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Potential for Phosphorus Toxicity in Zinc-Stressed Corn and Potato

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ABSTRACT

Corn (*Zea mays* L., 'Illinois WF 9×38-11') and potato (*Solanum tuberosum* L., 'Russet Burbank') were grown in dithizone purified nutrient solutions to contrast relationships between dry matter yield, tissue phosphorus (P) concentration, and tissue zinc (Zn) concentration as they influence the development of Zn deficiency and P toxicity. Treatments consisted of Zn at 0, 0.14, and 0.41 μM in factorial combination with P at 0.02, 0.10, 1.0, and 3.0 mM. Yield and tissue concentration of P and Zn were affected by statistically significant P-Zn treatment interactions in both species. Corn plants developed Zn deficiency symptoms and responded to nutrient solution Zn when plant growth was not limited by inadequate nutrient solution P. Corn plants grown in nutrient solutions containing 0 μM Zn and 3.0 mM P contained 3.39% P in leaf tissue and had significantly lower yields than did plants grown in nutrient solutions containing 1.0 mM P. Even though no visual symptoms were evident, P toxicity probably was responsible for the reduction in yield. Potato plants responded to nutrient solution Zn when growth was not limited by inadequate P but did not exhibit visual symptoms of Zn deficiency. Zinc-deficient potato plants containing in excess of 2.22% P in leaf tissue exhibited probable P toxicity symptoms characterized by puckering of leaf edges, thickening and upward curling of leaves, and leaf necrosis. Excessive concentration of P in leaf tissue of Zn-deficient potato was the result of increased mobilization and translocation of P from roots to above-ground parts, increased total P uptake, and concentration of P resulting from restricted growth. Excessive levels of P in corn leaf tissue were primarily the result of concentration of P due to restricted growth. Zinc concentration in tissue of both species was reduced by growth response dilution, but Zn uptake by plants receiving low levels of Zn was not reduced by increasing nutrient solution P concentrations. Apparent accentuation of Zn deficiency by P application is explained on the basis of accumulation of toxic levels of P in Zn-deficient plants. Species such as potato which show increased P uptake and increased mobilization and translocation of P to tops when under Zn stress are probably more susceptible to P toxicity.

Additional Key Words: *Zea mays* L., *Solanum tuberosum*, dilution effects, nutrient uptake.

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DEVELOPMENT OF ZINC (Zn) deficiency and its apparent accentuation following phosphorus (P) fertilization has become known as a "P-induced Zn deficiency." The interaction is observed predominantly when plants are grown on soils or growth media low in available Zn, and it can be corrected or prevented by modest Zn applications (Olsen, 1972). Mechanisms which have been proposed to explain the interaction include (i) P-Zn interactions within the soil, (ii) dilution of Zn in plant tissues by growth response to P, (iii) reduced uptake or translocation of Zn in the presence of added P, and (iv) P interference with the utilization of Zn by the plant (Olsen, 1972). Recent investigations (Loneragan et al., 1979) have demonstrated that at least three distinct phenomena contribute to the P enhancement of Zn deficiency in subterranean clover (*Trifolium subterraneum* L.). Two of these phenomena induce true Zn deficiency, whereas the third results in symptoms

similar to some expressions of Zn deficiency. Where ferruginous sand was used as the growth medium, application of P fertilizer induced a true Zn deficiency by depressing Zn absorption. This suggested to Loneragan et al. (1979) that P-enhanced bonding of Zn to oxides and hydroxides of iron (Fe) and aluminum (Al) may be important in some soils. Where P limited growth on siliceous sand, additional P induced a true Zn deficiency by promoting growth which diluted plant tissue Zn to concentrations below the critical level. Where P did not limit growth, additional P did not induce a Zn deficiency but increased P concentrations in plant tops to toxic levels. Where plants were marginally Zn deficient, added P produced P toxicity symptoms in addition to characteristic Zn deficiency symptoms which enhanced the apparent severity of the Zn deficiency.

Elevated levels of P in tops of Zn-deficient plants have been reported for corn (*Zea mays* L.), potato (*Solanum tuberosum* L.), and other crops. Correction of Zn deficiency in corn usually reduces P concentration but not P uptake by tops (Jackson et al., 1967; Sharma et al., 1968; Terman, Giordano, and Christensen, 1975; Henning³). Correction of Zn deficiency in potato often reduces both P concentration and P uptake by plant tops (Boawn and Leggett, 1964; Henning³). Under field conditions in Oregon, Jackson and Carter (1976) reduced P uptake by potato tops by as much as twofold when Zn deficiency was corrected. While correction of Zn deficiency decreases P concentration in both corn and potato, P uptake data in the literature suggest that P concentration-yield relationships are fundamentally different in Zn-deficient corn than in Zn-deficient potato and that potato may be more subject to P toxicity than corn when Zn is marginally deficient.

This study was undertaken to contrast the relationships between dry matter yield, tissue P concentration, and tissue Zn concentration as they influence the development of Zn deficiency and P toxicity in corn and potato.

EXPERIMENTAL PROCEDURE

Corn (*Zea mays* L., 'Illinois WF 9×3-11') and potato (*Solanum tuberosum* L., 'Russet Burbank') plants were grown in nutrient solutions containing Zn and P in amounts which ranged from deficient to adequate. Treatments consisted of three Zn levels (0, 0.14, and 0.41 μM ZnSO₄·7H₂O = Zn₀, Zn₁, and Zn₂, respectively) in factorial combination with four levels of P (0.02, 0.10, 1.0, and 3.0 mM KH₂PO₄ = P₁, P₂, P₃, and P₄, respectively).

Initial nutrient solution concentrations were:

Corn-
2.5 mM Ca(NO₃)₂, 1.0 mM Mg(NO₃)₂, 23 μM H₃BO₃, 6.3 μM MnCl₂·4H₂O, 0.16 μM CuSO₄·5H₂O, 0.25 μM H₃MoO₄·H₂O, and 50 μM Fe-EDTA;

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³ S. J. Henning. 1971. Zinc-phosphorus relationships in five plant species. M.S. Thesis. Oregon State University, Corvallis.

Potato—

2.5 mM Ca(NO₃)₂, 1.0 mM Mg(NO₃)₂, 0.75 mM MgSO₄, 11.6 μM H₃BO₃, 3.16 μM MnCl₂·4H₂O, 0.16 μM CuSO₄·5H₂O, 0.25 μM H₂MoO₄·H₂O, and 25 μM Fe-EDTA

An additional 5 μM Fe-EDTA was added every other day to corn nutrient solutions to prevent Fe deficiency. Nutrient solution concentrations of K₂SO₄ decreased from 2.74 to 1.25 mM for corn and from 1.49 to 0 mM for potato as the KH₂PO₄ concentration increased from 0.02 to 3.0 mM, such that at any P level, the initial K concentrations were 5.5 and 3.0 mM K for corn and potato, respectively. Glass distilled water was used in preparing nutrient solutions. Contaminating levels of Zn were removed from all macronutrient stock solutions using a dithizone-CCl₄ purification procedure adapted from Snell and Snell (1949).

Corn seeds were germinated in acid-washed quartz sand which had been moistened with a solution of 0.05 mM Ca(NO₃)₂, 0.2 mM Mg(NO₃)₂, and 0.25 mM K₂SO₄. When seedlings attained a height of 7 to 10 cm, 24 uniform seedlings were removed from the sand, and the seed coats and endosperms were removed. Seedlings were threaded through holes drilled in corks and held in place with dacron batting. Corks containing seedlings were suspended through holes in covers over plastic pots containing the nutrient solutions. Experimental units consisted of one seedling in 2 liters of nutrient solution. Two replicates of each of the 12 treatments were placed in a growth chamber maintained at 27°C during a 16-hour day and at 21°C during an 8-hour night. Nutrient solutions were aerated continuously and brought to volume daily. Nutrient solution pH values were adjusted to 6.0 initially; they were readjusted to 6.0 twice daily with dilute solutions of HCl and KOH. Plants were grown for 20 days, at which time they were harvested and separated into leaf, stem plus immature leaves, and root components. Roots were washed free of nutrient solution with glass distilled water.

Seed potatoes were washed with glass distilled water, soaked in a 2% solution of thiourea for 1 hour, and placed in a light-tight germination box maintained at 20°C. When the potato eyes were about 1 mm in size, a hemispherical seed piece 1.9 cm in diameter was cut out around the eye with a small melonball scoop. Seed pieces were dipped in a 1% solution of Captan and allowed to suberize for 12 hours before being planted in nursery-grade Perlite moistened with glass distilled water. Seed pieces in Perlite were placed in the germination box until the sprouts attained a height of 10 to 15 cm. They were then removed from the germination box and placed on a greenhouse bench for ten days. At this time, 24 uniform sprouts were removed from the Perlite and the seed piece was cut off. Potato sprouts were threaded through corks and placed in the nutrient solutions. Experimental units consisted of one seedling in 2 liters of nutrient solution. Two replicates of each of the 12 treatments were placed on a greenhouse bench where daylight hours were bracketed with supplemental lighting to provide a 16-hour day and an 8-hour night. Greenhouse temperature was maintained between 20 and 30°C. Nutrient solutions were aerated continuously and brought to volume daily. The pH values of the nutrient solutions were adjusted to 6.0 every two days with dilute solutions of HCl and KOH. Plants were grown for 31 days, at which time they were separated into leaves, stems plus petioles, and roots. Roots were washed free of nutrient solution with glass distilled water.

Plant materials were dried in an oven at 75°C, weighed, and ground in a Wiley mill with stainless steel parts. Ground plant samples were digested in nitric and perchloric acids. Plant materials were analyzed for Zn with a Perkin-Elmer Model no. 303 atomic absorption spectrophotometer. Phosphorus was determined by the vanadate-molybdate method. Analysis of variance of the data was conducted using procedures outlined for completely random, 3 by 4 factorial experiments with two replications (Snedecor and Cochran, 1967).

RESULTS

Yield

Dry matter yields and tissue concentrations of P and Zn for corn and potato tops, and roots are shown in Fig. 1, 2, 3, and 4, respectively. Yields of both species were influenced by statistically significant P-Zn interactions. Variance ratios (F Statistics) used to test for significance of main effects and interactions are sum-

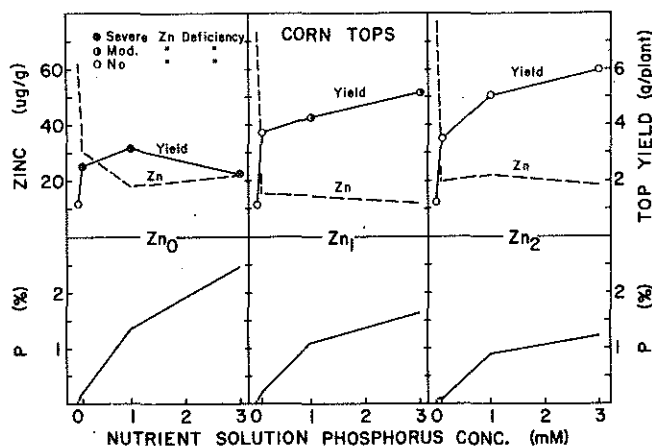


Fig. 1.—Dry matter yield, P concentration, and Zn concentration of corn plant tops as influenced by nutrient solution levels of P and Zn.

marized in Table 1. Inadequate P severely limited the growth of both species at the P₁ level; no response to Zn was measured. Top yield of both species increased as nutrient solution P was increased to the P₂ level but was maximized at the P₂ level only where Zn was added. At this P level, yields were not increased by increasing nutrient solution Zn from the Zn₁ to the Zn₂ level because inadequate P limited growth. Increasing P to the P₃ level increased corn yields slightly at the Zn₀ and Zn₁ levels and markedly at the Zn₂ level. Corn yields were further increased by increasing P to the P₄ level

Table 1—Variance ratios, *F*, for treatment effects on corn and potato dry matter yield, Zn and P concentrations in plant tissue, and Zn and P uptake by plant parts.

Species	Parameter measured	Plant part	Variance ratio, <i>F</i> , for main effects and interaction		
			P	Zn	P × Zn
Corn	Dry matter yield	Roots	26.8**	12.3**	3.7*
		Leaves	107.1**	139.9**	19.6**
		Total top	146.4**	86.8**	15.2**
	Zn concentration	Roots	4.1*	5.6*	0.7
		Leaves	122.3**	2.5	4.3*
		Total top	158.6**	2.7	3.6*
	P concentration	Roots	506.5**	19.5**	1.2
		Leaves	310.2**	44.3**	18.1**
		Total top	330.2**	27.9**	10.5**
	Zn uptake	Roots	2.4	7.0**	0.5
		Leaves	16.3**	55.1**	5.7**
		Total top	6.4**	41.0**	4.2*
P uptake	Roots	274.8**	11.6**	13.0**	
	Leaves	154.3**	1.5	6.1**	
	Total top	281.2**	5.5*	4.1**	
Potato	Dry matter yield	Roots	28.5**	18.0**	3.8*
		Leaves	82.3**	18.8**	3.5*
		Total top	61.5**	22.5**	4.7*
	Zn concentration	Roots	27.8**	29.7**	11.6**
		Leaves	129.2**	64.5**	3.7*
		Total top	175.8**	57.7**	16.2**
	P concentration	Roots	452.7**	74.6**	29.6**
		Leaves	67.7**	25.3**	9.5**
		Total top	88.1**	32.8**	13.0**
	Zn uptake	Roots	10.1**	170.4**	5.6**
		Leaves	73.5**	81.4**	11.1**
		Total top	29.9**	188.2**	4.8*
P uptake	Roots	42.3**	23.7**	8.1**	
	Leaves	25.1**	5.8*	2.3	
	Total top	27.5**	5.3*	2.0	

** Variance ratio, *F*, indicates statistically significant differences at the 0.05 and 0.01 probability levels, respectively.

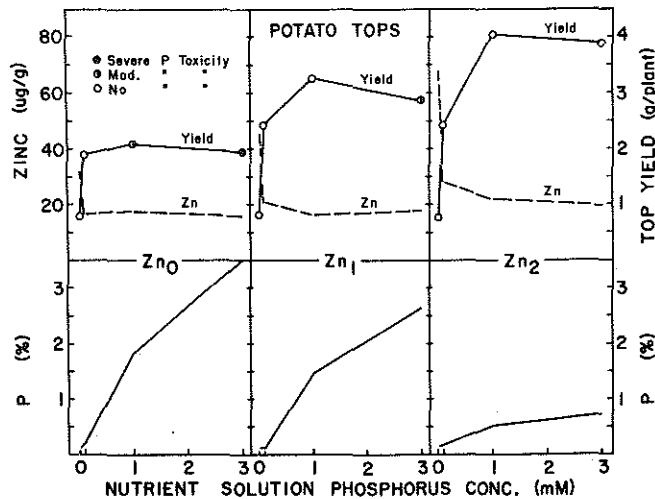


Fig. 2—Dry matter yield, P concentration, and Zn concentration of potato plant tops as influenced by nutrient solution levels of P and Zn.

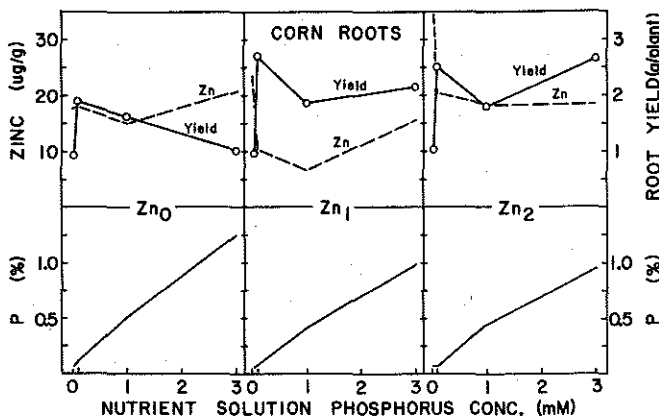


Fig. 3—Dry matter yield, P concentration, and Zn concentration of corn plant roots as influenced by nutrient solution levels of P and Zn.

when Zn was added but were significantly reduced when no Zn had been added. Potato top yields increased significantly at the Zn_2 level, increased slightly at the Zn_1 level, and remained constant at the Zn_0 level as nutrient solution concentration was increased to the P_3 or P_4 levels. Potato top yield was maximal in the P_3Zn_2 nutrient solution treatment.

Deficiency Symptoms

Time at which visual symptoms of P and Zn deficiency and P toxicity appeared, as well as relative ratings of their severity, are given in Table 2. Corn plants in the P_1 treatments exhibited symptoms of P deficiency on the 8th day after being placed in the nutrient solution. These plants had thin stems and narrow leaves. Dark purple coloration on the stem also extended up the midrib of the leaves when the experiment was terminated at 20 days. Plants in the P_2 , P_3 , and P_4 treatments with no added Zn (Zn_0) exhibited Zn deficiency symptoms at 11 days. At harvest, these plants exhibited the characteristic Zn deficiency symptoms of chlorotic bands on either side of the midrib and severe stunting due to shortened internodes. Plants in the

Table 2—Severity and day of appearance of P and Zn deficiency symptoms in corn and potato and P toxicity symptoms in potato.

Treatment	Corn			Potato				
	Deficiency symptoms ¹		Day observed	Deficiency symptoms		Toxicity symptoms ¹		
	P	Zn		P	Zn	P	Day observed	
P_1Zn_0	S	N	8	S	N	10	N	—
P_2Zn_0	S	N	8	S	N	10	N	—
P_3Zn_0	S	N	8	S	N	10	N	—
P_4Zn_0	N	S	11	M	N	18	N	—
P_2Zn_1	M	N	15	M	N	18	N	—
P_3Zn_1	M	N	15	M	N	18	N	—
P_4Zn_1	N	S	11	N	N	—	M	29
P_2Zn_2	N	M	16	N	N	—	N	—
P_3Zn_2	N	N	—	N	N	—	N	—
P_4Zn_2	N	S	11	N	N	—	S	25
P_2Zn_1	N	M	16	N	N	—	M	27
P_3Zn_2	N	N	—	N	N	—	N	—

¹ N = no deficiency (toxicity) symptoms; M = moderate deficiency (toxicity) symptoms; S = severe deficiency (toxicity) symptoms.

P_2Zn_1 and P_2Zn_2 treatments showed symptoms of P deficiency at 15 days. Zinc deficiency appeared on day 16 on the plants in the P_3Zn_1 and P_4Zn_1 treatments. Severity of Zn deficiency symptoms was not accentuated by increasing concentrations of P in the nutrient solution, nor was there any visual expression of P toxicity.

Time and order of appearance of deficiency and toxicity symptoms in potato differed from those observed for corn. The first deficiency observed was P deficiency on plants in the P_1 treatment after 10 days. These plants were small, and the leaves were dark green in color with the undersides of the leaves showing a dark purple coloration at harvest. At 18 days, plants at the P_2 level exhibited P deficiency symptoms. Potato plants at the P_2Zn_0 and P_3Zn_1 levels did not exhibit symptoms characteristic of Zn deficiency as described for the Russet Burbank potato (Boawn and Leggett, 1964). These plants were Zn deficient as evidenced by the yield increase which occurred when additional Zn was added (Fig. 2). Symptoms appearing on plants in the P_3Zn_0 , P_4Zn_0 , and P_4Zn_1 treatments were characterized by puckering of the leaf edges, thickening and rolling upward of the leaves, and grayish-brown necrosis. With the exception of the absence of "fern leaf"-type terminal growth, these are the same symptoms which Boawn and Leggett (1964) described as severe Zn deficiency symptoms in Russet Burbank potato. We believe, for the following reasons, that these symptoms are characteristic of P toxicity in Zn-deficient potato rather than being characteristic of Zn deficiency per se. First, Zn-deficient plants in the P_2Zn_0 and P_3Zn_1 treatments contained 16.1 and 16.2 $\mu\text{g Zn/g}$, respectively, and did not exhibit symptoms; plants in the P_3Zn_0 , P_4Zn_0 , and P_4Zn_1 treatments contained 17.5, 15.6, and 17.9 $\mu\text{g Zn/g}$, respectively, and exhibited symptoms. Second, the severity of the symptoms was more closely related to the P concentration in plant tissue at harvest than to nutrient solution Zn concentration or to Zn concentration in the plant tissue. Plants from the P_4Zn_0 treatment contained 3.54 and 4.08% P in total tops and leaves at harvest, respectively, and they showed the earliest and most severe expression of symptoms. Symptoms next appeared on P_4Zn_1 plants containing 2.64% P in total

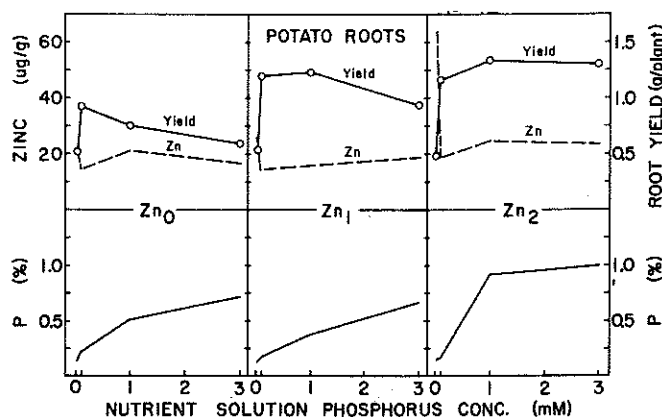


Fig. 4—Dry matter yield, P concentration, and Zn concentration of potato plant roots as influenced by nutrient solution levels of P and Zn.

tops (3.29% in leaves) and appeared last on P_3Zn_0 plants containing 1.83% P in total tops (2.22% in leaves). When Zn deficiency occurred in corn, in contrast, it appeared on the same day, irrespective of nutrient solution P level or plant tissue P concentration at harvest. Finally, field grown plants reported by Boawn and Leggett (1964) as having severe Zn deficiency symptoms contained from 0.64 to 2.0% P in leaf tissue. At these leaf P concentrations, the symptoms observed by Boawn and Leggett (1964) could have been P toxicity symptoms mistaken for an enhancement of Zn deficiency as suggested by Loneragan et al. (1979).

P Concentration and Uptake

While corn plants did not exhibit visual symptoms of P toxicity, the statistically significant decline in dry matter yield associated with increasing nutrient solution P concentrations from the P_3 to the P_4 level without added Zn (Fig. 1) suggests that plants in the P_4Zn_0 treatment were indeed suffering from P toxicity in addition to Zn deficiency. Tissue concentrations of P in corn plants from the P_4Zn_0 treatment were 2.45% P in the total top and 3.39% P in leaves. Maximum plant tissue P concentrations measured when Zn was adequate were 1.24 and 1.42% P in total tops and in leaves, respectively, for the P_4Zn_2 treatment. At the P_1 , P_2 , and P_3 nutrient solution levels, there were no differences between total top and leaf P concentrations except where Zn was deficient and P was near optimum. Under these conditions (treatments P_3Zn_0 and P_3Zn_1), P concentrations in leaf tissue were 1.22-fold greater than P concentration in total tops.

Phosphorus uptake by roots, leaves, and total top of corn (Table 3) increased as nutrient solution P concentration was increased from the P_1 to the P_4 level. At the P_1 , P_2 , and P_3 levels, addition of Zn to the nutrient solution had no effect on P uptake by any of the fractions. At the P_4 level, root uptake of P was increased by increasing Zn concentration in the nutrient solution, while P uptake by leaves and total tops increased significantly and then decreased slightly as Zn was increased from the Zn_0 to the Zn_1 and Zn_2 levels. Phosphorus uptake data indicate that reductions in corn plant P concentration associated with increasing levels of Zn in the nutrient solution were largely the result of dilution of plant P by a growth response to Zn. Comparable relationships bet-

Table 3—Phosphorus uptake by roots, leaves, and tops of corn and potato as influenced by P and Zn treatments.

Treatment	Phosphorus uptake					
	Corn			Potato		
	Roots	Leaves	Total top	Roots	Leaves	Total top
	mg/plant					
P_1Zn_0	0.5	0.5	0.9	0.7	0.7	1.0
P_1Zn_1	0.5	0.6	0.9	0.7	0.6	1.0
P_1Zn_2	0.7	0.7	1.0	0.7	0.7	0.9
P_2Zn_0	1.8	1.8	3.8	1.9	2.9	4.1
P_2Zn_1	2.2	1.9	3.8	2.0	3.7	5.0
P_2Zn_2	1.8	2.1	3.6	1.9	2.6	4.0
P_3Zn_0	8.3	24.3	42.5	3.8	28.4	38.1
P_3Zn_1	7.6	22.2	45.9	4.5	34.5	47.2
P_3Zn_2	7.7	26.8	45.7	12.1	12.7	20.1
P_4Zn_0	12.4	36.6	54.7	4.2	56.1	68.5
P_4Zn_1	20.9	51.6	83.2	6.2	60.3	78.6
P_4Zn_2	24.8	43.8	74.3	12.9	18.4	27.5
L.S.D., 5%	2.8	8.7	10.7	2.9	22.2	27.7

ween dry matter yield and plant P concentration have been reported by Terman et al. (1972, 1975) for corn grown in soil.

Relationships between potato plant dry matter yield and tissue P concentration were somewhat different as illustrated in Fig. 2 and 4 for total tops and roots, respectively. Potato top P concentrations were lower in the presence of adequate levels of Zn in the nutrient solution than would be expected if the reduction in P concentration was due simply to dilution by a growth response to Zn. Highest P concentrations measured in potato plants from the P_4Zn_2 treatment were 0.71 and 0.86% P in total tops and leaves, respectively, as contrasted to P concentrations of 1.24 and 1.42% in the total tops and leaves, respectively, of corn plants grown in a comparable nutrient solution. The relationship between potato root yield and root tissue P concentration shown in Fig. 4 helps explain why tops of potato plants adequately supplied with Zn contain lower P concentrations than would be predicted based on dilution by yield response to Zn. Potato plants grown in nutrient solutions containing adequate (P_3) or excessive (P_4) levels maintain significantly higher P concentrations in roots when the plants are adequately supplied with Zn (Zn_2) than when plants are Zn deficient (Zn_0 and Zn_1).

Phosphorus uptake by all potato plant fractions (Table 3) increased as nutrient solution P concentration increased. Where nutrient solution P concentration limited growth (P_1 and P_2), P uptake by potato, like corn, was unaffected by nutrient solution Zn level. At the P_3 and P_4 levels, however, correction of Zn deficiency resulted in marked increases in P uptake by roots and even more striking reductions in P uptake by leaves and total tops. The net effect was that Zn-deficient potato had a higher total P uptake than did potato plants adequately supplied with Zn.

Phosphorus concentration and uptake data for potato are similar to those of Paribok and Alekseeva-Popova (1965), showing higher P concentrations in above-ground portions and lower P concentrations in roots of Zn deficient pea (*Pisum* spp.) and tomato (*Lycopersicon esculentum*) compared to plants adequately supplied with Zn. These authors also found that (i) Zn-deficient plants translocated more P to above-ground portions where it accumulated in leaves

as inorganic phosphate, and (ii) that total P uptake was greater by Zn-deficient plants than by Zn-adequate plants.

Zinc Concentration and Uptake

Zinc concentration in both corn and potato was affected by statistically significant P-Zn interactions (Table 1). Relationships between Zn concentration in total top of corn and potato are shown in Fig. 1 and 2, respectively. Where P was extremely deficient (P_1), increasing levels of Zn in the nutrient solution increased Zn concentration in corn and potato tops significantly without affecting yield. Increasing Zn concentration from the Zn_0 to the Zn_1 level in the P_2 level nutrient solution increased corn yield and decreased plant concentration of Zn. At P_3 and P_4 levels, increasing nutrient solution Zn concentrations from Zn_0 to Zn_1 levels increased corn yield significantly and decreased Zn concentration in plants slightly. Increasing nutrient solution Zn from the Zn_1 to the Zn_2 level increased corn yield additionally as well as Zn concentration in plants. Zinc concentration in corn leaves averaged 1.26 times greater than that in total tops, but the relationship between Zn concentration and yield was the same. These relationships between tissue Zn concentration and corn plant yield at the P_3 and P_4 levels are typical of the effect often observed when extreme micronutrient deficiencies are corrected (Steenbjerg, 1951).

Figure 2 illustrates that correction of Zn deficiencies in nutrient solutions containing P at the P_2 , P_3 , and P_4 levels generally increased potato top yield and Zn concentration. Zinc concentrations in potato leaves at the P_1 , P_2 , and P_3 levels averaged 1.13 times higher than that in total tops, but yield-concentration relationships were the same.

Zinc uptake data for leaves and tops of corn and potato are given in Table 4. Increasing levels of Zn in the nutrient solution increased Zn uptake by both species. This effect was most pronounced at the P_3 and P_4 -nutrient solution levels where yield was the greatest. Zinc uptake by corn leaves and tops decreased as nutrient solution P concentration was increased from the P_1 to the P_2 level; it remained the same or increased slightly as P was increased from the P_2 to the P_4 level. Zinc uptake by potato leaves and tops remained the same or increased at all Zn levels as nutrient solution P was increased from the P_1 to the P_4 level, with the exception that Zn uptake declined as P was increased from the P_3Zn_2 to the P_4Zn_2 level.

DISCUSSION

Increased mobilization and translocation of P from roots to above-ground parts, increased total P uptake, and concentration of P resulting from restricted growth acted in concert to produce excessive concentrations of P in the above-ground parts of Zn-stressed potato plants. Loneragan et al.⁴ have reported that okra (*Abelmoschus esculentus* L. Moench) responds similarly to Zn stress. Phosphorus concentrations at or above 2.2% in potato leaf tissue (1.8% in total tops) produced probable P toxicity, manifested by puckering of leaf edges, thickening and rolling upward of leaf edges, and leaf necrosis. While P toxicity at times appears to accen-

Table 4—Zinc uptake by leaves and tops of corn and potato as influenced by P and Zn treatments.

Treatment	Zinc uptake			
	Corn		Potato	
	Leaves	Total top	Leaves	Total top
	µg/plant			
P_1Zn_0	60	72	13	25
P_2Zn_1	67	82	14	36
P_3Zn_2	74	93	17	50
P_2Zn_0	39	53	21	30
P_2Zn_1	39	58	37	51
P_2Zn_2	52	70	37	67
P_3Zn_0	26	55	25	36
P_3Zn_1	35	61	36	53
P_3Zn_2	79	112	58	89
P_4Zn_0	31	49	22	30
P_4Zn_1	35	61	36	51
P_4Zn_2	78	110	50	75
L.S.D., 5%	14	20	7	9

tuate Zn deficiency, it is important to recognize that excessive P concentrations in leaf tissue are the result, not the cause, of Zn deficiency in potato. In studies with Zn-stressed pea and tomato, Paribok and Alekseeva-Popova (1965) found that increased translocation of inorganic P from roots and accumulation of inorganic P in tops occurred at the expense of organic P fractions, suggesting that the processes of esterification of P in Zn-deficient plants were disturbed. Paribok and Alekseeva-Popova (1965) were unable to conclusively identify a cause for increased P uptake by Zn-stressed plants, but they speculate that, because organic P compounds in roots are rapidly hydrolyzed, the active P absorption process is intensified, or, alternatively, that passive uptake of P is intensified by increased root cell membrane permeability. They conclude that if the latter mechanism pertains, accumulation of nutrients other than P might also be expected. Accumulation of excessive levels of Fe by Zn-deficient corn grown on some soils in Oregon has been reported previously (Jackson et al., 1967; Henning³).

That the increased P uptake by Zn-deficient potato in this study is not simply an artifact resulting from high P availability in nutrient solution culture is borne out by the data of Jackson and Carter (1976). They found that Zn-stressed potato plants not fertilized with P had a higher uptake of P by tops than did Zn-adequate plants when grown in the field on a soil judged deficient in P based upon potato tuber yield responses to P fertilizer application.

In contrast to potato, P uptake by corn tops was not significantly reduced when Zn deficiency was corrected. Reductions in plant tissue P concentrations accompanying corn yield responses to correction of Zn deficiencies can be explained largely as dilution effects. This is consistent with lack of evidence of increased P uptake by Zn-deficient corn grown in the field. Because Zn-deficient corn plants do not exhibit increased P uptake and accumulation in leaves to the same degree as do Zn-deficient potato plants, they are probably less susceptible to P toxicity. Phosphorus toxicity probably can oc-

⁴ J. F. Loneragan, D. L. Grunes, R. M. Welch, E. A. Aduayi, A. Tengah, V. A. Lazar, and E. E. Cary. 1979. P accumulation and toxicity in relation to Zn supply. p. 1975. Agron. Abst.

cur in corn, however, when extremely Zn-deficient plants are exposed to very high levels of available P, as evidenced by the reduced yield measured for the P_4Zn_0 treatment. Zinc concentrations in tissues of corn plants deficient in Zn, as judged by the presence of Zn deficiency symptoms and yield response to added Zn, ranged from 15 to 49 $\mu\text{g Zn/g}$ in leaf tissue and from 12 to 31 $\mu\text{g Zn/g}$ in total tops. Tissue Zn concentrations tended to be reduced by increased yield associated with each added increment of nutrient solution P and by the first increment of nutrient solution Zn. The fact that the tissue Zn concentrations in Zn adequate plants (Zn_2 treatments) fall within the range of tissue Zn concentrations measured for Zn deficient plants points up the difficulty of establishing critical Zn concentrations in tissue where interaction with P is present. Zinc concentration in leaves of potato plants judged to be Zn deficient, based upon yield response to added Zn, ranged from 16.3 to 20.5 $\mu\text{g Zn/g}$. Potato plants with leaf Zn concentrations of 25 $\mu\text{g Zn/g}$ appeared normal, had the highest yields, and had sharply reduced concentrations of P in above-ground parts.

Failure to observe Zn deficiency symptoms on corn and potato grown in Zn_2 nutrient solutions (Table 2) and failure to measure a reduction in Zn uptake by plants in the Zn_0 and Zn_1 nutrient solutions as nutrient solution P concentrations were increased from the P_2 to the P_4 level (Table 4) suggests that high P availability per se is not responsible for the development and apparent accentuation of Zn deficiency in plants. A more plausible explanation of the apparent accentuation of Zn deficiency by P fertilizer applications is that P accumulates and may become toxic in Zn-deficient plants. Zinc-deficient species such as potato, which show increased P uptake, increased mobilization and translocation of P, and concentration of P due to limited dry matter production would be expected to be more subject to P toxicities than would species such as corn in which

concentration of P results primarily from reduced growth.

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