Plant and Soil 69, 327–339 (1982). 0032-079X/82/0693-0327$01.95 Ms. 5143

Response of cassava to VA mycorrhizal inoculation and phosphorus application in greenhouse and field experiments

R. H. HOWELER, L. F. CADAVID and E. BURCKHARDT*
CIAT, Apartado Aereo 6713, Cali, Colombia SA

Received 25 June 1982

Key words Cassava *Manihot esculenta* Crantz Mycorrhiza Phosphorus response VA mycorrhiza

Abstract Cassava (*Manihot esculenta* Crantz) was grown in the greenhouse and in the field at different levels of phosphorus applied, with or without inoculation with VA mycorrhiza in sterilized or unsterilized soil. When grown in a sterilized soil to which eight levels of P had been applied the non-inoculated plants required the application of 3200 kg P ha^{-1} to reach near-maximum yield of plant dry matter (DM) at 3 months. Inoculated plants, however, showed only a minor response to applied P. Mycorrhizal inoculation in the P check increased top growth over 80 fold and total P uptake over 100 fold.

Relating dry matter produced to the available P concentration in the soil (Bray II), a critical level of 15 ppm P was obtained for mycorrhizal and 190 ppm P for non-mycorrhizal plants. This indicates that the determination of critical levels of P in the soil is highly dependent on the degree of mycorrhizal infection of the root system. In a second greenhouse trial with two sterilized and non-sterilized soils it was found that in both sterilized soils, inoculation was most effective at intermediate levels of applied P resulting in a 15–30 fold increase in DM at 100 kg P ha^{-1}. In the unsterilized soil inoculation had no significant effect in the Quilichao soil, but increased DM over 3 fold in the Carimagua soil, indicating that the latter had a native mycorrhizal population less effective than the former.

When cassava was grown in the field in plots with 11 levels of P applied, uninoculated plants grown in sterilized soil remained extremely P deficient for 4–5 months after which they recuperated through mycorrhizal infection from unsterilized borders or subsoil. Still, after 11 months inoculation had increased root yields by 40%. In the non-sterilized soil inoculation had no significant effect as the introduced strain was equally as effective as the native mycorrhizal population.

These trials indicate that cassava is extremely dependent on an effective mycorrhizal association for normal growth in low-P soils, but that in most natural soils this association is rapidly established and inoculation of cassava in the field can only be effective in soils with a low quantity and quality of native mycorrhiza. In that case, plants should be inoculated with highly effective strains.

Introduction

Cassava (*Manihot esculenta* Crantz) is a tropical root crop that grows reasonably well on many very acid and low-P soils[6]. However, in Latin América phosphorus (P) remains the main limiting nutrient, and in many soils yields can be doubled or tripled with the application of this element. Recent work on the mycorrhizal dependence of the crop[7,10,15,17,18] has shown that cassava is highly dependent on a VA mycorrhizal association. This association improves

*Soil Scientist and Research Assistants of the Soil Program at Centro Internacional de Agricultura Tropical – CIAT.

the uptake of P, and thus the efficiency of applied P fertilizers[3,13]. Because cassava has a coarse and inefficient root system it was the only species that responded to mycorrhizal inoculation in well-stirred nutrient solutions of low P concentrations[8,9]. Since the cost of fertilizer P is 2–3 times higher than that of N and K, it is of extreme importance to maximize the efficiency of P uptake through cultural practices[12] which enhance a high native mycorrhizal population, or through artificial inoculation. The objective of this study was to determine the response of cassava to P applications and mycorrhizal inoculations and to evaluate the effectiveness of the native mycorrhiza vis-a-vis the introduced species under both greenhouse and field conditions.

Materials and methods

Greenhouse trials

The two greenhouse trials were conducted with sterilized or unsterilized soil from Santander de Quilichao and Carimagua, the former classified as a typic Dystropept[11] from the southern part of the Cauca Valley in Colombia, and the latter classified as a Haplustox[4] from the Eastern Plains of Colombia. The chemical characteristics of these soils are shown in Table 1. Soils were sterilized with methyl bromide about a week before planting.

In the first trial pots with 8 kg soil were planted with cassava tip cuttings of M Mex 59 previously rooted in a misting chamber, in small peat pots. Two g of mycorrhizal cassava roots were placed under each cutting for the inoculated treatments, while the same amount of autoclaved inoculum was used for the non-inoculated treatments. Soil from Quilichao was mixed with the equivalent of 1000 kg ha^{-1} dolomitic lime, 200 kg N ha^{-1} as NH_4NO_3, 200 kg ha^{-1} as KCl, 25 kg Mg ha^{-1} as $MgSO_4.7H_2O$ and 20 kg Zn ha^{-1} as $ZnSO_4.7H_2O$. Nine P treatments were established ranging from 0 to 3200 kg P ha^{-1} applied as $Ca(H_2PO_4)_2.H_2O$ with three replications. The soil was incubated for 6 weeks at field capacity prior to sterilization. A week later the cassava plantlets with peat pots were transplanted into the treated soils. After three months plants were cut at soil level, the topgrowth was dried, weighed and analyzed after HNO_3–$HClO_4$ digestion. The fibrous roots were removed and examined for root infection after clearing in KOH and staining with trypan blue[14]. Soil samples were taken and analyzed for Bray II (0.1 *N* HCl + 0.03 *N* NH_4F) extractable P, as well as pH, exchangeable Al, Ca, and Mg.

In the second trial the experimental procedure was essentially the same except that both sterilized

Table 1. Chemical characteristics of soils used in greenhouse and field trials

	% O.M.	ppm P (Bray II)	pH	meq 100 g^{-1}			
				Al	Ca	Mg	K
Greenhouse							
Quilichao	7.1	1.8	4.3	2.8	1.8	0.7	0.18
Carimagua	3.4	1.4	4.1	3.1	0.37	0.17	0.08
Field							
Quilichao	6.5	1.8	5.1	1.1	4.4	0.3	0.23

and non-sterilized soils were used from Quilichao and Carimagua to which 5 levels of P were applied ranging from 0 to 3000 kg P ha^{-1}. Tip cuttings of cultivar CM 91-3 were used and plants were harvested after only two months.

Field trial

Since inoculation can only be practical in the field if it can have significant effects on the yield of roots from plants grown from stakes in non-sterilized soil and harvested at 10–18 months, a trial was planted at CIAT–Quilichao to determine mycorrhizal effects in fieldgrown cassava. This station is located at 990 m above sea level in southern Colombia and chemical characteristics of the soil are shown in Table 1. Mean monthly temperature is 24.8°C and annual precipitation is 1850 mm. The trial was established on plots which three years earlier had received 11 levels of P, ranging from 0 to 1130 kg P/ha applied as triple superphosphate broadcast and incorporated. At that time beans (*Phaseolus vulgaris*) were planted for one semester after which the plots remained in grass fallow. The residual effect of P application on the available P in the soil at time of cassava planting is shown in Table 4. Half of each plot was covered with plastic and methyl bromide was injected at a rate of 0.1 kg m^{-2}. Care was taken not to contaminate these sterilized subplots with unsterilized soil during cultural practices. Mycorrhizal root inoculum was collected from highly infected cassava plants in a nearby field; roots were chopped to 0.5–1 cm pieces and 1.5 g of inoculum was placed directly below the stake (cv. CM 91-3) at time of planting. In addition, plants were inoculated with 100 g sand containing about 35 mycorrhizal spores per g. The same amount of autoclaved sand and root inoculum was used in the 'non-inoculated' treatments. Thus the trial had main plots of 11 P levels, subplots of sterilized or unsterilized soil and subsubplots of inoculated or non-inoculated plants. Cassava stem cuttings were planted vertically at a distance of 80 × 75 cm and each plant was fertilized with the equivalent of 100 kg N ha^{-1} as urea, 50 kg K ha^{-1} as KCl and 20 kg Mg ha^{-1} as $MgSO_4.7H_2O$, band applied after planting.

At 3½ months plant height was determined and upper fully expanded leafblades were sampled and analyzed for N, P, K and Zn. At 11 months plants were harvested and fresh root yields were determined. Fibrous roots of each treatment were examined to determine the degree of mycorrhization.

Results and discussion

Greenhouse trials

In the first trial there was a clear response to P already after two weeks and to mycorrhizal inoculation after three weeks. The non-inoculated plants remained small with typical symptoms of P deficiency up to the level of 1600 kg applied P ha^{-1}, with maximum plant growth reached only with 3200 kg P ha^{-1}. In the inoculated plants, however, there was no visual response to P and the P-check plants appeared as vigorous as the non-inoculated plants with 3200 kg P ha^{-1} applied. Mycorrhizal responses were most dramatic at low and intermediate levels of applied P (Plate 1).

Fig. 1 shows that non-inoculated plants required 3200 kg P ha^{-1} to reach maximum dry matter (DM) yield, and even with 800 kg P ha^{-1} plants remained extremely small and P deficient. Inoculated plants showed only a minor P response to 200 kg P ha^{-1}, and plants to which no P had been applied produced the same DM yield as non-inoculated plants with 1600 kg P ha^{-1}.

In the P check inoculation increased DM yield from 0.42 to 34.6 g $plant^{-1}$, which is an 80 fold increase. Inoculation not only increased dry weight but also

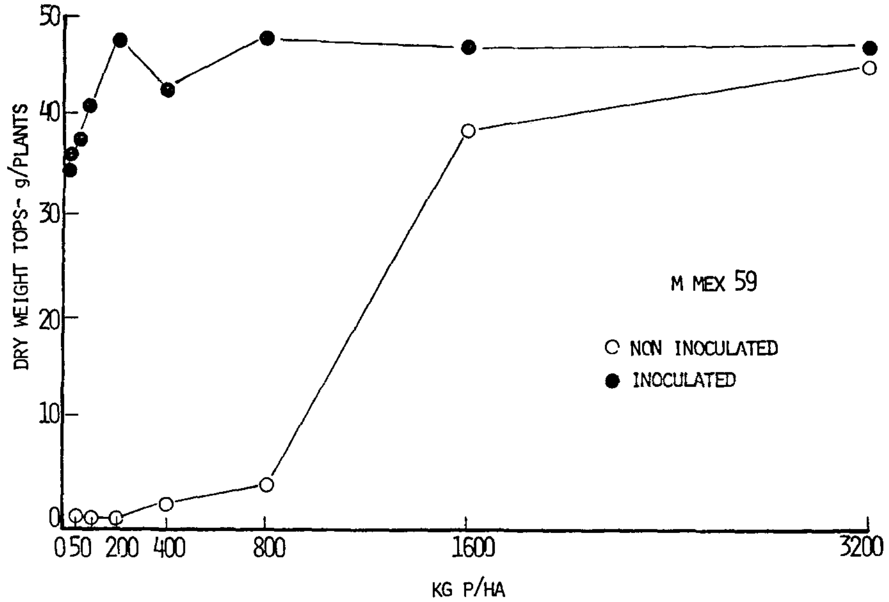

Fig. 1. The effect of various levels of applied P on dry weight of tops of inoculated and non-inoculated cassava grown in sterilized soil from CIAT – Quilichao.

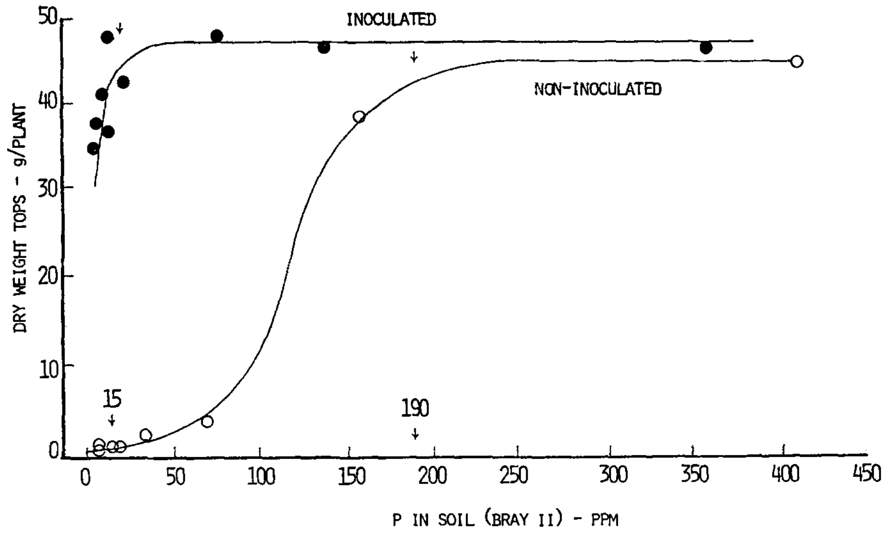

Fig. 2. Relation between dry weight of tops of inoculated and non-inoculated cassava and the available P content in sterilized Quilichao soil. Arrows indicate the critical P-level corresponding to 95% of maximum yield.

the P content of the tissue, even at the highest level of applied P, as shown in Table 2. Inoculation tended to decrease the K, N and Zn contents of the tops mainly due to better growth and dilution of nutrients in the tissue. The total uptake of all nutrients increased markedly due to inoculation, but mainly due to increases in DM. The total P uptake increased at all levels of applied P, but was marked in the P-check and at low levels of applied P where inoculation increased P-uptake over 100 fold.

Fig. 2 shows that there was a clear relationship between the dry matter of tops and the available P (Bray II) content of the soil after harvest. The critical level, corresponding to 95% of maximum DM yield, was found to be 15 ppm for inoculated and 190 ppm for non-inoculated plants. The critical level determined for root yield from field experiments generally varies between 8 and 10 ppm[2,6]. Thus the level found for inoculated plants in this trial was slightly higher, but that for non-inoculated plants was markedly higher than those determined in the field. This indicates that in the field cassava plants must be generally well-infected with mycorrhiza. Moreover, variations often observed in the determination of critical levels in the field may be due to variations in the degree of mycorrhizal infection. That critical levels of available soil P are vastly different for mycorrhizal and non-mycorrhizal plants, as observed in this experiment, is contrary to data reported by Howeler *et al.*[7] for cassava grown in sterilized and non-sterilized Australian soil. In that case near-maximum yield for mycorrhizal and non-mycorrhizal plants were obtained at approximately the same level of P applied, corresponding to 6–7 t P ha^{-1}, or more than twice the requirement in the present experiment. This could be due to a much higher P fixing capacity of the Australian soil or due to a more effective mycorrhizal strain used in the Colombian trial. In fact, the Colombian strain is a *Glomus* species, not yet described in the literature (Schenk, personal communication). It is also one of the most effective strains so far identified and tested in Colombia (Sieverding, personal communication).

Table 2 shows the effect of inoculation and P applications on the degree of mycorrhizal infection. In the inoculated treatments, both the infection and the effectiveness in terms of P uptake were highest at intermediate levels of 50 and 100 kg P ha^{-1}. These are levels of P application that often give maximum yields in field experiments[2] and that are economically feasible for many farmers. The observation of maximum effectiveness at intermediate levels of P application corresponds with similar results obtained in a sterilized and non-sterilized Australian soil[7] and has been reported by other workers[1]. Thus, Mosse *et al.*[13] reported that even mycorrhizal plants can not absorb appreciable amounts of P from very P depleted soil, while it is also widely recognized that mycorrhizal effects decrease at high levels of P application[3,5,17].

In the second experiment the response to inoculations was determined in both sterilized and unsterilized Carimagua and Quilichao soil. Fig. 3 shows that in both soils there was a good DM response to P applications, reaching maximum

Table 2. Effect of P applications on P content and total P absorption of tops, and on mycorrhizal infection of roots of inoculated and non-inoculated plants of M Mex 59 grown on sterilized Quilichao soil

P-application (kg ha^{-1})	% P in tops		P absorption by tops (mg plant^{-1})		Root infection*	
	Non-inoc.	Inoc.	Non-inoc.	Inoc.	Non-inoc.	Inoc.
0	0.05	0.08	0.2	27.7	0	1.7
25	0.07	0.07	0.5	25.5	0	2.2
50	0.04	0.11	0.3	41.3	0	2.6
100	0.05	0.12	0.3	49.4	0	2.6
200	–	0.17	–	81.0	0	2.4
400	0.06	0.17	1.2	73.0	0	2.0
800	0.09	0.17	3.4	86.0	0	1.5
1600	0.15	0.16	58.3	75.3	0	1.0
3200	0.20	0.25	90.5	118.3	0	1.0

* Visual evaluation of hyphae and vesicles: 0 = no infection and 3 = high infection.

Table 3. Effect of P application on P content and total absorption of tops of inoculated and non-inoculated plants of CM 91-3 grown on sterilized and unsterilized Quilichao and Carimagua soils

Soil and P application (kg ha^{-1})	P content (%)				P absorption (mg plant^{-1})			
	SN*	SI	UN	UI	SN	SI	UN	UI
Quilichao								
0	0.09	0.17	0.15	0.15	0.27	8.62	1.89	0.90
100	0.09	0.27	0.16	0.16	0.28	25.68	11.20	10.97
300	0.11	0.26	0.23	0.16	1.89	32.40	25.41	13.12
1000	0.16	0.24	0.17	0.18	27.71	44.04	17.51	18.72
3000	0.29	0.29	0.20	0.25	62.90	58.67	15.24	25.45
Carimagua								
0	0.08	0.14	0.14	0.13	0.54	6.37	3.30	5.08
100	0.07	0.31	0.25	0.17	0.51	33.98	11.07	24.16
300	0.08	–	0.20	0.17	0.75	21.18	16.86	19.75
1000	0.25	0.25	0.17	0.17	39.40	43.05	25.14	24.53
3000	0.34	0.27	0.22	0.27	69.53	62.50	54.45	63.85

* SN = Sterilized soil, Non-inoculated plants.
SI = Sterilized soil, Inoculated plants.
UN = Unsterilized soil, Non-inoculated plants.
UI = Unsterilized soil, Inoculated plants.

yield at 1000 kg P/ha^{-1} in Quilichao and at 3000 kg P ha^{-1} in Carimagua soils. In both sterilized soils there was a marked response to inoculation, increasing shoot dry weight 15 times in Carimagua and 31 times in Quilichao soil at 100 kg P ha^{-1}. In both soils inoculation also markedly increased the P content of tops (Table 3) resulting in an increase in total P uptake of 66 fold for Carimagua and 92 fold for Quilichào soils at 100 kg P ha^{-1}. However, in the unsterilized soil, there was no significant effect of inoculation in the Quilichao soil, but a marked effect in the Carimagua soil. In the latter inoculation increased dry weight of tops three fold at 100 P but only 38% at 300 P. The lack of response in unsterilized Quilichao soil is probably due to the fact that plants were inoculated with a strain collected from the same site. Thus, the introduced strain was the same as the dominant native strain and placement of infected root inoculum did not result in a better root infection than that obtained from spores in the unsterilized soil. In the Carimagua soil, however, the introduced strain from Quilichao was more effective than the local strains, resulting in a positive response to inoculations, at least at the three lower levels of applied P. Thus the effect of inoculation in unsterilized soil is highly dependent on the effectiveness and the competition from local strains. Table 3 shows that in the unsterilized soils inoculation did not increase the P content of the tops, except at the highest level of applied P. Thus, the total P uptake of inoculated plants was significantly higher in the sterilized soil than in the unsterilized soil. This may be due to a lack of competition of the introduced strains with native micro-organisms in the sterilized soil, or to the presence of soil pathogens in the unsterilized soil.

Field trial

Table 4 shows that the application of 11 levels of P three years earlier resulted in a range of available P levels in the soil from 1.8 to 117.3 ppm. Although plants suffered from two hail storms in the first two months after planting, most recuperated quickly. At 3½ months there was a good visual response to inoculation in the sterilized but not in the unsterilized soil. In the latter there was only a very minor plant height response to P eventhough the low P plots had soil-P levels was below the critical level of 8–10 ppm[6]. In the sterilized soil inoculation increased the average plant height from 44 to 55 cm, while in the unsterilized soil plant height was 48 cm, irrespective of inoculation.

Table 4 shows the P content of youngest fully expanded leaves at 3½ months. In the non-inoculated treatments in sterilized and unsterilized soil there was a response to P-application, but in the inoculated treatments there was no response to P. Surprisingly, all treatments including the non-inoculated plants in sterilized soil, had high P concentrations in the tissue, above the critical level of 0.4%[6]. However, highest P concentrations were found in inoculated plants grown in sterilized soil, which also showed the best plant growth and highest concentrations of K. Nitrogen and Zn concentrations were high but not related to P applications or mycorrhizal treatments.

Table 4. Residual effect of P application on available P content of soil before planting and the P content of youngest fully expanded leaves (Yfel) of $3\frac{1}{2}$ months old inoculated or non-inoculated cassava plants grown in sterilized or unsterilized soil in CIAT-Quilichao

P-application kg ha^{-1})	Soil P (Bray II) (ppm)	% P in Yfel-blades			
		SN*	SI	UN	UI
0	1.8	0.44	0.62	0.41	0.56
33	2.2	0.42	0.48	0.44	0.58
67	2.9	0.39	0.45	0.42	0.46
141	6.8	0.53	0.56	0.41	0.41
253	17.9	0.56	0.62	0.40	0.46
310	25.8	0.64	0.65	0.65	0.59
458	27.7	0.54	0.56	0.56	0.47
603	42.3	0.63	0.62	0.57	0.66
734	56.3	0.57	0.56	0.53	0.61
869	36.3	0.70	0.67	0.57	0.51
1131	117.3	0.46	0.58	0.55	0.53
Mean		0.53	0.58	0.50	0.53

* See Table 3.

Table 5. Effect of P application on root yield and degree of root infection of 11-months old cassava, CM 91-3, grown with and without inoculation on sterilized and unsterilized soil in CIAT-Quilichao

P-application (kg ha^{-1})	Fresh root yield (10^3 kg ha^{-1})				Degree root infection			
	SN*	SI	UN	UI	SN*	SI	UN	UI
0	31	50	33	35	0.6	1.6	0.5	1.0
33	28	51	44	41	0.9	1.2	1.0	0.9
67	32	50	40	40	1.0	1.3	1.0	0.6
141	30	68	40	46	0.6	1.2	0.8	1.5
253	29	43	42	33	1.6	1.3	0.3	1.3
310	55	51	34	32	1.5	1.6	0.6	0.8
458	46	57	42	31	1.0	1.5	1.0	1.3
603	41	54	40	43	1.8	1.3	1.0	0.6
734	37	59	28	37	1.1	1.6	0.6	1.3
869	38	52	41	37	0.5	1.8	1.3	0.8
1131	47	46	33	35	0.9	1.8	0.3	1.3
Mean	38	53	38	37	1.0	1.5	0.8	1.0

* See Table 3.

** Visual evaluation of hyphae and vesicles: 0 = no infection and 3 = high infection.

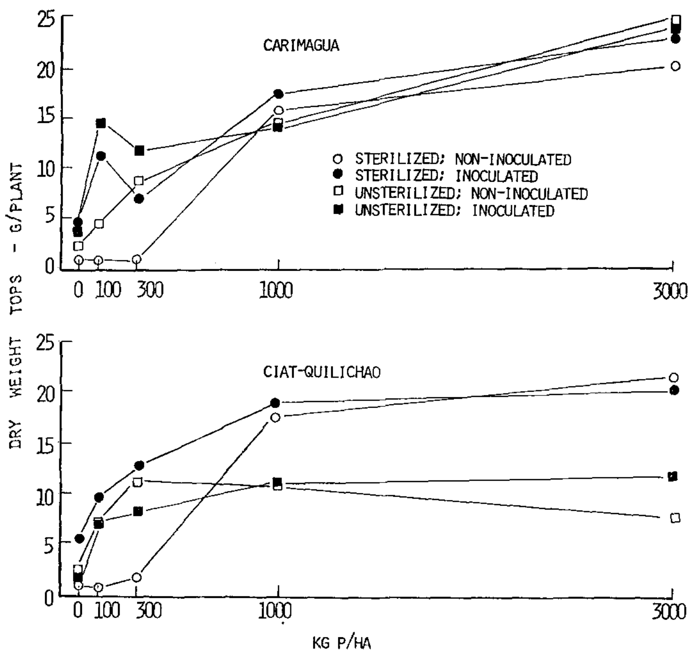

Fig. 3. The effect of applied P and mycorrhizal inoculation on the dry weight of tops of cassava grown in sterilized and unsterilized soil from Carimagua and CIAT – Quilichao.

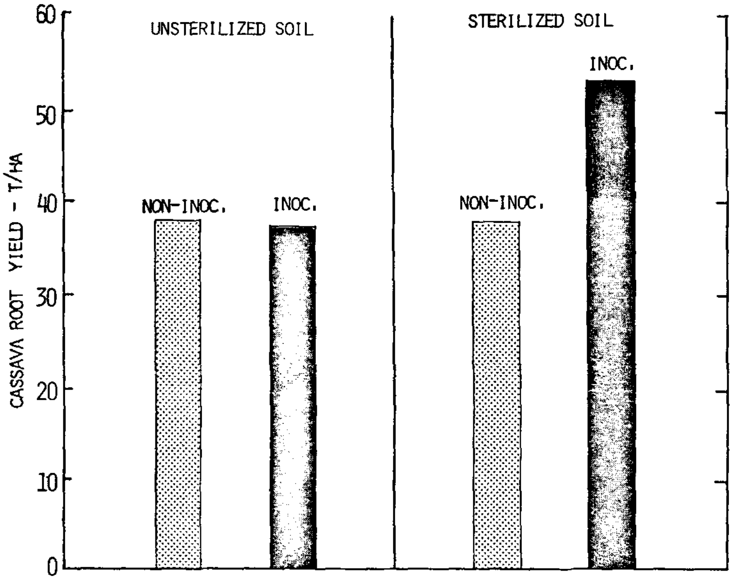

Fig. 4. The root yield response to mycorrhizal inoculation of 11-months old cassava (CM 91–3) grown in sterilized and unsterilized soil in CIAT – Quilichao. Data are averaged over 11 P treatments.

In the sterilized soil responses to inoculation were quite marked (see Plate 2) up to 5–6 months, after which the non-inoculated plants started to recuperate, first in the borders where plant roots became infected after penetration in unsterilized walkways. Recuperation then continued throughout the plot probably due to infection from the unsterilized subsoil. At time of harvest at 11 months most visual responses to sterilization and inoculation had disappeared.

Root yields and the degree of root infection at 11 months are shown in Table 5. There was no statistically significant effect of P applications, but a highly significant overall effect of both soil sterilization and inoculation. Fig. 4 shows that in unsterilized soil, averaged over P applications, there was no effect of inoculation, but in sterilized soil inoculation increased yields from 38 to

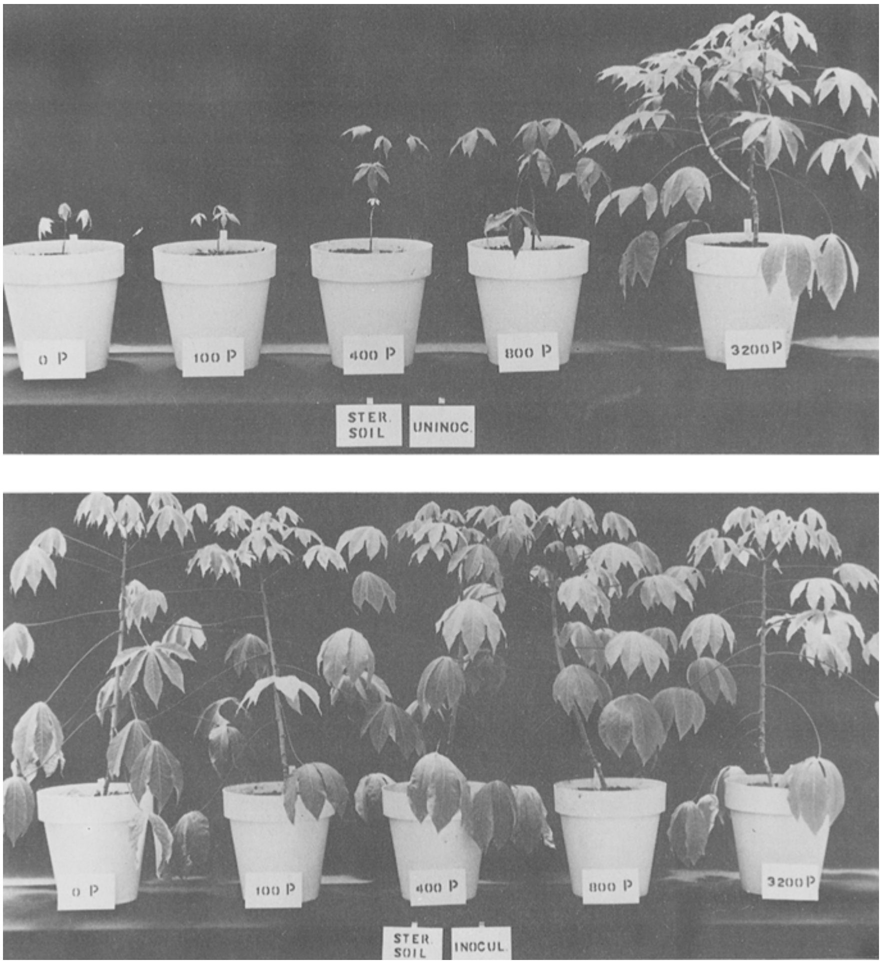

Plate 1. Response of cassava (M MEX 59) to P application (kg P ha^{-1}) in a sterilized soil from CIAT – Quilichao in the absence and presence of a mycorrhizal association.

53×10^3 kg ha^{-1}, *i.e.* a 40% increase in root yield due to mycorrhizal inoculation. Although this is highly significant, it is still an under-estimation of the importance of mycorrhiza in cassava, because of the recuperation of non-inoculated plants grown in sterilized soil once plant roots reached the unsterilized borders and subsoil. At harvest these plants were equally infected with mycorrhiza as the inoculated plants in unsterilized soil and even better infected than non-inoculated plants in unsterilized soil (Table 5). The inoculated plants in sterilized soil had a significantly higher infection, both in terms of hyphae and vesicles, than other mycorrhizal treatments and this resulted in greater plant height, higher P and K levels in leaves and ultimately a higher root yield. A better appreciation of the importance of mycorrhiza might be obtained by considering only one P treatment in one replication (shown in Plate 2) in sterilized soil. In this case the non-inoculated plants had only a minor root infection and did not recuperate, resulting in a root yield of only 8.7×10^3 kg ha^{-1} compared with 63×10^3 kg ha^{-1} in neighbouring but inoculated plants. This 7 fold increase in yield due to a better mycorrhizal infection is not of the same order of magnitude as the 30–80 fold increases in top DM obtained with tip

Plate 2. The effect of mycorrhizal inoculation (right) on the growth of cassava (CM 91–3) in a sterilized plot (0.01 ppm P in soil solution) in CIAT – Quilichao. In the back the same response in a non-sterilized soil.

cuttings in pot experiments in the same soil (see above), but is definitely an indication that cassava is highly dependent on a mycorrhizal association for P uptake from low P soils. When grown on these soils cassava can be called 'obligately mycorrhizal'.

The fact that no responses were observed in unsterilized soil is mainly because the introduced strain was collected from the same site as the native strains present in the unsterilized soil. As mentioned above, this is the most efficient strain isolated from Colombian soils so far, and belongs to an as yet undescribed species of *Glomus**. It is expected that in other soils with less effective native strains, and/or with low mycorrhizal populations, inoculation with this *Glomus* species might have a beneficial effect. Field trials are presently underway to test this hypothesis. In addition, new mycorrhizal species are being isolated and tested to search for even more effective strains, with good adaptation to acid soils and good competitive ability with local strains.

In both field and greenhouse trials with Quilichao soil best growth and yields were consistently obtained in sterilized soil with inoculated plants. The poorer growth in unsterilized soil, especially at high levels of applied P (Fig. 3) may be due to:

1. strong competition between the introduced strain and native microorganisms, making the former less effective
2. presence of soil pathogens, which affect cassava producion without causing visible symptoms.
3. the release of some essential minor elements such as Zn during the sterilization process or
4. an excessive mycorrhizal infection from native strains causing a carbohydrate drain on the plant, as suggested by Stribley *et al.*[16].

In the latter case, the P content of plant tissue would be greater in unsterilized soil, as observed in the Australian soil[7], but this was not the case in the present trial (see Table 4). The third hypothesis of Zn release by sterilization is born out by plant analyses, which generally show a higher Zn content in plants growing in sterilized than in unsterilized soil, but whether this is a direct or indirect effect of sterilization on plant growth is not quite clear. In any case, the effect was not very significant in the present field trial. The possible presence of unknown soil pathogens is presently being investigated. In that case, the elimination of these pathogens or of other competing microorganisms through soil fumigation in combination with mycorrhizal inoculation might be effective in increasing yield, but it is doubtfull that this would be an economic alternative to higher P fertilizer applications.

* Name: *Glomus manihotis* (Schenk *et al.* In press)

References

1 Abbott L K and Robson A D 1977 Growth stimulation of subterranean clover with vesicular arbuscular mycorrhizas. Aust. J. Agric. Res. 28, 639–649.
2 Centro Internacional de Agricultura Tropical 1982 Cassava Program Annu. Rep. 1981.
3 Daft M J and Nicolson T H 1969 Effect of Endogone mycorrhiza on plant growth. II. Influence of soluble phosphate on endophyte and host in maize. New Phytol. 68, 945–952.
4 Guerrero R 1971 Soils of the Colombian Llanos Orientales – composition and classification of selected soil profiles. Unpublished Ph. D Thesis, Dept. Soil Science, North Carolina State Univ. Raleigh, N.C.
5 Hayman D S 1975 The occurrence of mycorrhiza in crops as affected by soil fertility. *In* Endomycorrhiza. Proc. Symp. Univ. Leeds, July 22–25, 1974. Eds. F A Sanders, B Mosse and P B Tinker. Academic Press, London. pp 495–509.
6 Howeler R H 1981 Mineral nutrition and fertilization of cassava (*Manihot esculenta* Crantz). Centro Internacional de Agricultura Tropical, Series 09 EC–4, Cali, Colombia.
7 Howeler R H, Edwards D G and Asher C J 1979 The effect of soil sterilization and mycorrhizal inoculation on the growth, nutrient uptake and critical P concentration of cassava. Paper presented at Vth Intern. Symp. Trop. Root Crops. Manila, Philippines, Sept. 17–21, 1979 (*In press*).
8 Howeler R H, Edwards D G and Asher C J 1981 Application of the flowing solution culture techniques to studies involving mycorrhizas. Plant and Soil 59, 179–183.
9 Howeler R H, Asher C J and Edwards D G 1982 Establishment of an effective mycorrhizal association on cassava in flowing solution culture and its effect on phosphorus nutrition. New Phytol. 90, 229–238.
10 IITA Annu. Rep. 1976 International Institute of Trop Agric. Ibadán, Nigeria. pp 80–81.
11 Instituto Geografico 'Agustin Codazzi' 1976 Estudio General de Suelos de los Municipios de Santander de Quilichao, Piendamó, Morales, Buenos Aires, Cajibío y Caldono. Volúmen XII No. 4. 466 p.
12 Kruckelmann H W 1975 Effects of fertilizers, soils, soil tillage and plant species on the frequency of Endogone chlamydospores and mycorrhizal infection in arable soils. *In* Endomycorrhiza. Proc. Symp. Univ. Leeds July 22–25, 1974. Eds. F A Sanders, B Mosse and P B Tinker. Academic Press, London pp 511–525.
13 Mosse B, Powell C Ll and Hayman D S 1976 Plant growth responses to vesicular arbuscular mycorrhiza. IX Interactions between VA mycorrhiza, rock phosphates and symbiotic nitrogen fixation. New Phytol. 76, 331–342.
14 Phillips J M and Hayman D S 1970 Improved procedures for cleaning roots and staining parasitic and vesicular arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. 55, 158–161.
15 Potty V P 1978 Occurrence of vesicular arbuscular mycorrhiza in certain tuber crops. J. Root Crops 4, 49–50.
16 Stribley D P, Tinker P B and Rayner J H 1980 Relation of internal phosphorus concentration and plant weight in plants infected by vesicular-arbuscular mycorrhizas. New Phytol. 86, 261–266.
17 Yost R S and Fox R L 1979 Contribution of mycorrhizae to P nutrition of crops growing on an oxisol. Agron. J. 71, 903–908.
18 Zaag P van der, Fox R L, Pena R S and Yost R S 1979 Phosphorus nutrition of cassava, including mycorrhizal effects on P, K, S, Zn, and Ca uptake. Field Crops Res. 2, 253–263.