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Phosphorus uptake parameters of alfalfa and corn as influenced by P and Ph.

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PHOSPHORUS UPTAKE PARAMETERS OF ALFALFA AND CORN AS INFLUENCED BY P AND pH.

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KEY WORDS: Phosphorus influx, Root absorption power, Shoot and root growth rate, Transport to shoot

ABSTRACT

The effects of growth medium P and pH on growth, phosphorus uptake, transport and influx kinetics in alfalfa and corn were studied. Increasing P from 100 to 1000 µM and increasing pH from 5.5 to 6.5 reduced growth and rate of growth of shoot and root in corn. Overall growth of alfalfa was unchanged due to varying P and pH levels. In both crops, greater root length was recorded for low P levels. Alfalfa recorded lower P influx (I_n) and root absorption power (α) than corn. In corn, I_n and α slightly declined with increasing pH; however, in alfalfa at high P, I_n and α increased with increasing pH. Higher I_n and lower α were recorded at higher P. In both crops, higher P transport (Ts) were recorded at higher P level. With the exception of alfalfa at lower P level, increasing pH increased Ts. In both crops, Imax reduced with increasing

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pretreatment P. The Imax in alfalfa increased with increasing pH and in corn it decreased with increasing pH. The Km in both crops followed similar trends as that of Imax.

INTRODUCTION

Plant species differ in their ion absorption characteristics (9,13,36). These differences in ion uptake may be due to root morphology, rate of growth, ion uptake mechanisms, or internal nutrient demand (2,3,4,7,12,14,20,22,23,31,33,36,38,39). Plant demand for any given nutrient is a function of its internal ionic concentration and its rate of growth. If the external nutrient supply is not limiting, the metabolic demand of the plant can be of dominating importance in determining the quantity of nutrients absorbed. In the present study plant growth and its internal ionic concentrations were modified by growing plants into solutions having different levels of P and pH. The pH of the growth medium influences the forms of ion present and growth and functions of the plant roots (5,7,17,18, 26,27). The objectives of this research were to study the effects of growth medium P and pH levels on shoot and root growth, growth rate, P uptake and transport and influx kinetics in alfalfa and corn.

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MATERIALS AND METHODS

Experiment 1

Plant growth conditions

Seeds of alfalfa (*Medicago sativa* L. var. Iroquois) and corn (*Zea mays* Var. SX111-159696-32C5) were germinated in moist filter paper immersed in aerating water. Five day old seedlings were suspended in plastic pots containing nutrient solution. Five corn seedlings per 2 liter pots and 18 alfalfa seedlings per liter pot were used in this study. The composition of the nutrient solution was 2.5 mM Ca, 1 mM Mg, 1 mM K, 3 mM N, 2.0 mM

S, 46 μM B, 0.8 μM Zn, 0.3 μM Cu, 0.5 μM Mo, 9 μM Mn and 75 μM Fe as Fe-DTPA (diethylenetriamine pentaacetic acid). In this study, plants were grown at 3 nutrient solution pH levels (5.5, 6.5, and 7.5) and at 2 P levels (100 and 1000 μM P as KH_2PO_4). Corn was grown only at two pH levels mainly because in a preliminary study, the growth of corn at pH 7.5 was extremely poor. Nutrient solutions were renewed daily, and desired P and pH levels were maintained. Experiments were carried out in the greenhouse during the months of July and August. Plant growth pots were suspended in fiber glass drums where the water was circulated to keep the nutrient solution temperature of growth pots at 25 ± 2° C.

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Determination of P influx kinetics

Ten days before the harvest, growth containers were moved from greenhouse to climatically controlled growth rooms. In growth rooms, a day temperature of 28°C for 16 hours at 550 $\mu E\ sec^{-1}m^{-2}$ of light and 8 hours dark period at 22°C was maintained. Two days before the depletion studies, concentrations of ions in growth medium were reduced to half and pH of the nutrient solution was adjusted according to the growth treatment. Thirty hours before depletion time, solution was completely devoid of P in all the studies. On the day of depletion, solution composition of all other ions were brought to normal level and added with 10-15 μM P as KH_2PO_4. The P in solution was labelled with carrier free ^{32}P having activity of 3 μCi/liter, to facilitate measurements of P at low concentrations. A Beckman Scintillation counter having Beta spectrophotometer with automatic quench correction was used in determining ^{32}P activities. Ion influx kinetics were measured at solution pH similar to the one used for growth. Ion influx was assumed to follow Michaelis-Menten kinetics so that the relation between ion concentration and uptake was expressed in terms of Imax, the maximum influx, and Km the Michaelis-Menten

constant, which is the concentration where influx is one-half Imax. The P influx parameters were determined by the solution depletion method of Claassen and Barber (8) as modified by Nielsen and Barber (29). In this experiment the depletion studies for alfalfa were carried when plants were 30 days old and for corn they were carried at 20 days of growth. At the completion of depletion studies, plants were harvested and roots were immersed for 2 min in 10 mM Na_2SO_4 and washed 3 times in deionized water.

Experiment II

Alfalfa and corn plants were grown in greenhouse and other experimental details were similar to Experiment I. In this study, during the growth phase, the nutrient pH was maintained at 5.0 and P level was 500 µM. Phosphorus influx studies were carried at a pH of 4, 5, 6, 7, and 8. At the time of depletion, alfalfa was 32 days old and corn was 22 days old.

Determination of Growth and P uptake parameters.

Plant samples were wet ashed in the H_2SO_4 and H_2O_2 and P was determined by the method of Murphy and Riley (28).

The root length was determined by Tennants (35) method. The relative root growth rate, kr was determined as follows:

$$kr = [\ln L2 - \ln L1]/[T2 - T1] \quad [1]$$

where L refers to root length (cm/plant) and T refers to time in seconds. The subscript 1 refers to initial (5 days) and 2 refers to the plant age at final harvest. The relative shoot growth rate, ks, was calculated using equation 1 and root length was substituted for shoot weight (g/plant).

The nutrient influx rate into roots, I_n, (pmoles $cm^{-1}sec^{-1}$) was calculated as follows:

$$I_n = [(U2 - U1)/(T2 - T1)] \; [(\ln L2 - \ln L1)/(L2 - L1)] \quad [2]$$

where U refers to P ion content in plant (mmoles/plant). The rate of ion transport to shoot Ts was calculated by Pitman's (31) method.

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TABLE 1
Alfalfa and Corn Growth Parameters as Influenced by Growth Medium P and pH.

Treatment P	pH	Shoot wt.	Root wt.	Root Length	Kr	Ks
µmoles		----------g/plant----------		---m/plant---	--sec^{-1}X10^6--	
				Alfalfa		
100	5.5	0.16 ± 0.03†	0.024 ± 0.01	12.7 ± 3.38	2.68	2.36
	6.5	0.15 ± 0.05	0.025 ± 0.01	12.4 ± 0.93	2.68	2.29
	7.5	0.15 ± 0.01	0.024 ± 0.01	11.4 ± 3.48	2.63	2.32
1000	5.5	0.17 ± 0.01	0.024 ± 0.01	12.4 ± 0.25	2.68	2.38
	6.5	0.15 ± 0.01	0.023 ± 0.01	10.7 ± 1.01	2.61	2.31
	7.5	0.13 ± 0.01	0.024 ± 0.01	10.6 ± 0.14	2.60	2.24
				Corn		
100	5.5	1.70 ± 0.13	0.34 ± 0.01	63.3 ± 13.82	3.81	3.60
	6.5	1.48 ± 0.36	0.32 ± 0.08	86.9 ± 7.18	4.06	3.48
1000	5.5	1.26 ± 0.45	0.28 ± 0.05	71.2 ± 2.97	3.90	3.34
	6.5	1.09 ± 0.35	0.25 ± 0.09	55.8 ± 22.68	3.68	3.24

† Mean ± Standard deviation.

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TABLE 2
Phosphorus Uptake and Transport in Alfalfa and Corn as Influenced by Nutrient Medium P and pH.

Treatment P	Treatment pH	Concentration	P Parameters I_n	α	T_S
µmoles		g/kg	pmoles $cm^{-1}sec^{-1}$	$cm\ sec^{-1} X 10^{-6}$	nmoles $g^{-1}sec^{-1}$
			Alfalfa		
100	5.5	5.3 ± 0.01†	0.080 ± 0.01	11.59 ± 1.64	0.44 ± 0.06
	6.5	5.1 ± 0.08	0.066 ± 0.01	9.57 ± 0.62	0.37 ± 0.03
	7.5	5.0 ± 0.02	0.076 ± 0.01	11.01 ± 1.53	0.36 ± 0.01
1000	5.5	5.6 ± 0.02	0.078 ± 0.01	1.13 ± 0.01	0.43 ± 0.03
	6.5	5.9 ± 0.09	0.080 ± 0.01	1.16 ± 0.08	0.43 ± 0.08
	7.5	6.9 ± 0.08	0.091 ± 0.01	1.32 ± 0.12	0.49 ± 0.57
			Corn		
100	5.5	5.1 ± 0.08	0.173 ± 0.01	14.54 ± 0.71	0.53 ± 0.11
	6.5	5.5 ± 0.05	0.125 ± 0.04	10.50 ± 3.03	0.55 ± 0.11
1000	5.5	6.0 ± 0.14	0.181 ± 0.01	1.52 ± 0.01	0.58 ± 0.24
	6.5	6.9 ± 0.04	0.170 ± 0.01	1.43 ± 0.04	0.65 ± 0.12

† Mean ± Standard deviation.

$$Ts = [(Us2 - Us1)/(T2 - T1)] \quad [(\ln W2 - \ln W1)/(W2 - W1)] \quad [3]$$

where Us refers to P content in shoot and W refers to shoot wt.

The root absorption power or root uptake coefficient, α, for P was calculated using the following equation (30).

$$\alpha = [(I_n)/(2\pi ro\ C)] \quad [4]$$

where ro is the mean root radius which was 0.019 cm for corn and 0.011 cm for alfalfa and C is the mean ion concentration in solution (moles cm^{-3}).

RESULTS AND DISCUSSIONS

Plant growth parameters

Table 1 lists the shoot and root growth parameters of alfalfa and corn. Growth of alfalfa, as well as Kr and Ks did not change due to varying pH and P levels. However, a slight reduction in root length was observed at high pH level for both concentrations studied. At lower P and pH 7.5, alfalfa recorded about 9% higher root length than at higher P. In corn lower P gave higher growth, kr and ks for shoot and roots than higher P treatment. At pH 5.5, the corn shoot and root growth at low P were 36 and 22% higher than that of high P. The relation between ks and increasing ambient P have been reported for grasses (7) and lucerne (38). In any given P, increasing pH reduced corn shoot and root growth and ks. However at low P increasing pH increased corn root length. High P levels on the growth depressions have been reported for barley (32), clover (16), grasses (2,7), and rice (14). Reduction in growth at high P levels might be attributable to P toxicity in both crops.

Phosphorus uptake and transport

The pH of the growth media influence the availability of P by affecting its solubility. In alfalfa, at a lower ambient P levels, the shoot concentration of P slightly reduced with increasing pH (Table 2); whereas, at higher ambient P, concentration of P in shoot increased with increasing pH. In corn, P concentrations in shoot increased with increasing pH at both

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ambient P levels. Mahler (24), in a greenhouse study, did observe lower P concentrations in alfalfa at pH of 4.8. In his study, plant tissue P concentration did not appear to be affected by increasing soil pH once a threshold pH level of 5.0 had been reached. Above pH 5.0, P concentration ranged from 4.7 to 5.2 g/kg of tissue. Increase in P concentration with increasing external P supply have been reported for corn (19,21) and alfalfa (6).

The differences between species in their rate of ion absorption is widely reported (2,4,21,36). The rate of P absorption per unit root length, I_n, was greater for corn than for alfalfa (Table 2). Total shoot dry matter production in corn was about 9 times higher than for alfalfa and to meet its demands for nutrient requirements, corn roots have to work at much higher efficiency rate in absorption of P. The I_n, for alfalfa at pH 5.5. showed a decreasing trend with an increase in ambient P level; whereas, I_n values at higher pH levels increased with increase in P levels. In corn, at both pH levels, I_n increased with the increasing ambient P. In corn at both P levels, I_n declined with increasing pH. The concentration ratio of HPO_4^{2-} and $H_2PO_4^-$ is pH dependent factor. Hendrix (18) reported a 10 fold reduction in P absorption by bean plant when the pH was raised from 4 to 8.7. Tang and Laudelout (34) did observe a maximum P uptake by rice at pH 5.6 and uptake declined with increasing pH. Jungk and Barber (21) observed an increase in I_n for P in corn with an increase in P levels from 10 to 100 μM and I_n remained the same even after external P concentration was raised to 1000 μM. Christie and Moorby (7) did observe an increase in I_n in three grass species with an increase in P levels from 0.1 to 968 μM P. In any given P level, increasing I_n values were in association with increasing ks; however, in alfalfa at high P levels, I_n reduced with increasing ks.

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TABLE 3
Growth Medium Pretreatment P and pH on P Influx Kinetics of Alfalfa and Corn.

Treatment P µmoles	pH	P influx kinetics Imax pmoles $cm^{-1}sec^{-1}$	Km µM
		Alfalfa	
100	5.5	0.03 ± 0.01†	1.79 ± 0.78
	6.5	0.15 ± 0.20	1.97 ± 2.28
	7.5	0.28 ± 0.21	0.82 ± 0.09
1000	5.5	0.02 ± 0.01	0.64 ± 0.44
	6.5	0.04 ± 0.01	0.91 ± 0.86
	7.5	0.03 ± 0.02	1.47 ± 0.77
		Corn	
100	5.5	0.11 ± 0.02	2.24 ± 0.86
	6.5	0.06 ± 0.01	1.17 ± 0.01
1000	5.5	0.05 ± 0.01	1.02 ± 0.23
	6.5	0.04 ± 0.01	0.80 ± 0.33

† Mean ± Standard deviation.

TABLE 4
Depleting Solution pH on P Influx Kinetics of Alfalfa and Corn.

Depletion Solution pH	P influx kinetics Imax pmoles $cm^{-1}sec^{-1}$	Km µM
	Alfalfa	
4	0.75 ± 0.44†	3.65 ± 1.20
5	0.58 ± 0.18	3.02 ± 0.38
6	0.95 ± 0.20	4.75 ± 0.07
7	0.55 ± 0.09	2.16 ± 0.10
8	0.98 ± 0.73	2.93 ± 0.77
	Corn	
4	0.55 ± 0.02	3.89 ± 0.28
5	0.90 ± 0.23	7.85 ± 2.64
6	1.05 ± 0.54	5.93 ± 4.34
7	0.50 ± 0.16	2.39 ± 0.41
8	0.45 ± 0.27	3.21 ± 2.69

† Mean ± Standard deviation.

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The root uptake coefficient, α, is a plant factor indicating the effectiveness of ion absorption by the root. The average α values in corn were higher than in alfalfa (Table 2). The α values in corn declined at higher pH, but such trends were not observed in alfalfa. Higher P levels recorded considerably lower α values in both crops. This shows that the demand for P was relatively stronger in the roots of plants that had been under P stress. Christie and Moorby (7) observed a reduction in α as external concentration of P increased, further they also reported a decline in α with advancing age of the plants.

With the exception of Ts for alfalfa at low P levels, the Ts values increased with increasing pH. In both crops, Ts values were higher for high P levels than for low P levels. Overall, corn recorded higher Ts values than alfalfa.

Phosphorus Influx Kinetics

The pH of the nutrient solution effects the ionic species of P in solution. At pH 5.0 about 97 percent of P is present as $H_2PO_4^-$; however, only about 18 percent is in this form at pH 8.0, the divalent ion HPO_4^{2-} being dominant at this pH (5,26). Several studies have indicated that P is taken up mainly or entirely as $H_2PO_4^-$ forms both at low and high solute concentrations (10,11,17,37). The pH dependence of P uptake is well documented (17,18,37). In alfalfa at both P levels the Imax increased with increasing pH (Table 3). In corn Imax reduced with increasing pH. In both crops high Imax recorded for plants grown at low P. The Km values almost followed similar trends as that of Imax. McBride and Menzel (25) while reviewing literature list the average Km for P of 6.1 µM for an intact roots with a range of 0.6 to 20.7 µM. The magnitude of Km and Imax for a given ion are susceptible to change according to the nutrient status of the tissue (15). Such effects are evident in our current findings. Table 4 lists the P influx kinetics for second experiment where depletion studies

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were carried at varying pH values even though plants were raised earlier at pH 5.0. In both the crops, pH of depletion solution appears to have less influence on magnitude of Imax and Km. From the obtained data of preliminary experiments it appears that in intact plant system influx rates of P are controlled by plant demand.

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