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MEGAN HUGHES (Name) for the degree of MASTER OF SCIENCE (Degree)

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Title: THE INFLUENCE OF MYCORRHIZAE ON THE MINERAL NUTRIENT CONTENT OF STRAWBERRIES AND RED RASPBERRIES

Abstract approved: Lloyd W. Martin

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The influence of mycorrhizae on the nutrient uptake of strawberries and red raspberries was investigated. On red raspberries innoculation with a mycorrhizal fungus resulted in increased P uptake and a greater concentration of P in the shoots of the plants. The strawberries were innoculated with 2 species of mycorrhizal fungus. Both resulted in higher P and N concentrations in the shoot, but one fungus produced higher concentrations than the other. Measurement of the total mycorrhizal root length showed that the fungus species which resulted in the highest P and N concentration also had the highest level of infection.

The Influence of Mycorrhizae on the Mineral Nutrient Content of Strawberries and Red Raspberries

by

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Note: This thesis is presented in the form of 2 papers to be submitted to the Journal of the American Society for Horticultural Science and 1 paper, as an appendix, to be submitted to HortScience. The format of the individual papers corresponds to that required by these journals.

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Let us never forget that the cultivation of the earth is the most important labor of man. When tillage begins, other arts follow. The farmers are the founders of civilization.

Daniel Webster

Those who labor in the earth are the chosen people of God.

Thomas Jefferson

Mycorrhizae and the nutrition of red raspberries[1/]

Megan Hughes [2/]

Oregon State University, Corvallis

Abstract. Mycorrhizal and non-mycorrhizal red raspberries were grown at 0, 22 and 44 ppm added soil P. Mycorrhizal plants had significantly higher concentration of P than non-mycorrhizal plants at all soil P levels. Total P uptake was greater in mycorrhizal plants than controls at 22 and 44 ppm added P. There were no differences between mycorrhizal and non-mycorrhizal plants in N, Mg, B and Zn concentrations at all P levels. Potassium concentration in mycorrhizal plants was lower than controls at 22 ppm added P but total K uptake was the same. Copper concentration was higher in mycorrhizal plants at the highest P level. There were significant effects due to P levels on the total uptake of all elements and on the concentration of all elements except Zn.

There are many reports of improved P nutrition of mycorrhizal versus non-mycorrhizal plants (8,5,3). The differences are greatest in soils of low P availability and are less important when soluble P is added (8, 4). Differences between mycorrhizal and non-mycorrhizal plants in concentrations of N, K, Ca, Na, Mg, Fe, Mn, Cu, B, Zn and Al have also been reported (1,5,9). However these results are incon-

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sistent and comparisons between controls and mycorrhizal plants were not usually valid since non-mycorrhizal plants were often small and suffering from acute P deficiency (11). When mycorrhizal strawberries were compared with non-mycorrhizal plants grown on soil with added P, no differences in P,N or Ca were found, but K was lower and Mg higher in the mycorrhizal plants (8). Mycorrhizal and non-mycorrhizal soybeans were grown at three levels of P and the highest concentration of P was found in mycorrhizal plants. There were higher P, N, Ca and Cu concentrations in the mycorrhizal plants at all levels of P but no differences in Mn, Mg, Fe or K (12). On a soil with very little available P the K concentration in mycorrhizal plants was lower and Mn, Mg, Cu and Zn concentrations were higher than in non-mycorrhizal plants (11).

This study was undertaken in an attempt to obtain non-mycorrhizal red raspberry plants with a P content similar to that of mycorrhizal plants; and to compare the effect of mycorrhizae on the levels of other nutrients.

Materials and Methods

A clay loam soil was used which averaged 12 ppm P by the dilute acid fluoride method (table 1). It was autoclaved for 2 hours to achieve partial sterilization. Phosphoric acid was added and mixed thoroughly to produce 3 treatments of 0, 22 and 44 ppm added P. Fifty ppm N as NH_4NO_3 and 62 ppm K as KSO_4 were added to each treatment. The soil was weighed equally into 36 pots and 1 raspberry cutting (Rubus idaeus L. cv. Meeker) was planted in each. The raspberries were propagated by root cuttings, sprouts from which were removed and

re-rooted to avoid mycorrhizal contamination from the original root. At the time of planting a suspension of approximately 10 spores of Glomus fasciculatus (Thaxter sensu Gerdemann) Gerdemann and Trappe was added to half the pots. G. fasciculatus is a common mycorrhizal fungus which infects a wide range of hosts (Trappe, personal communication). The other half of the pots received an equal volume of filtered leachate from the spores to introduce similar non-mycorrhizal organisms into both treatments.

After 8 months all the above-ground portions of the plants were harvested and total shoot dry weight was measured. The entire plant top was then ground and analyzed for elemental concentration. Potassium, P, Ca, Mg, Mn, Cu, B and Zn were measured by emission spectroscopy (2) and N was measured by modified Kjeldahl (14). Total plant uptake of each element was then calculated from the concentration data and the dry weight of each plant. The data were analyzed as a completely randomized design and the LSD was computed from the analysis of variance. The roots were sampled, stained by the method of Kruckleman (10) and checked for the presence or absence of infection.

Results and Discussion

Mycorrhizal plants had significantly (5% level) higher concentration of P than non-mycorrhizal plants at all soil P levels (fig. 2, table 2). Total P uptake was greater in mycorrhizal plants than controls at 22 and 44 ppm added P (fig. 3, table 3). There were no significant differences between mycorrhizal and non-mycorrhizal plants in N, Mg, B and Zn concentrations at all levels of P (table 2). Copper concentrations in mycorrhizal plants were higher than controls at the

highest P level. Potassium concentration in mycorrhizal plants was lower at 22 ppm added P, but total K was nearly the same (table 3), indicating the concentration difference was due to dilution by greater growth in the mycorrhizal plants. The same explanation may be applied to the lower Ca concentration in mycorrhizal plants at the 0 and 22 ppm added P levels. Mn levels in all plants were abnormally high, probably as a result of heat sterilization of the soil, which releases Mn. There were significant effects due to P levels on the total uptake of all elements and on the concentration of all elements except Zn.

The major difference in mineral nutrient levels between mycorrhizal and non-mycorrhizal plants was in P concentration. However, the P treatments did not produce differences in P concentration that were consistent and great enough to allow comparisons of mycorrhizal plants with controls at similar P levels, as was planned. Nevertheless, the lower K concentration and higher Cu concentration agree with previously reported results (8,11,12).

The mechanism by which mycorrhizae increase uptake of P has been well established (13). The ultimate limitation on P uptake is its slow diffusion into the depleted zone surrounding the root. Widely spread hyphae extend the absorbing surface beyond this depleted zone, bypassing this rate-limiting step and allowing increased P uptake. Calculations based on the extent and absorbing area of mycorrhizal hyphae show that this is physically possible. Apparently the hyphae do not have any special mechanism for extracting P from the soil, nor using unique forms of P, but they simply allow greater absorption of

P available in the soil.

It is also hypothesized (13) that the uptake of any element would be enhanced by mycorrhizae if it is slowly available and its soil diffusion rate is the limiting factor in its uptake. Thus, Zn and Mn should both be increased in mycorrhizal plants, as their diffusion rate in soils is low (15,7). Reports of Zn deficiencies in non-mycorrhizal plants have been made (6). The present study showed a slight but statistically insignificant increase in the Zn uptake of mycorrhizal plants. Mn was also higher in mycorrhizal plants, although not significantly, in spite of the very high levels which were taken up. The soil level of these 2 elements may have to be quite low in order for their uptake to be enhanced by mycorrhizae.

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Table 1. Soil test results for 2 samples of soil before sterilization.

Sample	pH	P (ppm)	K (meq/100 g)	Ca (meq/100 g)	Mg (meq/100 g)	CEC[y] (meq/100 g)	OM[z] (%)
1	6.5	19	.29	14.1	6.9	22.3	2.92
2	6.6	5	.26	14.7	7.3	22.9	3.76

[y]Cation exchange capacity

[z]Organic matter

Table 2. The nutrient concentration of red raspberries as affected by mycorrhizae and added soil P.

Treatments		Concentration of nutrients (dry wt. basis)								
		N	K	P	Ca	Mg	Mn	Cu	B	Zn
Mycorrhizae	ppm P	%					ppm			
Control	0	1.12[z]	.68	.09	1.64	.43	1394	11.8	114	72
	22	1.07	.78	.08	1.56	.35	1398	7.2	91	69
	44	.89	.56	.11	1.16	.29	1324	5.2	66	52
Innoculated[y]	0	1.24	.76	.14	1.45	.39	1391	10.2	115	59
	22	.98	.66	.12	1.37	.33	1453	6.3	78	62
	44	.89	.53	.14	1.22	.32	1565	10.6	69	58
LSD	(0.05)	.17	.07	.02	.19	.06	268	3.7	18	18

[y] innoculated with Glomus fasciculatus

[z] each value is the mean of 6 replications

Table 3. The nutrient uptake of red raspberry shoots as affected by mycorrhizae and added soil P.

Treatments		Shoot	Total shoot uptake								
		dry wt.	N	K	P	Ca	Mg	Mn	Cu	B	Zn
Mycorrhizae	ppm P	g/plant	mg/plant								
Control	0	4.10	45.90[z]	29.32	3.95	66.62	18.20	5.77	.05	.46	.31
	22	5.61	59.97	44.18	4.59	87.94	19.83	7.92	.04	.51	.39
	44	8.99	80.09	50.20	9.84	104.56	25.73	11.95	.05	.60	.46
Innoculated[y]	0	3.46	42.04	26.80	4.85	50.19	13.37	4.87	.04	.39	.20
	22	6.47	62.92	42.08	8.07	86.33	20.92	9.33	.04	.49	.38
	44	9.31	81.83	48.89	13.09	112.43	29.17	14.51	.10	.63	.55
LSD (0.05)		1.20	9.20	9.88	1.70	12.45	4.28	2.53	.30	.08	.13

[y] innoculated with Glomus fasciculatus

[z] each value is the mean of 6 replications

Fig. 1. Shoot dry weight as affected by soil P and innoculation with Glomus fasciculatus.

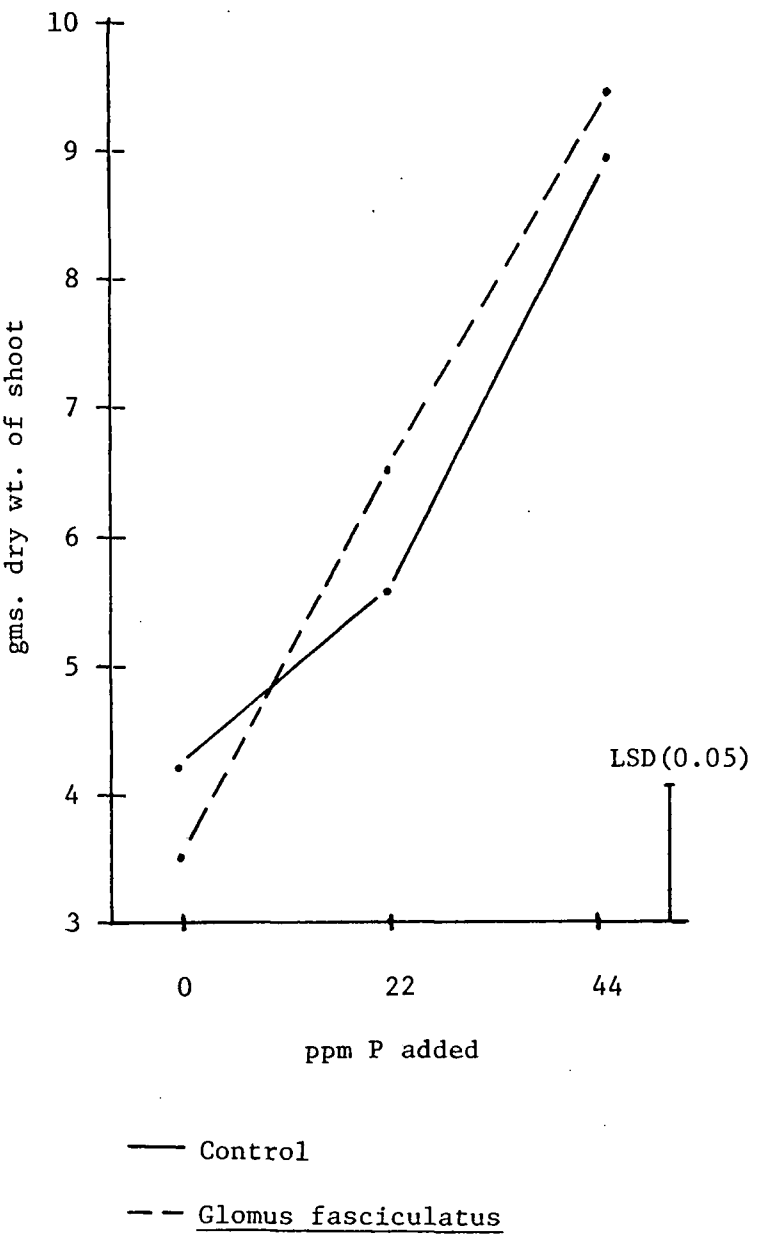

10
9
8
7
6
5
4
3
gms. dry wt. of shoot
LSD(0.05)
0
22
44
ppm P added
Control
Glomus fasciculatus

Fig. 2. P concentration (dry weight basis) as affected by soil P and innoculation with Glomus fasciculatus.

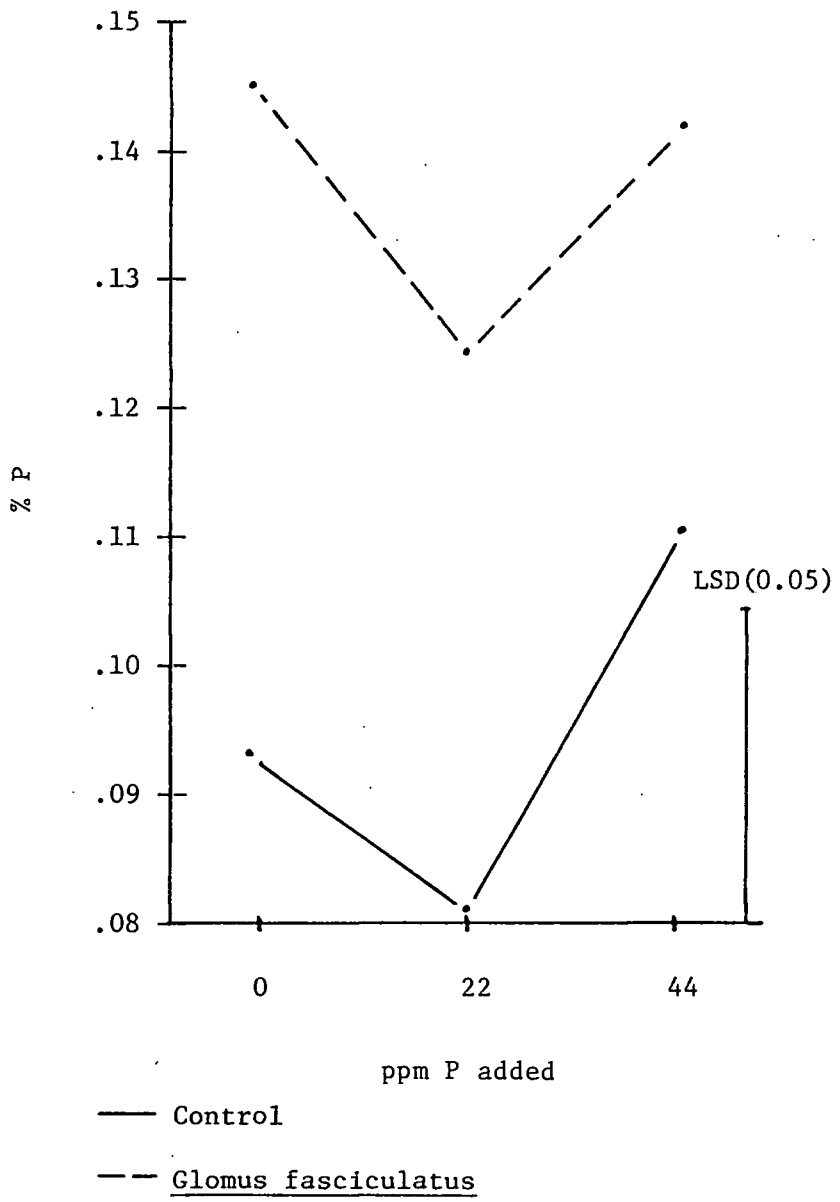
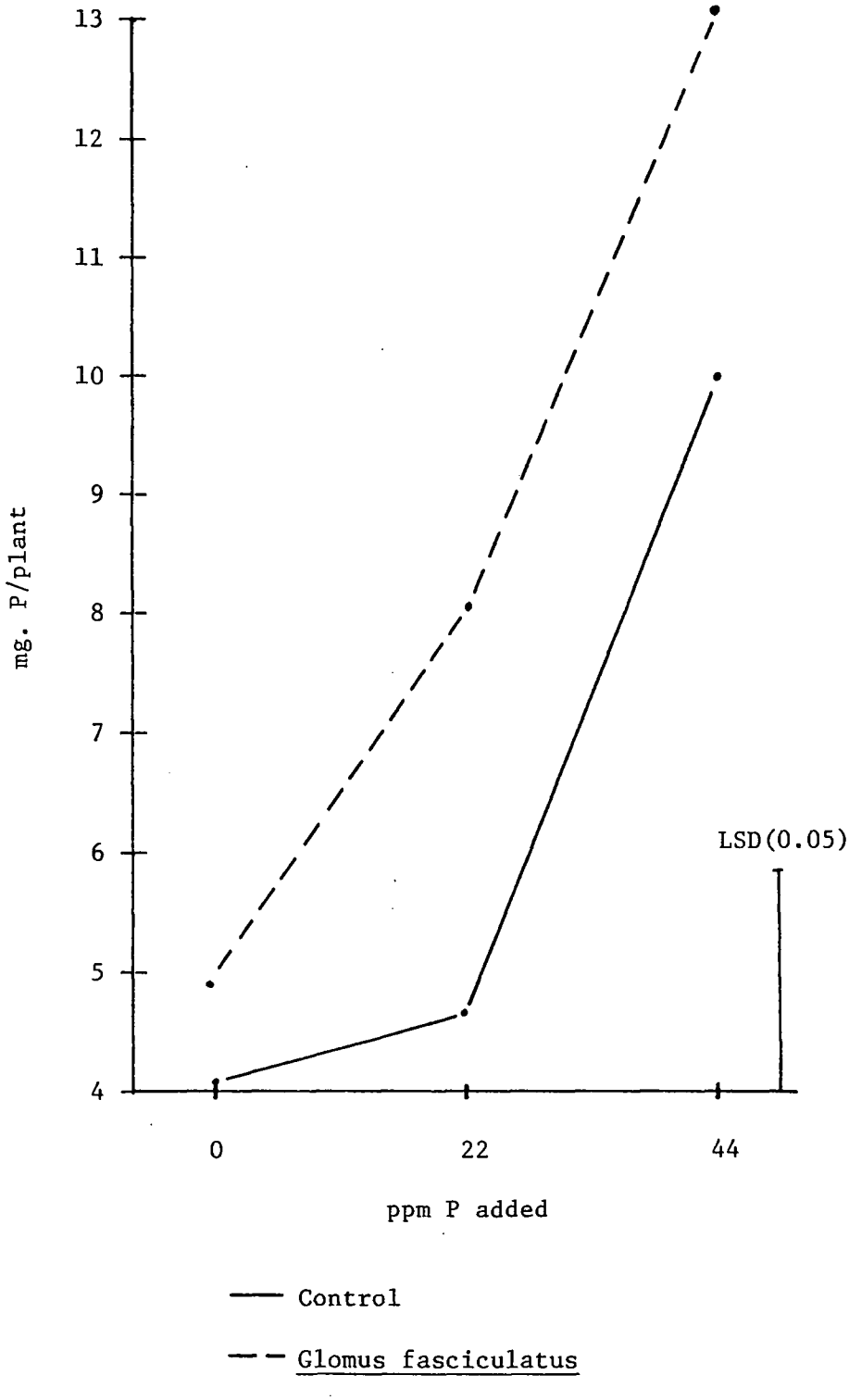

.15
.14
.13
.12
.11
.10
.09
.08
% P
LSD(0.05)
0
22
44
ppm P added
Control
Glomus fasciculatus

Fig. 3. Total shoot P as affected by soil P and innoculation with Glomus fasciculatus.


13
12
11
10
9
8
7
6
5
4
mg. P/plant
LSD(0.05)
0
22
44
ppm P added
Control
Glomus fasciculatus

Mycorrhizae and the nutrition of strawberries[1/]

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Abstract. Strawberries (Fragaria X ananassa Duches.) were grown at 3 levels of soil P and innoculated with 2 mycorrhizal fungus treatments: Glomus fasciculatus (Thaxter sensu Gerd.) Gerd. and Trappe, Gigaspora calospora (Nicol. and Gerd.) Gerd. and Trappe, and a control without mycorrhizal fungus. Both P and N concentrations in the shoots of innoculated plants were significantly higher than controls. Innoculation with Glomus fasciculatus resulted in the highest mycorrhizal root length and the highest % of infected root length out of the total. Innoculation with Glomus fasciculatus also resulted in the greatest concentration fo P and N in the shoots. Innoculation with Gigaspora calospora resulted in less infection and lower shoot concentration of P and N.

While mycorrhizal fungi have been found to produce growth substances and vitamins, and increase resistance to water stress in the host plant (14), their most important practical role is in plant nutrition. In particular, P uptake is greatly dependent on mycorrhizae. Numerous studies have shown that non-mycorrhizal plants are

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[2/] Department of Horticulture

generally lower in P concentration than mycorrhizal ones, and severe P deficiency often occurs in the absence of mycorrhizae (4,3,6).

Mycorrhizae may also promote the uptake of other elements. Peach seedlings grown in a low Zn soil were stunted and showed symptoms of Zn deficiency unless they were mycorrhizal (5). Other researchers have found differences between mycorrhizal and non-mycorrhizal plants in concentrations of other nutrient elements (1,4,8). However, because of the major role mycorrhizae play in P nutrition the effects of mycorrhizae on the uptake of other nutrients are difficult to interpret, since the non-mycorrhizal plants are often severely P deficient (11). More consistent evaluation of effects on other nutrients are obtained when non-mycorrhizal plants are given added P. Higher concentrations of N, Ca, Mg, Mn, Cu, and Zn, and lower concentrations of K in mycorrhizal plants have been found in experiments where controls received added P (6, 11, 15).

Individual species of vescicular-arbuscular (VA) endophytes will form mycorrhizae with a wide range of hosts, but some species are more beneficial to a particular host in a given soil than others. Onions innoculated with 7 different types of VA endophytes showed a wide range of growth responses (10). One strain produces a 15-fold increase in dry weight, whereas others resulted in little infection and only slightly increased growth. The strain that was most effective in one soil was only moderately so in a second soil in which several other strains produced more growth. This and other experiments led to the speculation that the specificity of a fungus depends more on its interaction with a soil type than with a particular

host (10).

The present study was designed to gain information on the effects of 2 different mycorrhizal fungi - Glomus fasciculatus and Gigaspora calospora - on the growth and mineral nutrition of strawberries at 3 levels of P. In addition, the relation between the extent of mycorrhizal infection and nutrient uptake was examined, as well as the effect of mycorrhizae on the levels of elements other than P.

Materials and Methods

A clay loam soil which averaged 12 ppm P (table 1) by the dilute acid fluoride method was autoclaved for 2 hours to achieve partial sterilization. Phosphoric acid was added and mixed thoroughly to produce 3 soil treatments of 0, 22 and 44 ppm added P. Fifty ppm N as NH_4NO_3 and 62 ppm K as K_2SO_4 were added to each treatment. The soil was weighed equally into 45 1-gallon pots and 1 strawberry was planted in each pot. The strawberries had been propagated in sterile medium from unrooted runners to avoid mycorrhizal contamination. At the time of planting a suspension of approximately 10 spores of Glomus fasciculatus was added to 1/3 of the pots and a suspension of approximately 10 spores of Gigaspora calospora was added to another third. The remaining pots received an equal volume of filtered leachate from the spores to introduce non-mycorrhizal contaminating organisms into all treatments.

The plants were grown in the greenhouse from June to January. All the above-ground portions of the plants were then harvested, dried to constant weight, and total dry weight was measured. The entire plant top was then ground and analyzed for elemental concentration.

Potassium, P, Ca, Mg, Mn, Cu, B and Zn were measured by emission spectroscopy (2) and N was measured by Kjeldahl (19). Total ahoot uptake of each element was then calculated.

The pots containing soil and roots were weighed and subsampled as follows: The soil in each pot was quartered and 2 opposite quarters were thoroughly mixed and quartered again. Two opposite quarters were again thoroughly mixed and quartered. One quarter was weighed and reserved for root sampling.

The soil samples were soaked in a 3% sodium hexametaphosphate solution to facilitate washing. The roots were quantitatively washed out before clearing, bleaching and staining (11). Total root length and total mycorrhizal root length were then measured by a sime-intercept technique (Ambler, J. R., Young, J. L. 1976. Techniques for determining vescicular-arbuscular rootlength. In press.)

Results

The dry weight of the aerial portion of the strawberry plants generally increased with increasing P levels. There were no significant differences in dry weight (5% level) due to fungus innoculation (fig.1).

There were significant differences due to fungus treatment in both P and N concentrations (fig. 2,4). Plants innoculated with Glomus fasciculatus had the highest concentration of P and N, while control plants were lower. Plants innoculated with Gigaspora calospora were intermediate in P and N concentration.

Total P uptake in the shoot was the same in all treatments at each level of P, except at the second P level where plants innoculated with Glomus fasciculatus had a much higher total P content (fig.3).

The effects of fungus innoculation on the concentrations of the other elements were not significant. In addition, P concentration differences were neither so consistent nor great as to allow comparisons of nutrient contents at equivalent P levels (table 2).

The results of the total root length measurements are shown in table 3. Ther greatest root length occurred at the highest P level in all treatments in plants innoculated with Glomus fasciculatus. Per cent of the total root length that was mycorrhizal and the actual length of infected roots is given in table 4. From this data it can be seen that innoculation with Glomus fasciculatus resulted in the highest infection, both in terms of root length infected and % of total root length infected.

Discussion

The 2 nutrients most affected by mycorrhizal innoculation were P and N. Both generally had their highest concentration in plants innoculated with Glomus fasciculatus and next highest in plants innoculated with Gigaspora calospora. Increased concentration and total uptake of P by mycorrhizal plants is usually found in studies of this nature and is thought to be due to the increased absorbing area of the mycorrhizal system (15). This is borne out by the measurements of both total and mycorrhizal root length in this study. The greatest mycorrhizal root length, both in absolute terms and as a % of total root length, occurred in plants innoculated with Glomus fasciculatus, which also had the highest P concentration. Plants innoculated with Gigaspora calospora had much less mycorrhizal root length, thus less absorbing area and lower P concentration.

The effects of mycorrhizal innoculation on N uptake observed in this study are much less easy to explain. Others who have found increased N uptake in mycorrhizal plants have ascribed it to improved P nutrition, not to fungal activity per se (13). In the present study N concentration decreased while total N uptake and dry weight tended to increase within each fungus treatment as soil P increased. However, there was a significant difference in N concentration between fungus treatments. Glomus fasciculatus resulted in the highest N concentration at 0 and 44 ppm added P. Since improved P nutrition within treatments resulted in a lower N concentration, the higher N concentration in mycorrhizal plants cannot be explained on the basis of P nutrition.

Since NO_3^- and NH_4^+, unlike $H_2PO_4^-$, are readily mobile in the soil, their replenishment by diffusion into the depleted area surrounding the root is not considered to be the rate-limiting factor in their uptake, a factor which is overcome in the case of P by an extensive mycorrhizal network. Thus mycorrhizae may improve N nutrition not as a result of their more extensive absorbing surface, but by some mechanism which accelerates other parts of the N uptake process. This may be an effect on the plants' uptake mechanism, or perhaps the fungi themselves have a more efficient means of absorbing N.

Both fungus treatments showed an increase in % root length infected at the highest P level. Previous reports showed a decrease in mycorrhizal infections at high levels of added P (7,13). High P levels in the host apparently make the root environment less attractive to the fungi (15). Since the initial level of P in the soil used in this study was quite low, the levels of P added were probably not

sufficient to discourage mycorrhizal infection.

The differences observed between the 2 fungi under similar soil and host conditions imply that selection of efficient strains of fungi for specific circumstances may be possible. So many factors may affect the host-fungus interaction, however, (soil type, climate, nature of the host and fungus, etc.) that the efficacy of a particular strain may have to be evaluated in each specific situation.

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Table 1. Soil test results for 2 samples of soil before sterilization.

Sample	pH	P (ppm)	K (meq/100 g)	Ca (meq/100 g)	Mg (meq/100 g)	CEC[y] (meq/100 g)	OM[z] (%)
1	6.5	19	.29	14.1	6.9	22.3	2.92
2	6.6	5	.26	14.7	7.3	22.9	3.76

[y]Cation exchange capacity

[z]Organic matter

Table 2. The nutrient concentration of strawberries as affected by mycorrhizae and added soil P.

Treatments		Concentration of nutrients (dry wt. basis)								
		N	K	P	Ca	Mg	Mn	Cu	B	Zn
Mycorrhizae	ppm P	%					ppm			
Control	0	1.12[z]	1.61	.24	.85	.34	1806	5.8	83	41
	22	1.87	1.87	.25	.85	.35	1405	6.2	87	45
	44	1.52	1.90	.30	1.11	.35	1431	5.6	75	47
Gigaspora	0	2.01	1.77	.25	.83	.34	1505	6.4	80	43
calospora	22	2.04	1.78	.27	.78	.35	1773	6.0	82	46
	44	1.76	1.83	.35	1.04	.34	.704	5.4	79	59
Glomus	0	2.21	1.64	.35	.80	.34	1495	7.6	77	53
fasciculatus	22	2.02	1.76	.35	.84	.35	1634	6.6	81	56
	44	1.88	1.84	.36	1.01	.36	1638	5.6	79	47
LSD (0.05)		.22	.19	.05	.08	.05	374	1.2	11	16

[z]Each value is the mean of 5 replications

Table 3. The nutrient uptake of strawberry shoots as affected by mycorrhizae and added soil P.

Treatments		Shoot	Total shoot uptake								
		dry wt.	N	K	P	Ca	Mg	Mn	Cu	B	Zn
Mycorrhizae	ppm P	g/plant	mg/plant								
Control	0	2.74	53.34[z]	44.05	6.62	23.20	9.49	4.83	.02	.23	.11
	22	3.06	56.07	57.32	7.51	26.12	10.73	4.19	.02	.26	.14
	44	5.50	81.91	107.52	16.12	61.33	19.21	7.56	.03	.41	.27
Gigaspora	0	2.74	55.27	48 92	6.93	22.83	9.18	4.07	.02	.22	.12
calospora	22	2.73	54.51	48.62	7.36	21.18	9.33	4.85	.02	.22	.12
	44	5.09	86.95	93.27	17.45	52.61	17.17	8.75	.03	.39	.31
Glomus	0	1.97	44.09	32.44	6.92	16.00	6.62	3.08	.01	.15	.10
fasciculatus	22	3.84	76.72	67.61	13.48	32.14	13.35	6.26	.03	.31	.23
	44	4.77	85.21	87.88	16.62	48.04	16.42	7.53	.03	.36	.22
LSD (0.05)		1.02	15.44	23.23	3.56	12.09	3.92	2.47	.01	.09	.11

[z]Each value is the mean of 5 replications

Table 4. Total root length of strawberries as affected by mycorrhizae and levels of added soil P.

P added	Mycorrhizae		
	Control	G.calo.[x]	G. fasc.[y]
ppm	cm		
0	2750c[z]	3350bc	2500c
22	3000bc	2750c	4000ab
44	4350a	4050ab	4350a

[x] Gigaspora calospora

[y] Glomus fasciculatus

[z] Values in any column followed by the same letter are not significantly different at the 5% level.

Table 5. Mycorrhizal root length of strawberries as affected by mycorrhizae and levels of added soil P.

P added	Mycorrhizae			
	G. calospora[w]		G. fasciculatus[x]	
ppm	cm	%[y]	cm	%[y]
0	70a[z]	2.1	305bc	12.2
22	73a	2.6	408c	10.2
44	253b	6.2	684d	15.7

[w] Gigaspora calospora

[x] Glomus fasciculatus

[y] % of total root length

[z] values in any column followed by the same letter are not significantly different at the 5% level.

Fig. 1 The response of shoot dry weight of strawberries to levels of added soil P and mycorrhizae.

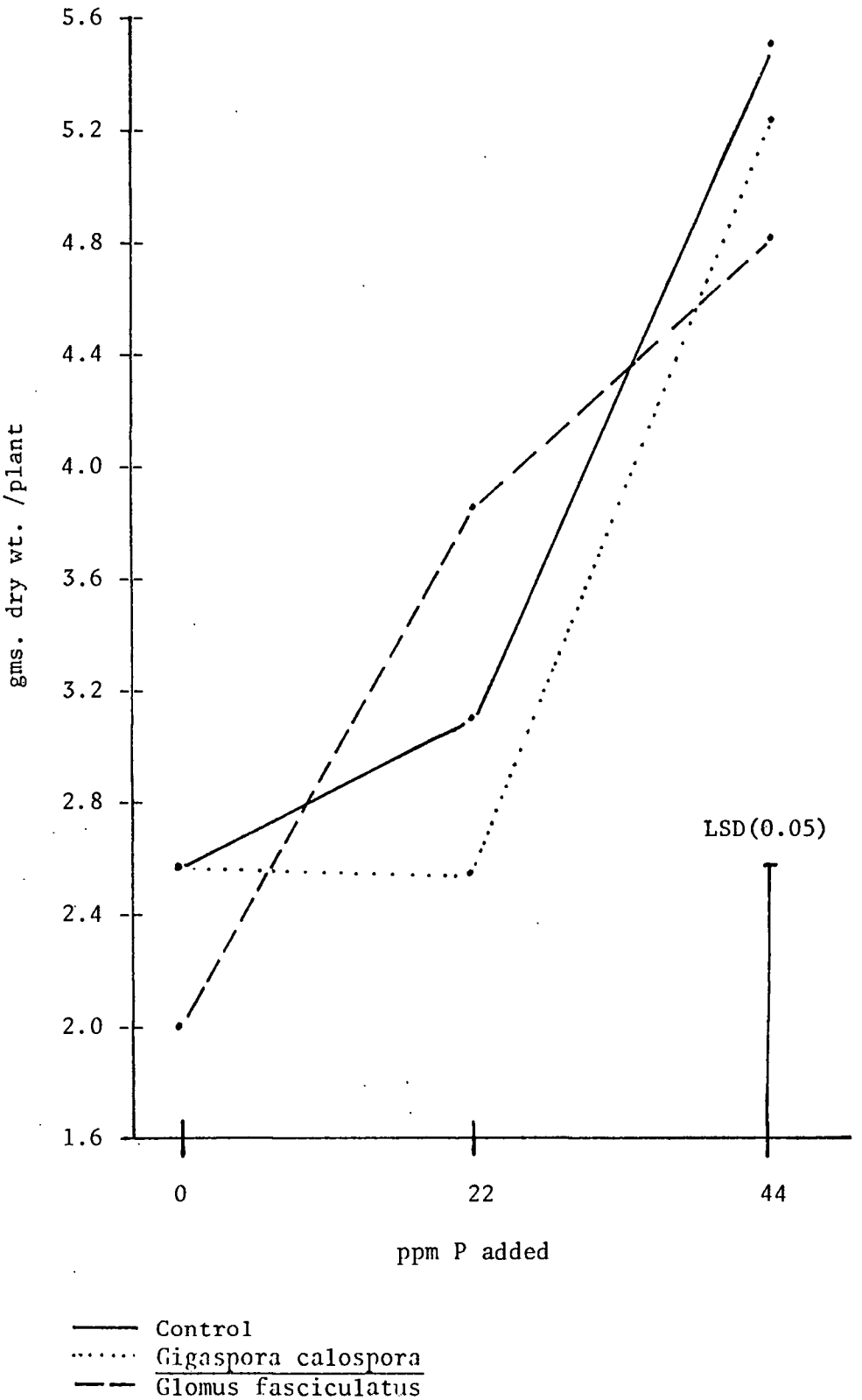

5.6
5.2
4.8
4.4
4.0
3.6
3.2
2.8
2.4
2.0
1.6
gms. dry wt. /plant
LSD(0.05)
0
22
44
ppm P added
Control
Gigaspora calospora
Glomus fasciculatus

Fig. 2 The response of shoot P concentration (dry weight basis) to levels of added soil P and mycorrhizae.

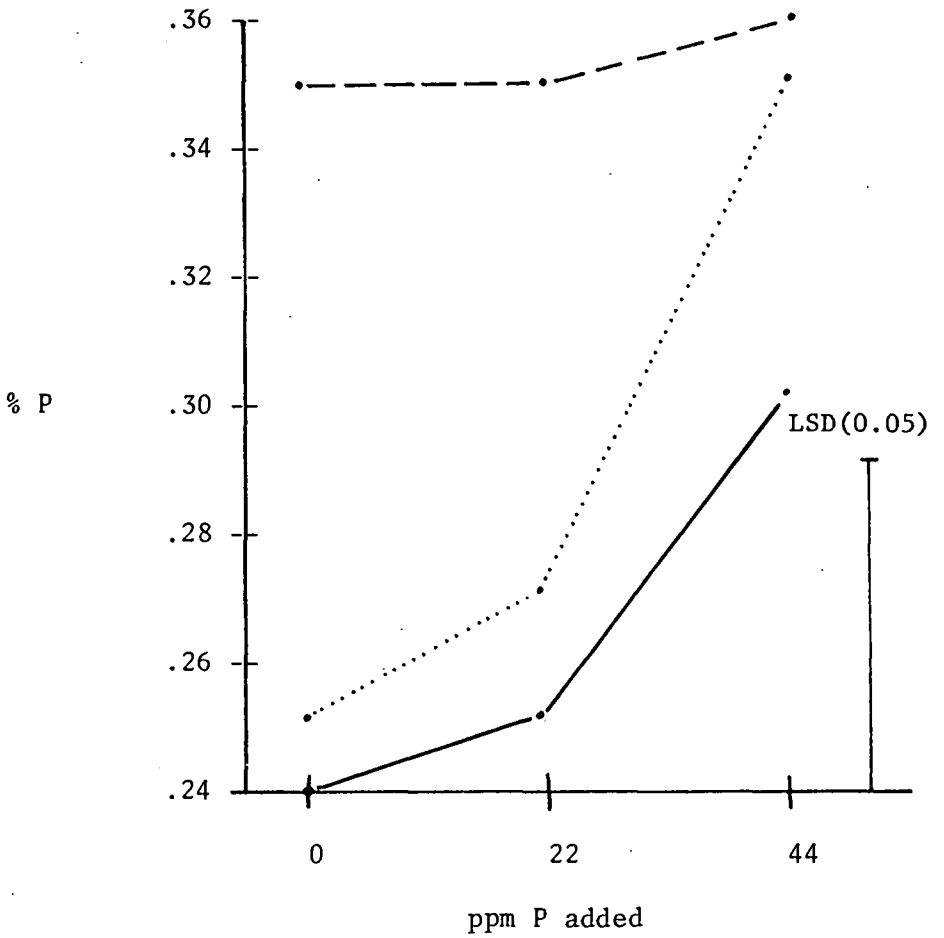

.36
.34
.32
% P
.30
.28
.26
.24
LSD(0.05)
0
22
44
ppm P added
Control
Gigaspora calospora
Glomus fasciculatus

Fig. 3. Total shoot P as affected by levels of added soil P and mycorrhizae.

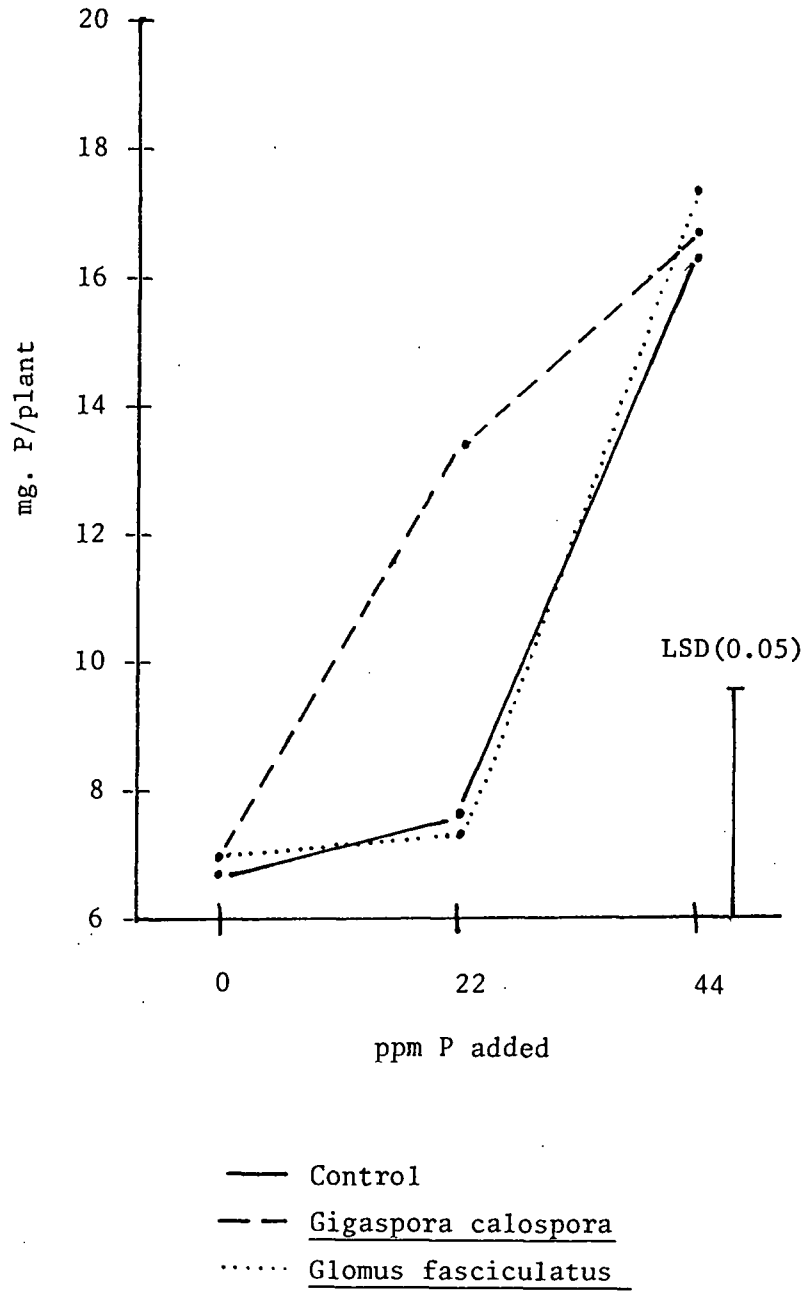
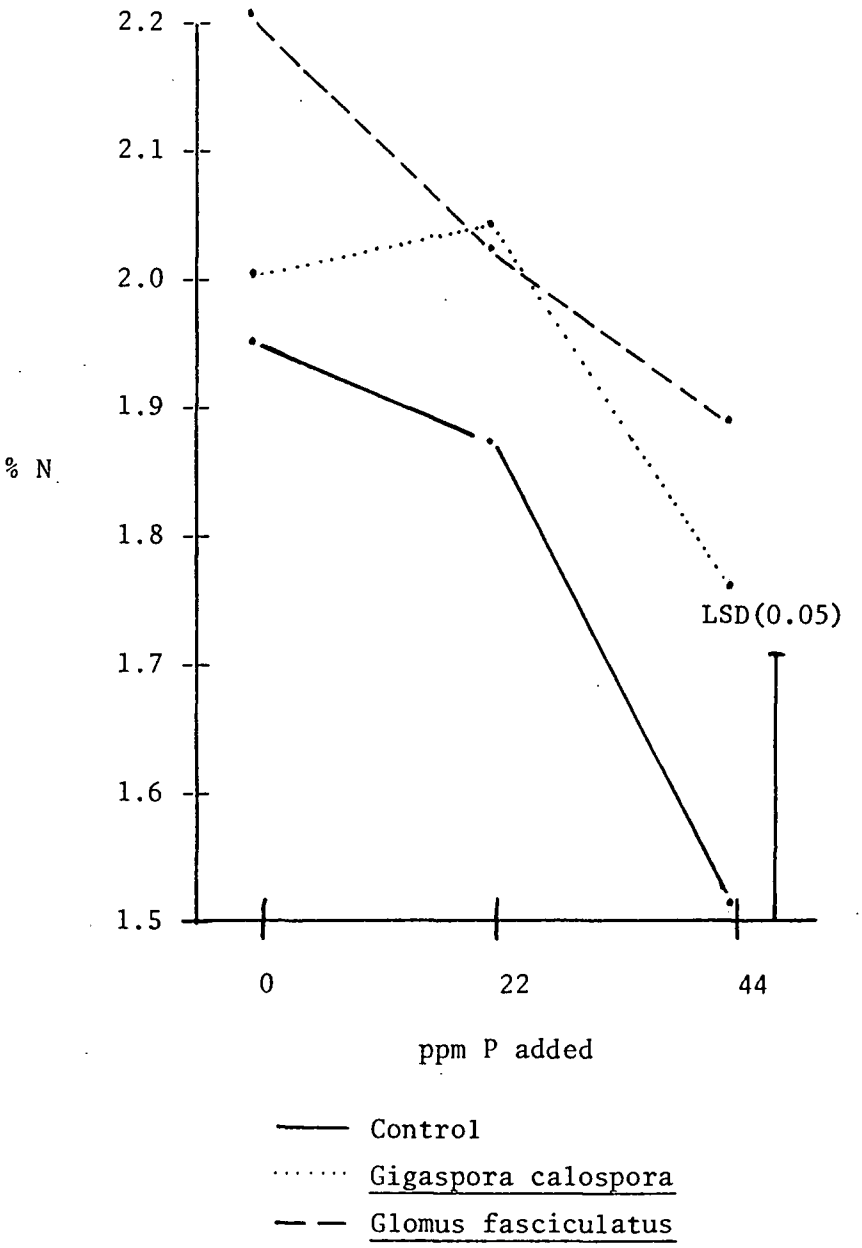

20
18
16
14
12
10
8
6
mg. P/plant
LSD(0.05)
0
22
44
ppm P added
Control
Gigaspora calospora
Glomus fasciculatus

Fig. 4. The response of shoot N concentration to levels of added soil P and mycorrhizae.


2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
% N
LSD(0.05)
0
22
44
ppm P added
Control
Gigaspora calospora
Glomus fasciculatus

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APPENDIX A

Elemental composition of red raspberry leaves as a function of time of season and position on cane[1/]

Megan Hughes [2/]

Oregon State University, Corvallis

Additional index words. Rubus idaeus L.

Abstract. Leaves of red raspberry (Rubus idaeus L. cv. Meeker) were sampled every 2 weeks through the season and at 7 different positions on the cane to determine the best time and positions for diagnostic leaf sampling. The last half of August and the positions identified as numbers 4, 5, 6, and 7 showed the least variation in nutrient concentrations and would be best for leaf sampling.

Leaf analysis is used to detect sub-optimal nutrition in a wide variety of crops. But before it can be used in this manner the type and magnitude of changes in leaf composition due to non-nutritional factors such as genotype, sampling date and leaf age must be determined.

The influence of genotype, age of plant and sampling date on leaf composition of red raspberries was investigated in British Columbia (3).

[1/] Received for publication _____, Oregon Agr. Expt. Sta. Tech. Paper No. _____.

[2/] Department of Horticulture

The youngest mature leaves of the primocanes were sampled and it was found that plant age did not significantly influence elemental concentrations, while date of sampling and genotype caused wide variation.

A similar study in Oregon, using the youngest mature leaves, produced such variable results that no conclusions could be drawn (Chaplin, unpublished). It was decided that the choice of "youngest mature leaf" was too dubjective to result in selection of leaves of equal age. A more precise means of identifying leaves to be sampled was needed. This study was undertaken to determine how elemental composition of leaves at specific positions varied through the season. Both leaf position and a period of the season could then be specified for more accurate diagnostic leaf sampling.

A uniform portion of a field of "Meeker" red raspberries was chosen for this study. Twenty samples were taken every 2 weeks during the period of July 16 to Sept. 9 in 1974. Each sample consisted of 3 moderate-sized canes (0.8-1.3 cm dia. at the base, approx. 180 cm tall) taken at random from the south side of one row. A separate row was used for each sample. The canes were than divided into 7 positions and leaves from all three canes were combined at each position. The positions were: the top 15 cm (6 in.)of the cane, measured from the tip of the longest leaf (this included the terminal and several unexpanded leaves), plus each successive 2 leaves down the cane (fig. 1).

Emission spectroscopy was used to determine leaf levels of K, P, Mg, Ca, Mn, B, Cu and Zn (1). Modified Kjeldahl (5) was used to

determine N levels.

Leaf concentrations of N, P and K were highest in the younger leaves and decreased steadily down the stem (figs. 2, 3, and 4). Nitrogen, P and K also showed a decline in concentration at each position through the season, especially in lower leaves (positions 4-7). As has been pointed out (2), these concentration decreases probably result from growth dilution as the leaves increase in dry weight. Similar results have been obtained with other crops, generally accompanied by an increase in N, P and K taken up by the leaves (4,6). Total uptake of nutrients was not measured in this study.

Concentrations of Mg and Ca were highest in lower leaves and decreased at upper positions (figs. 5,6). The concentrations showed a slight decrease through the season. Zinc and Mn concentrations both increased from upper to lower positions (figs. 7, 8). Zinc increased through the season while Mn decreased. Copper concentration was variable, with lower leaves generally higher in Cu (fig. 10). Leaf B decreased from upper to lower leaves (fig. 9). Levels at positions 4-7 remained nearly constant through the season, while younger leaves showed considerable fluctuation in B concentration.

The period of least flux of nutrient concentrations occurred in the last 2 weeks of August. This corresponded to a decline in rapid growth and, by the end of August, some plants had set terminal buds. However, at the last sampling date, all nutrient curves showed a sharp change. This was probably due to an unseasonable rain in early September, which caused the plants to resume growth. Normally the concentration curves would be expected to continue as they had in

August.

As the best correlation of leaf composition with plant mineral status occurs when the internal nutrient flux is at a minimum (6), the last half of August seems to be the best time to take leaf samples of red raspberries. Nutrient levels tended to be widely different at each sampling date at posirions 1-3, but levels at positions 4-7 did not vary as much. There would thus be less chance of variation due to position of leaf sampled by choosing leaves from position 4 or below. This specification overcomes the problem of subjectivity in deciding which is the "youngest mature leaf".

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Proc. 37:480-481.

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Fig. 1. Schematic drawing of red raspberry cane, showing 7 positions sampled.

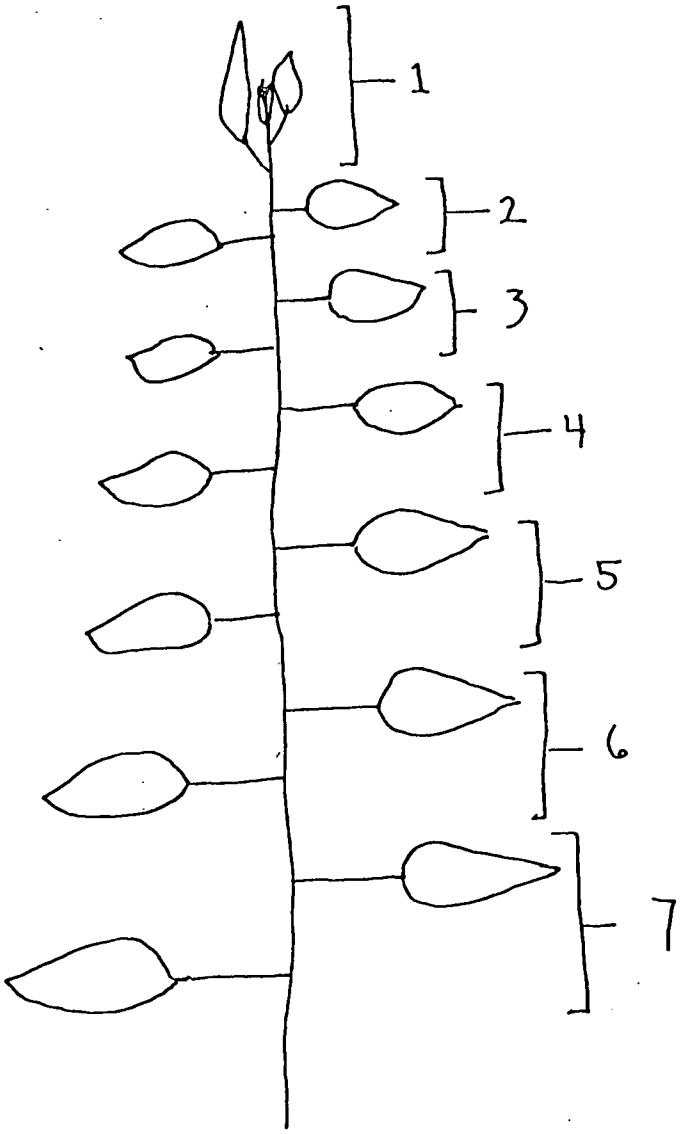

1
2
3
4
5
6
7

Fig. 2 N concentration (dry weight basis) of leaves at different positions as a function of sampling time.

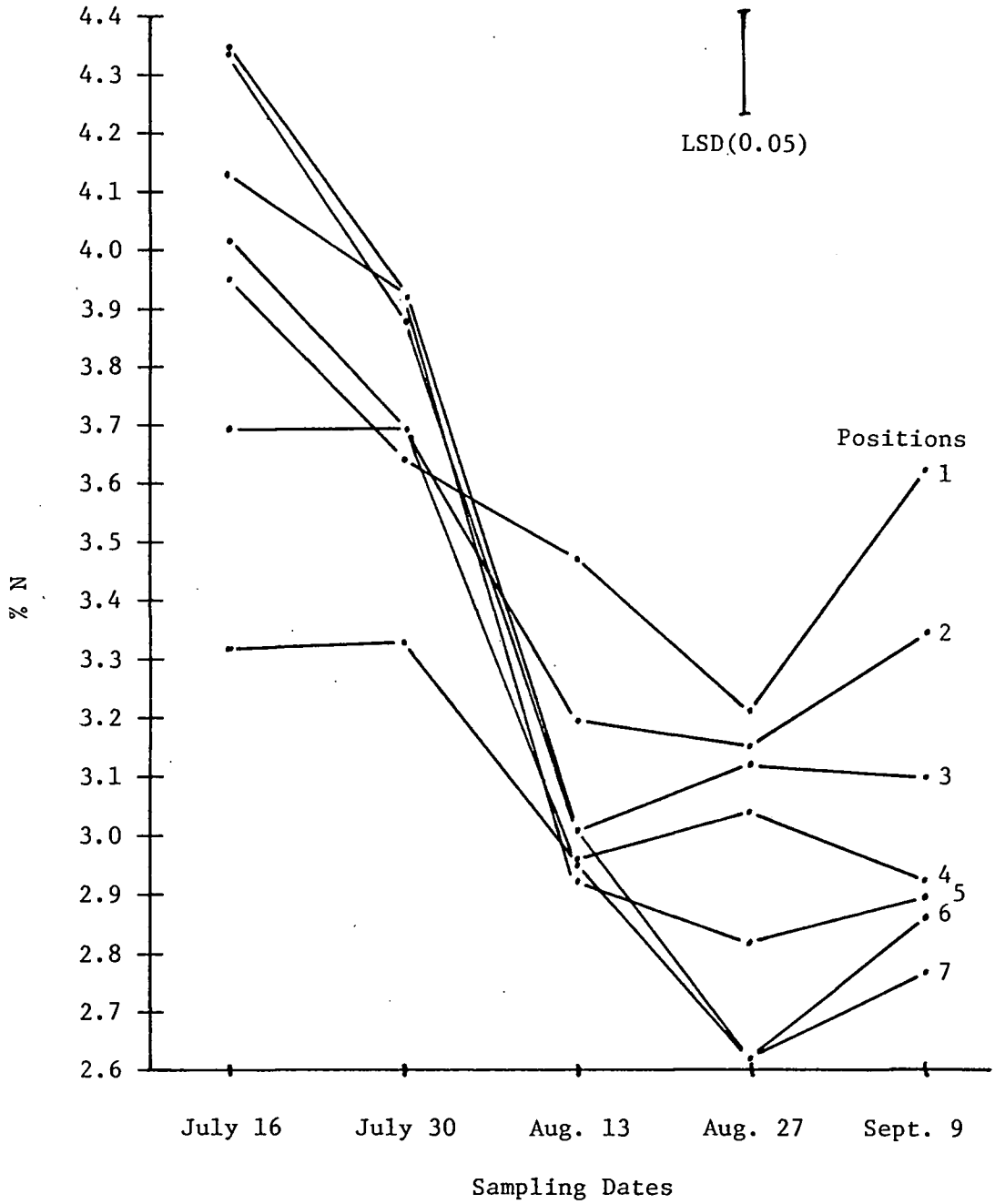

4.4
4.3
4.2
4.1
4.0
3.9
3.8
3.7
3.6
3.5
3.4
3.3
3.2
3.1
3.0
2.9
2.8
2.7
2.6
% N
LSD(0.05)
Positions
1
2
3
4
5
6
7
July 16
July 30
Aug. 13
Aug. 27
Sept. 9
Sampling Dates

Fig. 3 K concentration (dry weight basis) of leaves at different positions as a function of sampling time.

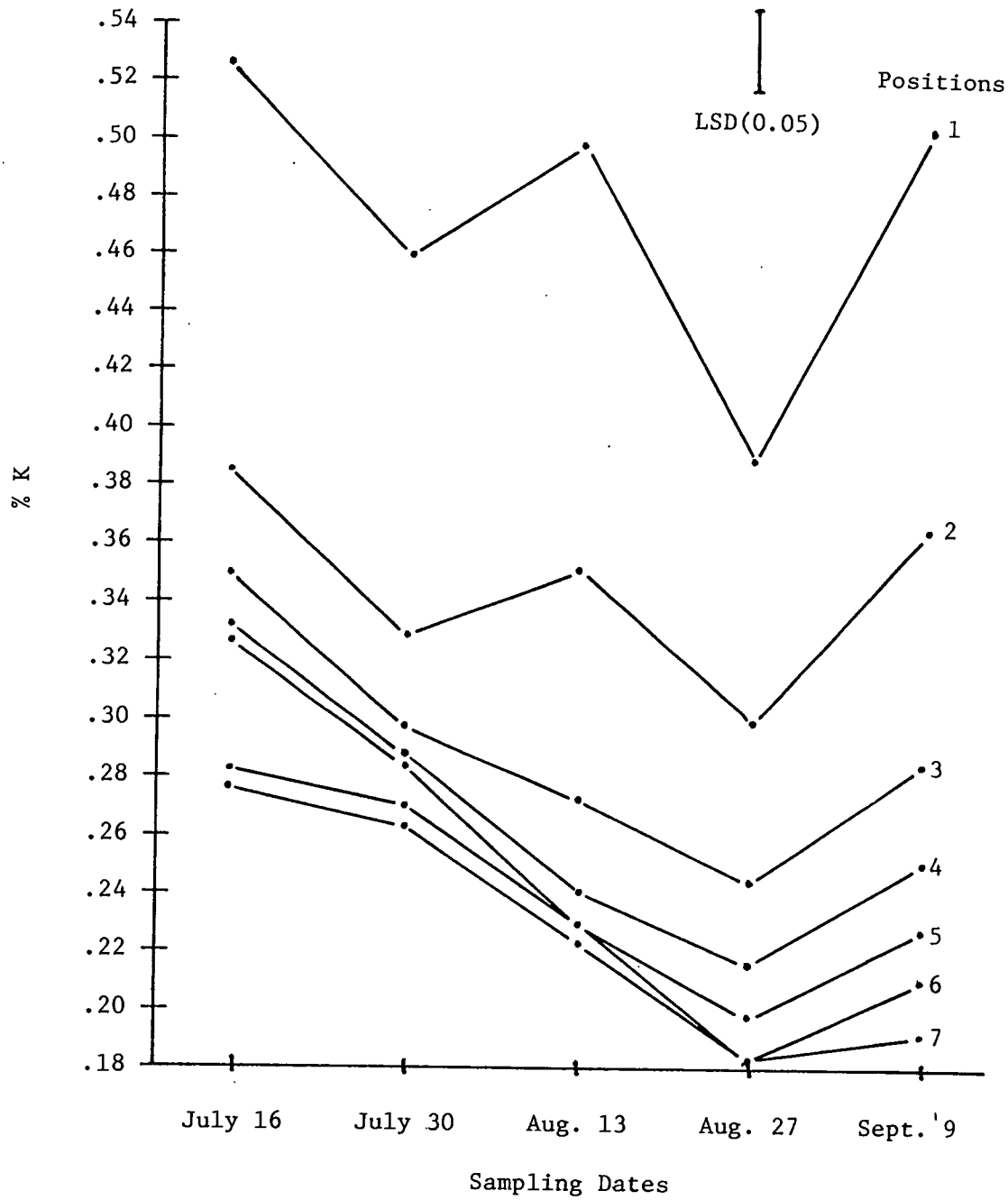

.54
.52
.50
.48
.46
.44
.42
.40
.38
.36
.34
.32
.30
.28
.26
.24
.22
.20
.18
% K
LSD(0.05)
Positions
1
2
3
4
5
6
7
July 16
July 30
Aug. 13
Aug. 27
Sept. 9
Sampling Dates

Fig. 4 P concentration (dry weight basis) of leaves at different positions as a function of sampling time.

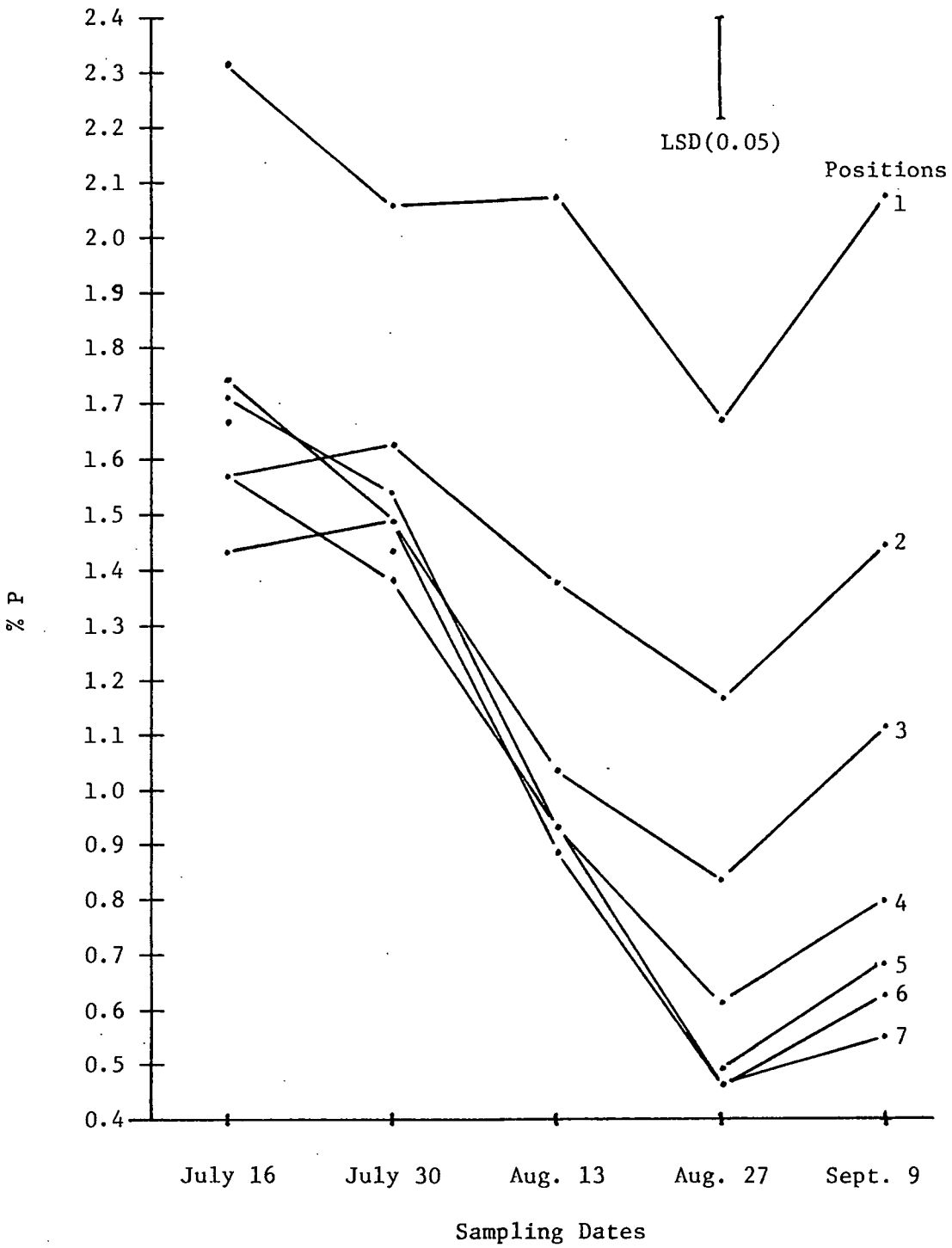

2.4
2.3
2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
% P
LSD(0.05)
Positions
1
2
3
4
5
6
7
July 16
July 30
Aug. 13
Aug. 27
Sept. 9
Sampling Dates

Fig. 5 Ca concentration (dry weight basis) of leaves at different positions as a function of sampling time.

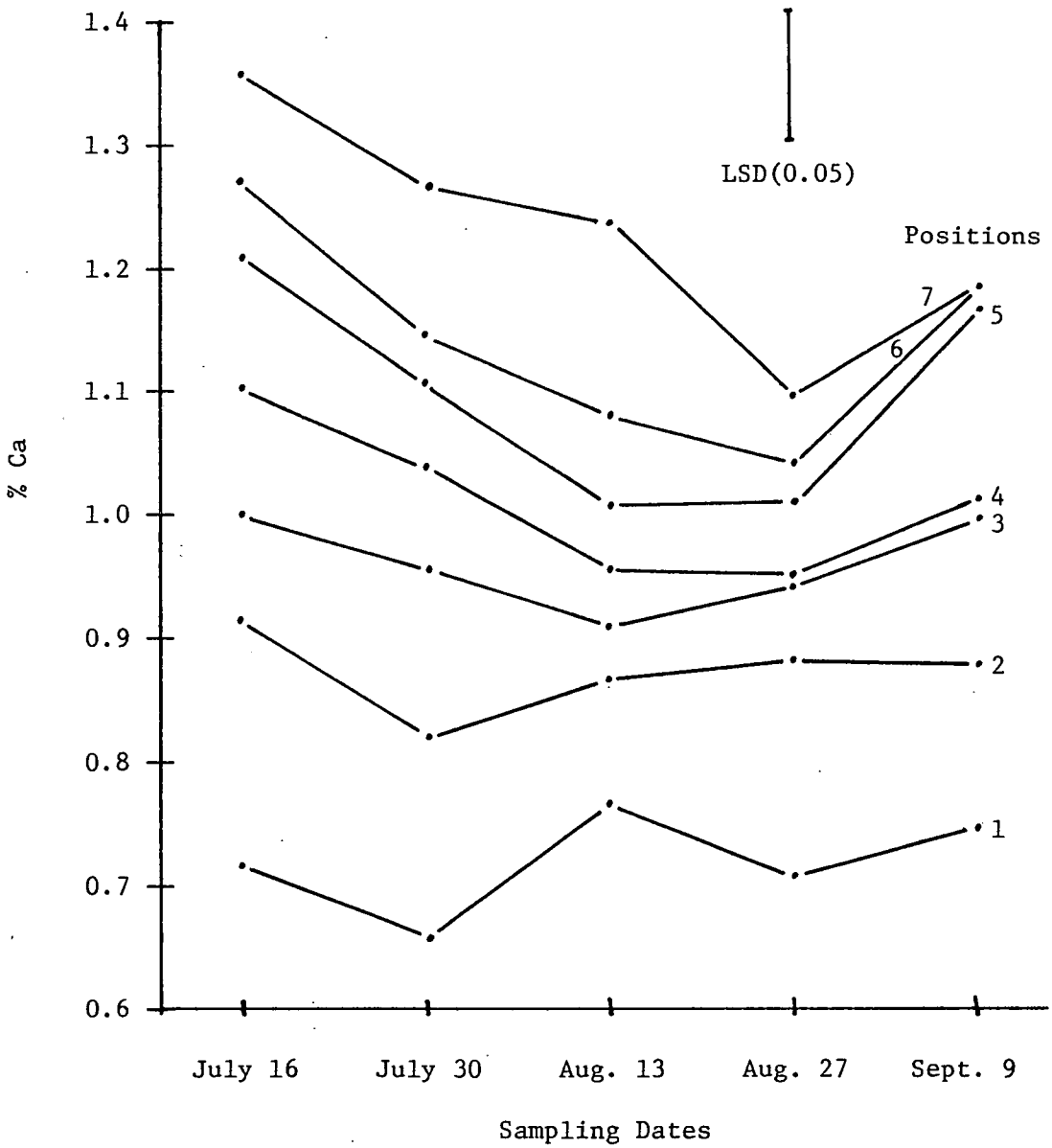

1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
% Ca
LSD(0.05)
Positions
7
6
5
4
3
2
1
July 16
July 30
Aug. 13
Aug. 27
Sept. 9
Sampling Dates

Fig. 6 Mg concentration (dry weight basis) of leaves at different positions as a function of sampling time.

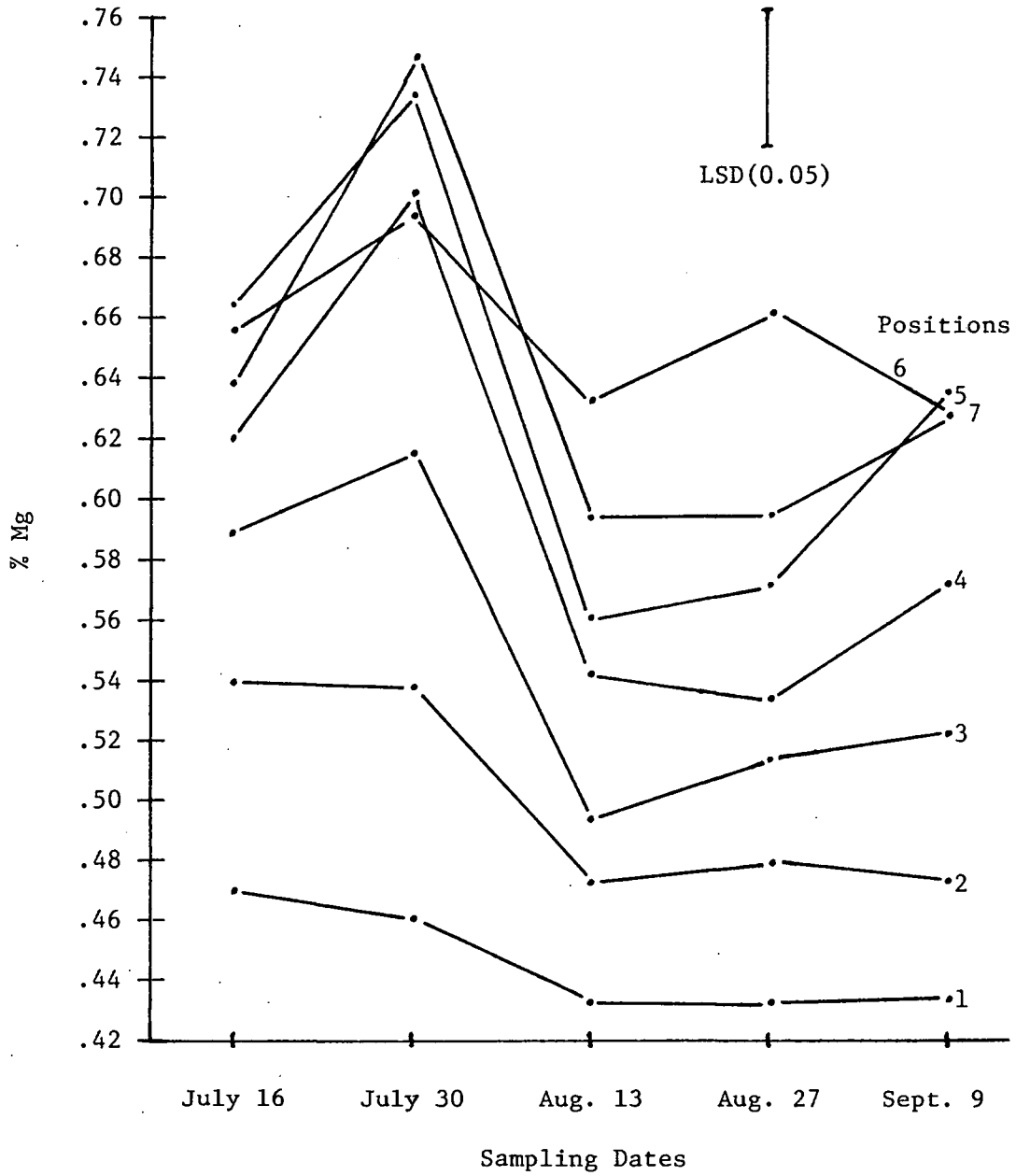

.76
.74
.72
.70
.68
.66
.64
.62
.60
.58
.56
.54
.52
.50
.48
.46
.44
.42
% Mg
LSD(0.05)
Positions
6
5
7
4
3
2
1
July 16
July 30
Aug. 13
Aug. 27
Sept. 9
Sampling Dates

Fig. 7 Mn concentration (dry weight basis) of leaves at different positions as a function of sampling time.

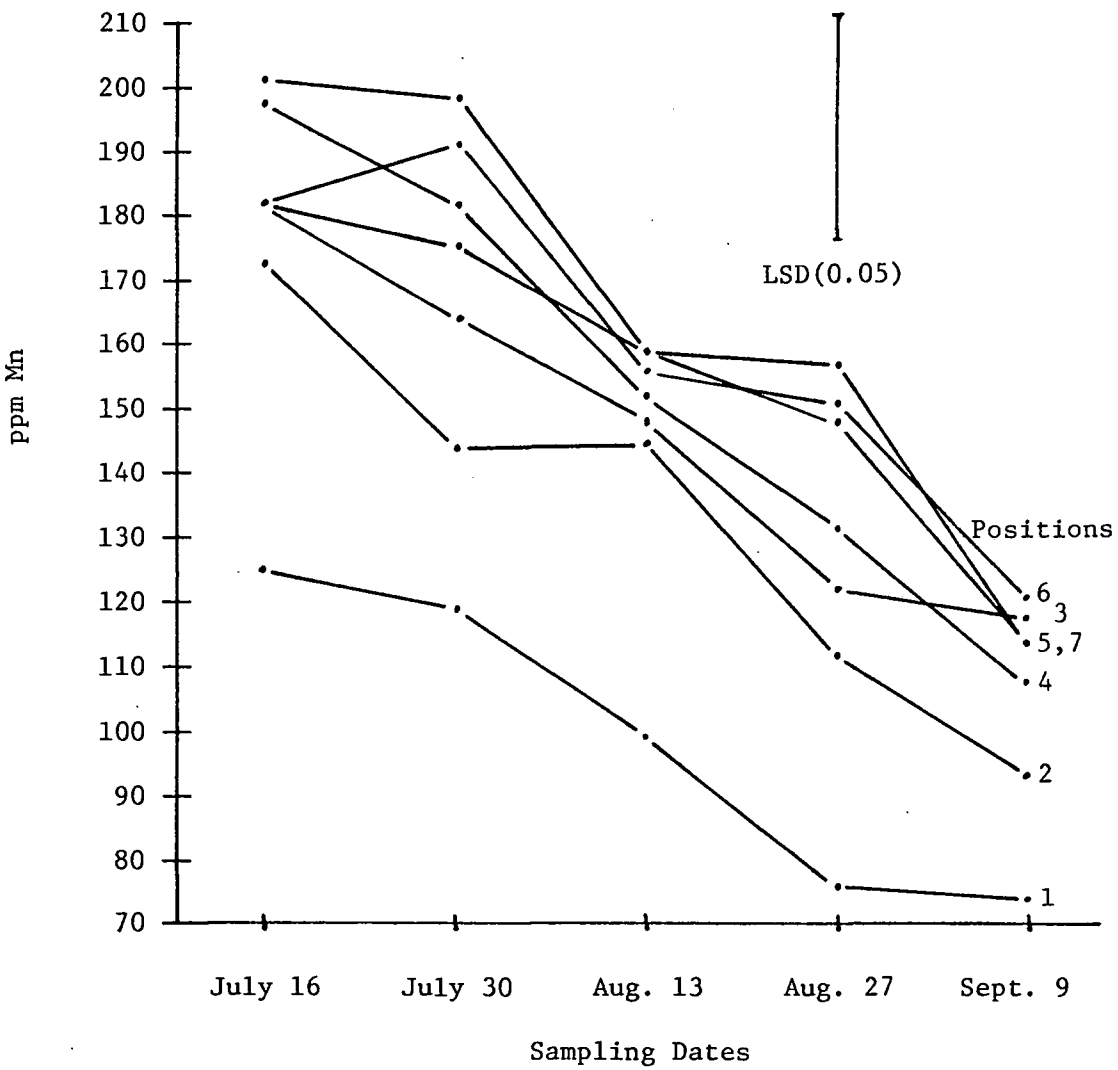

210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
ppm Mn
LSD(0.05)
Positions
6
3
5,7
4
2
1
July 16
July 30
Aug. 13
Aug. 27
Sept. 9
Sampling Dates

Fig. 8 Zn concentration (dry weight basis) of leaves at different positions as a function of sampling time.

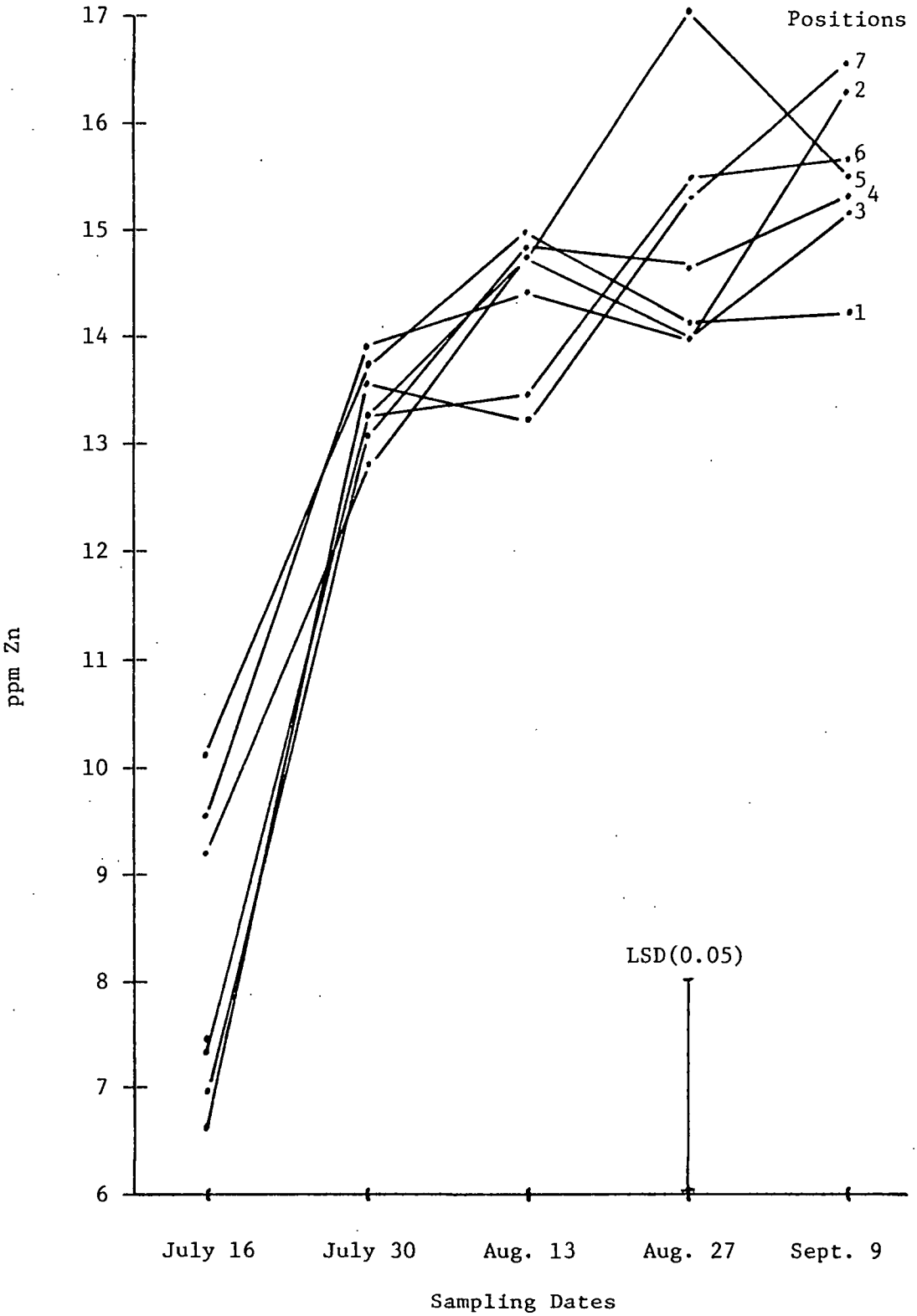

Positions
7
2
6
5
4
3
1
17
16
15
14
13
12
11
10
9
8
7
6
ppm Zn
LSD(0.05)
July 16
July 30
Aug. 13
Aug. 27
Sept. 9
Sampling Dates

Fig. 9 B concentration (dry weight basis) of leaves at different positions as a function of sampling time.

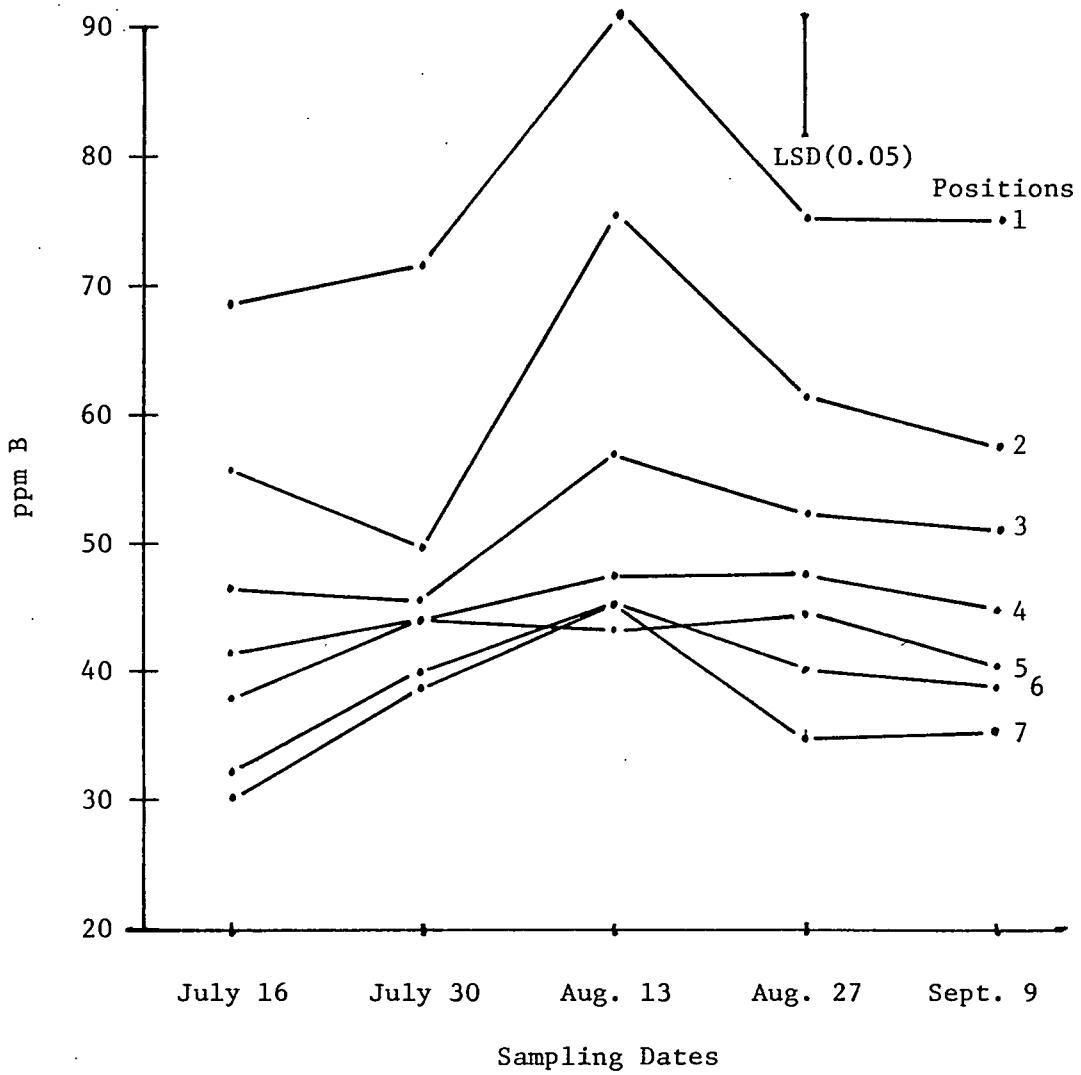
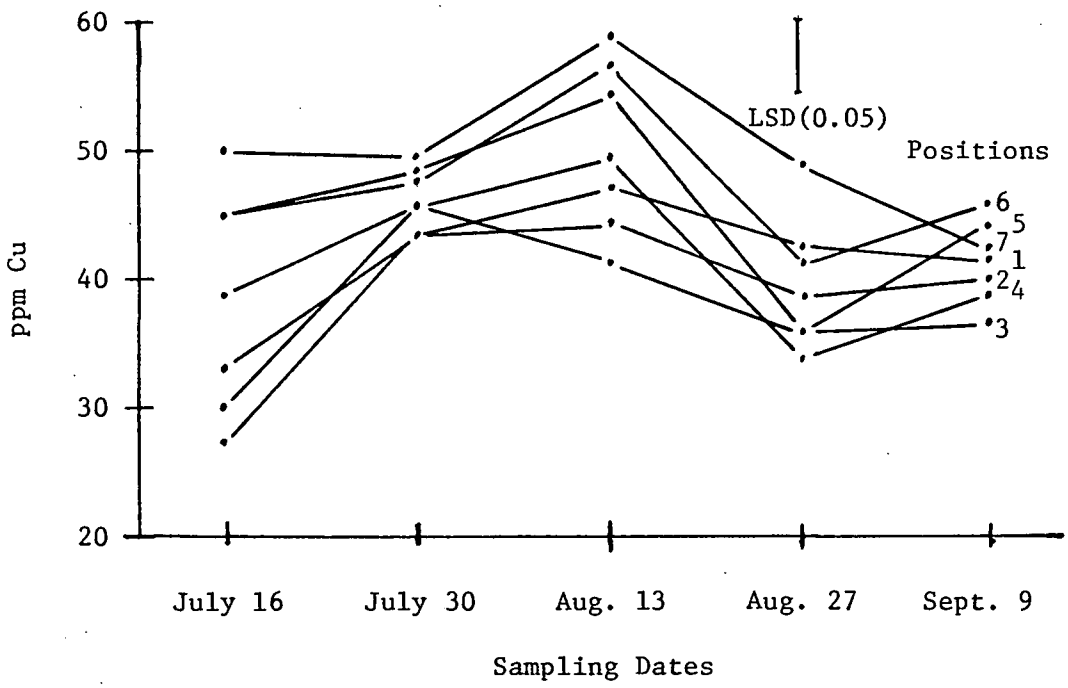

90
80
70
60
50
40
30
20
ppm B
LSD(0.05)
Positions
1
2
3
4
5
6
7
July 16
July 30
Aug. 13
Aug. 27
Sept. 9
Sampling Dates

Fig. 10 Cu concentration (dry weight basis) of leaves at different positions as a function of sampling time.


60
50
40
30
20
ppm Cu
LSD(0.05)
Positions
6
5
7
1
2
4
3
July 16
July 30
Aug. 13
Aug. 27
Sept. 9
Sampling Dates

APPENDIX B

LITERATURE REVIEW

An extensive review of the literature on vescicular-arbuscular mycorrhizae has been published by Gerdemann (1968). More recently Mosse (1973) reviewed the work since then. Rather than attempting to duplicate the efforts of these two reviewers, this review presents only a brief summary of work on the role of mycorrhizae in phosphorus nutrition. The recent work of Sanders and Tinker (1971, 1973) on the physical mechanism of improved P nutrition in mycorrhizal plants is discussed in detail.

Gerdemann (1964) was one of the first to notice that mycorrhizae seemed specifically involved in P uptake. He found that non-mycorrhizal plants showed P deficiency symptoms while mycorrhizal plants were larger, removed more P from the soil and had a larger per cent P in both tops and roots. Others, including Holevas (1966), Daft and Nicolson (1969) and Possingham (1971), working with strawberries, tomatoes and grapevines, respectively, reported similar effects of mycorrhizae on P nutrition.

Further indications of the role of mycorrhizae in P nutrition came with the discovery that the addition of P fertilizer to strawberries would simulate the effects of mycorrhizae (Holevas 1966). Ross (1971) and Daft and El-Giahmi (1974) repeated these results with soybeans and green beans, respectively. It was found that the addition of P usually improves the growth of non-mycorrhizal plants more than it does mycorrhizal ones and sometimes even reduces the growth of mycorrhizal plants (Mosse 1973).

However, the source and availability of the added P determines whether non-mycorrhizal plants can use it adequately. Murdoch et al. (1967) found that mycorrhizal and non-mycorrhizal maize grew equally well when P was added in a soluble form (super phosphate or mono-calcium phosphate). In a less soluble form (tricalcium phosphate, rock phosphate), mycorrhizal maize had a higher P concentration and grew larger than non-mycorrhizal plants. Similar results were reported by Daft and Nicolcon (1966) using apatite (slowly soluble), dicalcium phosphate (readily soluble) and tricalcium phosphate as phosphorus sources.

The question of whether the fungi themselves absorb P and transfer it to the host plant or whether mycorrhizal infection induces the plant roots alone to acquire more P was dealt with by Hattingh et al. (1973). They used autoradiography to measure ^{32}P accumulation by mycorrhizal and non-mycorrhizal onions. ^{32}P as $H_3{}^{32}PO_4$ added to the soil 27 mm from the root was taken up by mycorrhizal onion roots but not by non-mycorrhizal roots. However, when the hyphae growing from the roots were severed before the addition of labeled P mycorrhizal roots did not differ in ^{32}P content from non-mycorrhizal roots. The authors concluded that the fungi were directly responsible for P uptake, and that they enable plants to remove P from larger soil volumes beyond the immediate vicinity of the root surface.

Experiments by Hayman and Mosse (1972) and Mosse et al. (1973) gave further support to Hattingh's conclusion. Using various species and several soils labeled with ^{32}P they measured the ratio of ^{32}P

to total P 9specific activity) of mycorrhizal and non-mycorrhizal plants. If the specific activities differed it would indicate that mycorrhizal plants used P from different sources than did non-mycorrhizal plants. However, there was no significant difference between the two, enabling the authors to conclude that mycorrhizal roots did not have access to unique sources of P. They also concurred with the conclusion that greater exploration of the soil by mycorrhizae was responsible for greater P uptake.

Sanders and Tinker (1971) further refined the use of ^{32}P-labeled soil to pinpoint the means my which mycorrhizal plants accumulate P. Mycorrhizal and non-mycorrhizal onions were harvested on four occasions during 4.5 weeks. At each harvest total P contents of shoot and root, level of radioactivity and the P concentration and specific activity of the soil solution were measured. Not only the specific activity of the mycorrhizal and non-mycorrhizal plants but also that of the soil solution were similar. The authors believe this indicated that both groups of plants absorbed their P from the soil solution or forms in rapid equilibrium with it. They found it highly unlikely that the major effects of mycorrhizae are due to the fungus having special access to organic P or non-exchangeable inorganic P.

The area immediately surrounding the root surface is quickly depleted of P, with the result that the major factor limiting P uptake is the speed at which P in this zone is replenished by diffusion from other areas. Sanders and Tinker (1971, 1973), using the measurements discussed above, calculated a theoretical maximum of P inflow into the

depleted root zone. This figure, 3.5×10^{-14} mole/cm/sec, is close to the P influx rate for non-mycorrhizal plants, calculated from root length and P uptake measurements. The influx of P into mycorrhizal plants, however, was four times greater. Further calculations indicated that approximately 50 cm of hyphae per cm of infected root would be sufficient to account for the greater influx of P into mycorrhizal roots. Measurements made on the onion plants indicated they had about 80 cm hyphae per cm of infected root, or an average of 45 cm hyphae per cm of total root length. It appears that there was sufficient hyphae to absorb the extra P.

In order to elucidate the means by which this P was transported from its hyphal entry site to the plant root, the authors calculated the concentration gradient that would be necessary if the diffusion through the hyphae was at least as fast as through water. This concentration gradient - of the order of 4 moles $H_2PO_4^-$ /liter/cm - was thought too large for diffusion to account for the observed rates of P transport. They then postulated some form of mono- or bi-directional streaming through the hyphae. Calculation of the velocity of the bulk monoOdirectional flow needed to deliver the required amount of P at a concentration of 0.2% P gives 2.2 cm/hr. This velocity was considered reasonable.

Sanders and Tinker (1973) feel that mycorrhizal infection should be beneficial wherever the maximum diffusion of an ion into the depleted root zone is less than that required for optimum plant growth. This is supported by Gilmore (1971) who reports alleviation of Zn deficiency by mycorrhizae, and by Mosse (1973), who finds

increased Mn uptake in mycorrhizal plants. Both ions have low diffusion coeficients in the soil (Halstead and Barber, 1968; Warncke and Barber, 1971). Since molybdenum also has a low diffusion coeficient (Lavy and Barber, 1964), its uptake should also be enhances by mycorrhizae, although this has not yet been reported.

The precise, quantitative methods of Sanders and Tinker (1971, 1973) deserve to be expanded into other areas of mycorrhizal research. The Questions of mechanisms of hyphal uptake and translocation, transfer to the host, and which ions (or other substances) are involved could be profitably attacked with physical methods. More immediately practical research, such as the selection of specific strains of fungi for specific needs and the possibility of field innoculation, lends itself more to the field-oriented, qualitative research that is most prevalent in mycorrhizal investigations.

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