplanted to the field
D	Seeded with a Planet JR. No. 300 A

Classification for Canada (Canada Soil Survey Committee) it belongs to the podzol humo-ferric orthic and was placed in the Morin series[28]. Soil analyses were done as described by Plenchette *et al.*[25]. The pH of the soil was 5.9. It contained 0.13% N (Kjeldahl), 100 μg/g P (Bray II), 150 μg/g K, 880 μg/g Ca, 24 μg/g Mg, 7.1 μg/g Mn, 1.2 μg/g Zn, 24 μg/g Fe, 1 μg/g Cu.

The experiment was carried out in 1980. Plants previously grown in this soil were Broom-Corn Millet (*Panicum miliaceum* L.) in 1979, potato (*Solanum tuberosum* L.) in 1978, and before that the soil was fallowed. Broom-Corn Millet roots were collected in September 1979 and were to be found intensely mycorrhizal. However, spores could not be observed readily.

The soil was plowed, disced and rototilled in spring 1980 and amended with a basal fertilization of 100 kg $N\text{-}NH_4NO_3$/ha and 100 kg K–KCl/ha. No phosphorus was added and the fertilizers were incorporated in the soil with a spring tooth harrow in order to prepare the seedbed.

A complete randomized block design with four replications was used, each block containing two treatments (fumigated and non-fumigated soil). The experimental units for the 20 plant species were randomly distributed in each half block. Dowfume MC-2 (98 percent methyl bromide and 2 percent chloropicrin) was used as fumigant at the rate of 45 g/m^2. It was applied on a sunny day at the end of May; the moisture of the soil was 19% (w/w). The parts of the soil to be fumigated were covered with a clear 100 μm (4-mil) polyethylene sheet. The tins containing 681 g each of methyl bromide were placed at appropriate intervals under the plastic sheet, the edges of which were buried in a 20 cm deep furrow to provide an efficient seal. The tins were punctured by pressing them manually against the applicator's steel pin. During the day, soil temperature varied between 12°C and 15°C at a depth of 15 cm at the time of fumigation. The polyethylene sheets were removed after 3 days and the plantation started one week later.

Table 1 enumerates the plant species cultivated, the methods of propagation, the size of the experimental units, the number of plants per unit, the size of the samples and the parts of the plants harvested. At harvesting time, three months later, samples of plants were oven dried (65°C, 48 h) and the dry mass was measured. Data were analyzed using analysis of variance. Root samples were collected from each plant at harvesting time for staining and for determination of the root endomycorrhizal colonization (REC) index expressed as a percentage of microscope fields showing endomycorrhizal structures[26].

Results

Most of the plant species used in this study had a better growth in non-fumigated soil (Table 2). On the basis of the yield difference between plants growing in fumigated and non-fumigated soils, it was possible to distinguish three groups of plants. Group I consisted of plants which had a better growth in non-fumigated soil than in fumigated soil. All the horticultural (including ornamental) species grown in fumigated soil were severely stunted, especially the carrots. Tomatoes and potatoes were stunted less in fumigated soil. Group II included oat and wheat plants which grew almost the same in both treatments. Group III included cabbage and garden beet plants which grew significantly better in fumigated soil than in the non-fumigated one. The roots of all plants growing in non-fumigated soil were colonized by VA mycorrhizae, except for cabbage, garden beet and slender purple-osier willow. No VA mycorrhizae were found in the root systems of cabbage and garden beet, but ectomycorrhizae were present on the root of slender purple-osier willow.

Table 2. Yield, relative endomycorrhizal colonization (REC) index and relative field mycorrhizal dependency (RFMD) index for some plant species cultivated in fumigated and non-fumigated soil containing 100 µg/g of available phosphorus

Group	Plant species	Dry mass/plant†		REC index (%)	$RFMD^{100}$ (%)
		Fumigated soil	Non-fumigated soil		
I	Tartarian Honeysuckle	0.6	7.3**	24	91.6
	Common Ninebark	0.7	6.9**	12	90.2
	Slender Purple-Osier Willow	1.2	6.1**	ecto-mycorrhizae	80.2
	Currant	1.1	4.1**	39	74.6
	Marigold	3.3	12.5**	29	73.6
	Purple Leaf Sand Cherry	0.3	1.2**	26	72.2
	Spirea	5.2	17.2**	25	69.6
	Carrot	0.07	9.2**	66	99.2
	Garden Pea	1.3	40.3**	89	96.7
	Leek	0.5	11.9**	58	95.7
	Kidney Bean	0.7	13.3**	88	94.7
	Fababean	1.4	21.8**	62	93.5
	Sweet Corn	45.5	166.5**	69	72.7
	Pepper	4.1	12.1**	42	66.1
	Tomato	71.2	174.6*	50	59.2
	Potato	107.5	185.3*	44	41.9
II	Oat	208.9	170.9	79	0
	Wheat	155.5	155.6	55	0
III	Cabbage	175.6**	93.3	0	–
	Garden Beet	27.1**	5.6	0	–

(*), (**) Significantly different at 5% and 1% level of probability; analysis of variance.
† Except for oat and wheat which yield represents the dry mass of plants from 1 m row.

It is noticeable that ornamental species as a group had lower REC indices (Table 2) than horticultural crops including oat and wheat where the values of the REC indices were always higher than 40%. The highest REC indices were those of two legumes, the garden pea and the kidney bean. The spores found in the soil were not sufficiently abundant to provide clear identification of the fungal species. The intramatrical structures of mycorrhizal fungus in the roots of the different plant species did not vary markedly from one species to another, except for the size of the vesicles. The appearance of the vesicles suggested that at least some of the fungal material inhabiting the roots belongs to the genus Glomus. Mycorrhizae were not observed on plants growing in fumigated soil.

For each plant that formed mycorrhizae a mycorrhizal dependency value was calculated. It was called relative field mycorrhizal dependency (RFMD) index and was determined by expressing the difference between the dry mass of the

mycorrhizal plant and the dry mass of the non-mucorrhizal plant as a percentage of the dry mass of the mycorrhizal plant (Table 2). Yields were evaluated by weighing the harvested plant parts (Table 1), and the RFMD indexes calculated from these values.

$$\text{RFMD} = \frac{(\text{Dry mass mycorrhizal plant}) - (\text{Dry mass non-mycorrhizal plant})}{\text{Dry mass mycorrhizal plant}} \times 100$$

Carrots were the most mycorrhizally dependent plants of the experiment with a RFMD index of 99.2%. Legumes and leeks were also highly mycorrhiza dependent. Potato and tomato had the lowest mycorrhiza dependency with a RFMD index of 41.9% and 59.2%, respectively, and these plants belong to the same family. Oat and wheat had a RFMD index of 0% since there was no significant difference between the dry mass of the mycorrhizal and non-mycorrhizal plants.

The RFMD index was not determined for cabbage and garden beet since they failed to form mycorrhizae. A significant ($P < 0.05$) correlation ($R^2 = 0.50$) was found between the REC indices and the RFMD indices for horticultural plants, but not for ornamental plants.

Discussion

Menge *et al.*[21] numerically defined the mycorrhizal dependency (MD) by expressing the dry mass of a mycorrhizal plant as a percentage of the dry mass of a non-mycorrhizal plant at a given level of soil fertility. This method of calculation may lead to extremely high percentages such as that reported by Hall[10] for *L. scoparium* (13000%). We think that the highest level of mycorrhizal dependency should not exceed 100% and that the lowest should be 0%. Thus with the proposed method of calculation, the value of the mycorrhizal dependency is 100% when the plant fails to grow without mycorrhizae and 0% if the difference between the dry mass of the mycorrhizal plant and the dry mass of the non-mycorrhizal one is zero or not statistically significant because this difference is then considered not to be significantly different from zero. It is proposed that the acronym RFMD have a superscript that represents the level (in μg/g) of the available phosphorus of the soil, since, as stated by Menge *et al.*[21], the mycorrhizal dependency is linked with a given level of soil fertility and because it is well known that phosphorus is the element which is the most concerned in mycorrhizal development and efficiency.

In our experiment the soil contained 100 μg/g of available phosphorus and therefore the RFMD^{100} was determined. All horticultural crops had REC indices higher than 40%. For carrot, kidney bean, sweet corn, leek and potato, the P-fertility of the soil (100 μg/g) may be considered as low (Table 3) according to the criteria of the Conseil des Productions Végétales du Québec (C.P.V.Q.)[5]. The efficiency of mycorrhizae in soil of low P-fertility has been clearly

Table 3. Available soil phosphorus* classes for some crops according to the criteria published by the C.P.V.Q.** (1980).

Crop	Amount of available P in the soil (μg/g)		
	Poor (under)	Medium (between)	Sufficient (over)
Carrot	112	113–196	196
Kidney Bean	112	113–196	196
Leek	112	113–196	196
Potato	112	113–196	196
Sweet Corn	75	76–150	150
Oat	42	43– 85	85
Wheat	50	51–110	110
Cabbage	112	113–196	196
Garden Beet	112	113–196	196

* Bray-2 extractable soil phosphorus

** Conseil des Productions Végétales du Québec

demonstrated[14,23,25]. The P-fertility of the soil may have been too low to permit a normal growth of plants without the help of mycorrhizae. However plants having high phosphorus requirements may have very different RFMD indices since tomato had a $RFMD^{100}$ index of 41.9% and at the opposite carrot had a $RFMD^{100}$ index of 99.2%. In the case of legumes which had high $RFMD^{100}$ indices, it is likely that mycorrhizae are as much important for their phosphorus nutrition as Rhizobium is for their nitrogen requirements. Carrots had the highest $RFMD^{100}$ index, and this may be related to the specific root system of this plant. With a $RFMD^{100}$ index of 95.7% leek is a plant of great interest to work with because it is a plant that can be seeded, germinated and inoculated in the greenhouse and then transplanted in the field.

In the case of tomato and pepper an early and temporary growth stimulation was observed in fumigated soil. Such a phenomenon has been reported by Martin *et al.*[17] and Newcomb[24] and was attributed to the elimination of the soil-borne pathogens.

Plants from group II, oat and wheat, grew almost equally well in fumigated and non-fumigated soil and therefore with the method proposed the $RFMD^{100}$ was 0% for these plants. A soil having a P-fertility of 100 μg/g is considered to have sufficient phosphorus for oat and nearly sufficient for wheat (Table 3). This may explain why, despite the relative high REC indices of these plants, the mycorrhizal efficiency was very low in this case. Baylis[1] stated that plants with a graminoid root system were less dependent on mycorrhizae for their supplies of phosphorus.

Plants from group III, cabbage and garden beet, had a significantly better

growth in fumigated soil. These two plant species belong respectively to the Cruciferae and Chenopodiaceae consisting of species reported to be non-mycorrhizal[7]. More recently several species of these two families have been found to be sometimes mycorrhizal[12]. In this experiment cabbage and beet did not form mycorrhizae in natural soil. The better growth of these plants in fumigated soil can be explained by the destruction of the soil-borne pathogens and by the absence of competition with other organisms for the nutrients.

Except for cabbage and garden beet all the other plant species were naturally mycorrhizal. Slender purple-osier willow was the only one to form ectomycorrhizae.

Plants from group I grew normally in non-fumigated soil, and were mycorrhizal while plants in fumigated soil remained stunted. In the latter case the poor growth of plants may be attributed mainly to the absence of a mycorrhizal endophyte after soil fumigation. Kleinschmidt and Gerdemann[15] concluded that the primary reason for stunting following fumigation was inadequate nutrition of plants brought about by the destruction of mycorrhizal fungi. Stunting following fumigation was observed mostly in citrus[11,15,18,22,35] but also with other plants such as cotton[13], peach[16], soybean[31], white clover[27] and harwood species[3,6,29]. Sleeth[33] attributed the stunting problems in a nursery after fumigation to toxic bromide residues in the soil. More recently Tucker and Anderson[37] showed that methyl bromide gas dissipated rapidly after fumigation and that there was no more bromide in stunted plants than in nearby healthy plants.

In this experiment the poor growth of plants from group I in fumigated soil was not due to methyl bromide residues in the soil. Indeed, the early and temporary growth stimulation of tomato and pepper, the equally good growth of wheat and oat as well as the stimulation of cabbage and garden beet in the fumigated soil, could not have taken place in a toxic soil unless the sensitivity to methyl bromide of all the plant species used coincided with their mycorrhizal dependency. Under ideal conditions soil fumigation destroys all microbiological life in the soil, pathogenic fungi and bacteria as well as mycorrhizal fungi, nitrifying bacteria and rhizobia. The destruction of the nitrifying bacteria temporary inhibits the nitrification process and the poor growth of plants in fumigated soil could be attributed to this fact. However, the soil was fertilized with 100 kg/ha of $N–NH_4NO_3$. This quantity and this kind of nitrogen fertilizer were sufficient to assure normal growth of plants in a fumigated soil as indicated by the behaviour of oat, wheat, cabbage and garden beet. This explanation also probably applies to the three legumes species that did not form nodules in fumigated soil. The three species of legumes had high REC indices in natural soil and the lack of mycorrhizae in fumigated soil may be the reason for their poor growth.

The RFMD index should be of practical interest to anyone who would like to evaluate under a given set of field conditions the role played by the indigenous endomycorrhizal fungi with different plant species and the importance of

maintaining a high level of colonization on any given crop by appropriate cultural practices or by inoculation. It should also be useful in the selection of new crop cultivars. It is obvious that the mycorrhizal dependency can be determined under different conditions such as in greenhouse or by using selected mycorrhizal strains. In our opinion, the RFMD index should be used exclusively for experiments conducted under field conditions in the presence of the indigenous mycorrhizal fungi and with a sufficient N and K soil content.

This experiment shows the importance of VA mycorrhizae in agricultural and horticultural practice since among 20 plant species commonly cultivated, sixteen had $RFMD^{100}$ indices above 40% of which seven had $RFMD^{100}$ indices higher that 90%.

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