1987Plant Physiol. (1987) 84, 1319–1324
0032-0889/87/84/1319/06/$01.00/0

Nitrogen Enhancement of Phosphate Transport in Roots of *Zea mays* L.

II. KINETIC AND INHIBITOR STUDIES

Received for publication December 9, 1986 and in revised form May 11, 1987

FRANK W. SMITH AND WILLIAM A. JACKSON*
Division of Tropical Crops and Pastures, Commonwealth Scientific and Industrial Research Organization, Cunningham Laboratory, St. Lucia, Queensland 4067, Australia (F.W.S), *and Department of Soil Science, North Carolina State University, Raleigh, North Carolina 27695-7619* (W.A.J.)

ABSTRACT

Exposure to 1 millimolar ammonium pretreatments increased V_{max} for phosphorous uptake in dark-grown decapitated maize seedlings without a statistically measurable change in K_m. Sulfate uptake also was stimulated. The stimulation in phosphorous uptake due to ammonium pretreatment was greater in seedlings grown without phosphorous than in those grown with 25 micromolar phosphorous. The stimulus was not expressed unless the entire root system was pretreated with ammonium, and pretreatment of a part of the root system inhibited phosphorous uptake by the remaining part unless it also had been pretreated. Pretreatment with the amino acid analogs *p*-fluoro-DL-phenylalanine and L-azetidine-2-carboxylic acid (AZ) restricted phosphorous uptake in seedlings that were pretreated with ammonium and in those that were not, but the effect of ammonium pretreatment was not completely eliminated by the analogs. In general, translocation of the entering phosphorous was affected similarly to uptake by experimental treatments. Enhanced translocation, however, was not sufficient to account quantitatively for the increase in uptake, and an increased uptake was still evident when translocation was completely prevented by 50 micromolar AZ pretreatment.

Many agronomic studies on the banding of nitrogen (N) and phosphorous (P) fertilizers have shown that N increases the absorption of fertilizer P. While there are a number of soil related factors and interactions between the plant and soil that contribute to this effect (7, 16), it is recognized that the phenomenon is partially attributable to physiological reactions of the plant itself (16). Among the earliest studies to arrive at this conclusion was that of Cole *et al.* (5) who eliminated soil related factors and found up to 3-fold increases in P uptake by N pretreated maize plants grown in solution culture. They suggested a link between synthesis of N intermediates such as glutamine and the energy supply needed for anion uptake.

Other studies sought to explain the phenomenon by suggesting that N increased the rate of transfer of P across the root symplast to the xylem. Leonce and Miller (13) hypothesized that ammonium may increase the rate at which a phosphorous-carrier complex released P into the xylem. Later observations that N pretreatment stimulated P translocation to the tops relatively more than P uptake, led to the suggestion that the N effect was exerted on two quite distinct P transport systems: the initial uptake across the plasmalemma and the subsequent lateral movement of P to the xylem (21, 22). It was postulated that some N intermediates, presumably synthesized during the pretreatment phase, influenced these two processes.

We have shown that the stimulation of P uptake could be induced in decapitated maize seedlings by pretreatments with either nitrate or ammonium. In presence of ammonium, the stimulus took 6 to 8 h to develop and did not decay rapidly (20). Development of the stimulus therefore did not require participation by shoot-related processes. The present paper describes experiments designed to characterize further the nature of the stimulation of P uptake and translocation in these seedlings in which growth and functions of the root system is sustained by flow of materials from the endosperm (8).

MATERIALS AND METHODS

General Procedures. Corn genotypes DeKalb XL-45 and Pioneer Sargent were used in the experiments described here. Ammonium pretreatment increased P uptake and translocation to the xylem in both genotypes, but Pioneer Sargent tended to have lower translocation rates. Procedures for growing the seedlings and for pretreatment conditions have been described (20). The basal solution identified as sulfate-medium (20) was used in all experiments reported in this paper. It contained 1 mM $CaSO_4$, 500 μM K_2SO_4, 250 μM $MgSO_4$, 25 μM KH_2PO_4, trace elements at two-fifths the concentration in Hoagland solution, and 1 mg Fe L^{-1} as FeEDTA. Methods used for attaching xylem exudate collectors, handling of seedlings during the pretreatment and uptake phases, and subsequent analytical techniques were the same as those described previously (20) except where noted otherwise. Phosphorous uptake was obtained by dividing the quantity of ^{32}P removed from the ambient solution by its specific activity, and translocation of exogenous P was determined by dividing the quantity of ^{32}P in the xylem fluid collected during each 0.5 h interval by the specific activity of the ambient solution. Translocation of the P previously accumulated in the tissue prior to exposure to the labeled solutions (endogenous P) was determined by subtracting the exogenous P from the total P in the xylem. All data are presented per unit root fresh weight and are the means of four replications of four plants each unless otherwise noted.

Kinetic Studies. The effects of N pretreatment on kinetic parameters K_m and V_{max} were determined using detopped seedlings of genotype Pioneer Sargent. Seedlings were grown on basal medium and prepared as described above, but exudate collectors were not attached. After detopping, assemblies of seedlings were pretreated for 16 h in basal medium containing either 0 or 1 mM added as $(NH_4)_2SO_4$. The seedlings were then exposed for 3 min to basal medium containing 1.5, 2, 3, 5, 10, and 25 μM P as

KH_2PO_4, and then to identical solutions labeled with ^{32}P for 20 min. After a 3 min desorption period in unlabeled uptake solutions, the roots were blotted dry, divided into root and seed piece, weighed, ashed, and ^{32}P contents determined by liquid scintillation procedures. During the uptake and desorption periods, a small absorbent pad was kept over the cut 'stump' of each seedling to collect exudate. This was ashed with the plant material to enable total ^{32}P uptake to be determined. All solutions were maintained at 28° C and aerated continuously.

Initial P Status of Seedlings. The effect of the initial P status of the Pioneer Sargent seedlings was examined by comparing seedlings that had been grown continuously in P-free basal medium (−P) with seedlings grown in basal medium containing 25 μM P (+P). Pretreatment solutions containing either 0 or 1 mM N as ammonium sulfate were also made up in −P and +P media. All solutions used during the P uptake measurement phase of the experiment contained basal medium plus 25 μM KH_2PO_4 labeled with ^{32}P.

Comparison of Phosphate and Sulfate Uptake. Seedlings of Pioneer Sargent were grown as described above except that the basal solution contained 100 μM $MgSO_4$. Concentrations of major cations similar to those occurring in the normal sulfate medium were maintained by using chloride salts instead of sulfate salts. Pretreatment solutions contained either 0 or 1 mM ammonium. Sulfate and phosphate uptake were then measured by transferring seedlings back into −N basal culture solutions containing either 100 μM $^{35}SO_4^{-2}$ or 25 μM $H_2{}^{32}PO_4^-$. Uptake rates were calculated from the amount of labeled S or P which accumulated in the plant material and paper pads used to collect the xylem exudate. Tissues were prepared for scintillation counting by methods outlined by Clarkson et al (3).

Divided Root System Experiments. Following germination of Pioneer Sargent seeds in paper wraps (20), the primary root axis was excised at the base of each seed. This encouraged growth of two to four seminal roots per seedling. Two d later seedlings were selected and excess roots removed so as to leave each seedling with only two roots, each 4 to 6 cm long. One of these was trained through a hole in the wall of a dual compartment culture vessel. Both compartments were filled with aerated basal solution which was renewed each day. Seven d after germination had been initiated, solutions were drained from the culture vessels, holes in the walls of the culture vessels through which the trained roots passed were sealed with silicone grease, and aerated solutions containing N pretreatments were added. These pretreatments (referring to solutions in the compartment containing the seed (main root) and that containing the trained root, respectively) were: −N−N, +N+N, −N+N, +N−N, where +N refers to 1 mM ammonium added to the basal solution. Seedlings were not decapitated in this experiment, and there were seven replicates of each pretreatment. After 20 h, these pretreatment solutions were replaced by aerated basal solution. The trained root compartments contained ^{33}P-labeled solutions and the main root compartments contained ^{32}P-labeled solutions. Uptake from the labeled solutions continued for 2 h, guttation fluid being collected on paper pads during this period. The trained root was then cut from each seedling and both trained root and main root desorbed in unlabeled basal solution for 3 min, blotted dry, and weighed separately. The whole seedling together with the wick used to collect guttation fluid was oven dried, ashed, and ^{33}P and ^{32}P determined by dual label liquid scintillation procedures. Solution samples from each compartment of each culture vessel were also counted to check for cross-contamination of uptake solutions. No contamination was found.

Inhibitor Studies. Three experiments were conducted in which amino acid analogs were added to pretreatment solutions. The DeKalb XL-45 genotype was used in these studies. There were two replications of each pretreatment, and each culture contained four seedlings. In the first experiment the phenylalanine analog p-FPA[1] was used. Pretreatment solutions containing either 0 or 1 mM N as ammonium sulfate were established to provide concentrations of 0, 10, 20, 50, 100, or 200 μM p-FPA. Following 20 h in these pretreatment solutions, detopped seedlings were transferred back to basal culture solutions for 1 to 2 h and then to uptake solutions containing ^{32}P and 200 μM phenylalanine. Phosphate uptake and translocation were then monitored for 4 h.

The proline analog AZ was used in two similar experiments. Pretreatment solutions contained 0 to 100 μM AZ in one experiment and 0 to 50 μM AZ in the other. In both experiments, the ^{32}P uptake solutions contained 100 μM proline. Phosphate uptake and exudation was measured over a 4 h period.

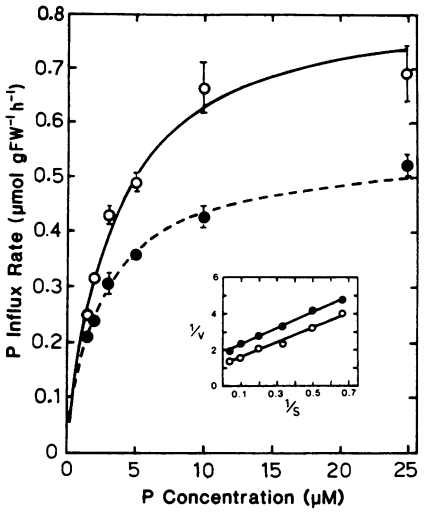

FIG. 1. Dependence of P uptake rates on external P concentrations by decapitated, dark-grown Pioneer Sargent maize seedlings which had been pretreated for 20 h in 1 mM ammonium (open symbols) or not pretreated (closed symbols). V_{max} = 0.546 (−N) and 0.875 (+N) μmol g^{-1} fresh weight $h^{-1} \cdot K_m$ = 2.47 (−N) and 3.51 (+N) μM P.

Table I. *Effects of P Concentration in the Basal Nutrient Medium and of 20-h Ammonium Pretreatment on N and P Concentrations in the Roots of Decapitated, Dark-grown Pioneer Sargent Corn Seedlings*

Values are the means of four replicate cultures.

Phosphorus Treatment	Ammonium Pretreatment	Root Tissue Concentrations	
		Phosphorus	Nitrogen
μM	mM	μmol g^{-1} fresh wt	
0	0	24.7	242
0	1	23.8	354
25	0	46.5	225
25	1	36.9	363
LSD (0.01)		4.2	17

RESULTS

Kinetic Studies. Over the range of external P concentrations from 1.25 to 25 μM, pretreatment with 1 mM ammonium increased V_{max} for phosphate uptake by 57% in Pioneer Sargent seedlings (Fig. 1) without a statistically measurable effect on K_m. Increased capacity for uptake rather than a marked effect on the

[1] Abbreviations: p-FPA, *p*-fluoro-DL-phenylalanine; AZ, L-azetidine-2-carboxylic acid.

affinity of the uptake system is indicated. In seedlings grown on 25 μM P, the relative response to N pretreatment varied among 14 separate experiments but the stimulation occurred in each.

Initial P Status of Seedlings. Growing Pioneer Sargent seedlings without P resulted in root P concentrations about 60% those of seedlings exposed to 25 μM P (Table I). Total N concentration of the root tissue was increased by ammonium pretreatment, the response being slightly greater in seedlings grown with 25 μM P. Phosphorous uptake was stimulated more by ammonium pretreatment when the seedlings were grown without P (Fig. 2A). A significant decrease in the uptake due to growth in 25 μM P was evident only in ammonium pretreated plants.

Without ammonium pretreatment, the initial translocation of exogenously supplied P to the xylem was slightly greater in plants grown with 25 μM P (Fig. 2B), but after the third hour, the rates were similar to those grown without P (Fig. 2B, inset). Ammonium pretreatment stimulated translocation of exogenous P in both low and high P seedlings with the effect being more pronounced on those grown in the absence of P. Exogenous P translocation approached steady state rates during the 3 to 4 h period. These rates, as a percentage of uptake, increased from 8.0 to 13.3% as a result of ammonium pretreatment in plants grown without P, and from 7.8 to 11.3% in plants grown with 25 μM P. The values are lower than those obtained with DeKalb XL-45 (*cf.* Fig. 3), but the pattern was the same.

Comparison of Phosphate and Sulfate Uptake. Ammonium pretreatment also enhanced sulfate uptake and translocation of the absorbed sulfur (Table II). The stimulation in P uptake in this experiment (18%) was not as marked as in other experiments and sulfate uptake was enhanced to about the same relative extent (19%). A greater proportion of the absorbed sulfate than phosphate was translocated to the xylem, but translocated sulfur was not enough to totally account for the stimulation in sulfate uptake.

Divided Root System. Phosphorous uptake by the main root was stimulated by ammonium pretreatment of that root only when the trained root was also pretreated (Table III A). On the other hand, uptake by the nonpretreated main root was inhibited if the trained root was pretreated. Uptake by the trained root was more variable than uptake by the main root but tended to respond similarly. Thus, both sets of data show that ammonium pretreatment of a part of the root system was largely ineffective in stimulating P uptake unless the other part was also pretreated. Further, they reveal an inhibitory effect on uptake by the nonpretreated part of the root system if the opposite part was pretreated. Total P uptake by the entire root system was therefore greatest only when both parts of the root system were pretreated; lack of pretreatment of a given part was not overcome by pretreatment of the other part.

Translocation of the exogenous P generally responded to pretreatment similarly to uptake (Table III B). There were some exceptions, however. Translocation by the trained root was significantly increased by its pretreatment when the main root was not pretreated, whereas uptake was not significantly enhanced. The decrease in P uptake by nonpretreated roots resulting from pretreatment of the opposite root was accompanied by only a marginal inhibitory effect on P translocation.

Inhibitor Studies. The relatively long time (at least 6 h) for the stimulus in P uptake to be initiated by ammonium and its persistence upon transfer to N-free media (20) suggest a possible involvement of protein synthesis in its induction. Addition of the analogs of phenylalanine (p-FPA) and proline (AZ) to root tissue has been shown to result in synthesis of ineffective protein (15, 17, 18) and, over longer periods, in reduced protein synthesis (15). Accordingly experiments involving presence of these analogs during the pretreatment period were conducted with genotype DeKalb XL-45 to determine if induction of the stimulus would be eliminated when synthesis of functional protein was impaired. In these experiments, root N concentrations following ammonium pretreatment were increased (175 ± 4 *versus* 124 ± 6 μmol g^{-1} fresh weight for ammonium-pretreated and controls, respectively) with no significant influence of the analogs.

Pretreatment for 20 h with 20 μM p-FPA decreased subsequent P uptake in seedlings that were simultaneously pretreated with 1 mM ammonium and in those which were not (Fig. 3A). There was no evidence of a recovery in P uptake rate during the uptake period indicating a relatively long-lasting inhibition, even though 200 μM phenylalanine was present in the uptake solution. Translocation of the absorbed P was also inhibited by p-FPA pretreatment (Fig. 3B). Increasing p-FPA to 200 μM did not reduce the P uptake rate further (Fig. 4A). The increase in P uptake arising from ammonium pretreatment (Fig. 4A, inset) was decreased by 10 μM p-FPA pretreatment but beyond that concentration there was no further decline. The increase in exogenous P translocation arising from ammonium pretreatment was not eliminated even at 200 μM p-FPA (Fig. 4B), although the tendency was for it to become progressively less with increasing p-FPA concentration (Fig. 4B, inset). In seedlings which were not pretreated with ammonium, translocation of the absorbed P was inhibited by the p-FPA treatments relatively more than was uptake (Fig. 4C)

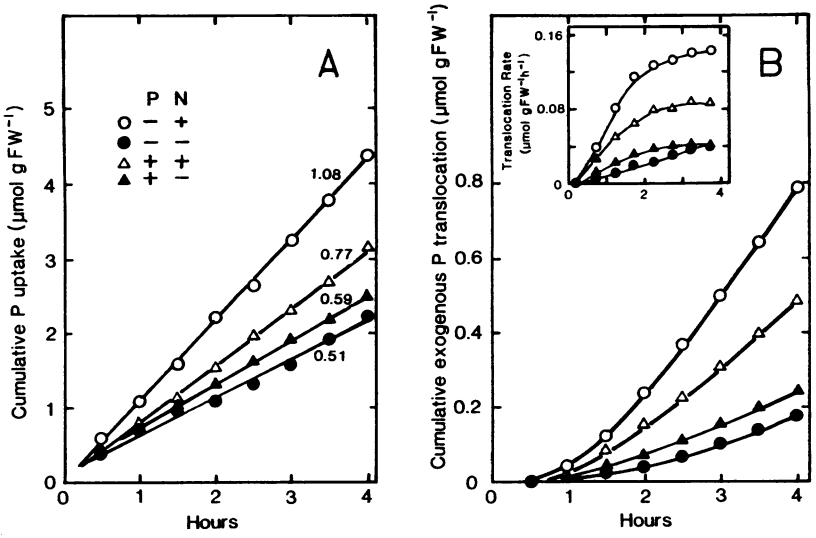

FIG. 2. Influence of ammonium pretreatment and presence of 25 μM P during growth on subsequent P uptake (A) and translocation of the exogenous P (B) by Pioneer Sargent maize seedlings. Numbers adjacent to the lines in (A) are the hourly uptake rates in μmol g^{-1} fresh weight h^{-1}. The inset in (B) shows the mean hourly translocation rates during each 0.5 h period.

Table II. *Influence of 20-h Ammonium Pretreatment on P and S Uptake and on the Percentage of the Absorbed P and S which was Translocated to the Xylem by Corn Seedlings*

Uptake was from 100 μM sulfate or 25 μM phosphate in the absence of ambient ammonium. Values are the means of four replicate cultures.

Ammonium Pretreatment	Uptake Time	Phosphate		Sulfate	
		Cumulative uptake	Deposited in xylem	Cumulative uptake	Deposited in xylem
mM	*h*	*μmol g⁻¹ fresh wt*	%[a]	*μmol g⁻¹ fresh wt*	%[a]
0	1			0.226	8.3
0	2	0.865	3.1	0.462	8.6
1.0	1			0.284	16.4
1.0	2	1.019	5.3	0.552	17.1
LSD (0.05)				0.032	3.9

[a] As percentage of uptake.

Table III. *Influence of 20 h Pretreatment with 1 mM Ammonium on P Uptake and Translocation of Exogenous P by the Main Root and a Trained Root of Corn Seedlings during a Subsequent 2 h Period*

Values are the means ± standard error of seven replicate cultures.

Pretreatment		Uptake by Main Root	Uptake by Trained Root	Total Uptake
Main Root	Trained Root			
			μmol g⁻¹ fresh wt h⁻¹	
A. Phosphorus uptake				
$+NH_4^+$	$+NH_4^+$	0.88 ± 0.09	1.36 ± 0.15	1.12 ± 0.20
$+NH_4^+$	$-NH_4^+$	0.66 ± 0.06	0.85 ± 0.06	0.75 ± 0.04
$-NH_4^+$	$+NH_4^+$	0.44 ± 0.02	1.19 ± 0.06	0.81 ± 0.04
$-NH_4^+$	$-NH_4^+$	0.61 ± 0.04	1.07 ± 0.12	0.84 ± 0.06
		Translocation by Main Root	Translocation by Trained Root	Total Translocation
B. Phosphorus translocation				
$+NH_4^+$	$+NH_4^+$	0.18 ± 0.03	0.17 ± 0.03	0.35 ± 0.05
$+NH_4^+$	$-NH_4^+$	0.09 ± 0.01	0.07 ± 0.01	0.16 ± 0.02
$-NH_4^+$	$+NH_4^+$	0.06 ± 0.01	0.17 ± 0.01	0.23 ± 0.02
$-NH_4^+$	$-NH_4^+$	0.08 ± 0.01	0.08 ± 0.01	0.16 ± 0.01

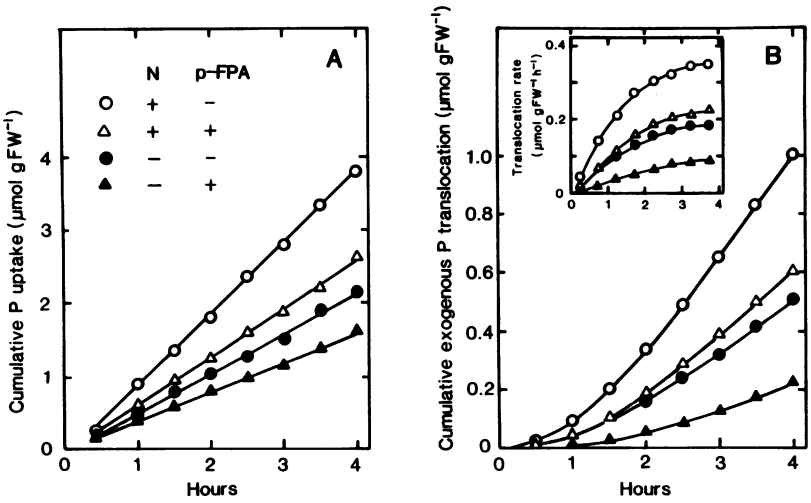

FIG. 3. Influence of pretreatments (20 h) with and without 1 mM ammonium, and with and without 20 μM p-FPA, on subsequent P uptake (A) and translocation of the exogenous P (B) by DeKalb XL-45 maize seedlings. Numbers adjacent to the lines in (A) are the hourly uptake rates in μmol g^{-1} fresh weight h^{-1}. The inset in (B) shows the mean hourly translocation rates during each 0.5 h period. The uptake solution contained 200 μM phenylalanine.

at all p-FPA concentrations employed.

Results of two experiments with the proline analog AZ indicate an influence on P uptake similar to that of p-FPA. Similar results were obtained from both and results from the experiment using 0 to 100 μM AZ are presented (Fig. 5). Phosphorous uptake by ammonium pretreated seedlings and by those not pretreated was inhibited by as little as 5 μM AZ during pretreatment (Fig. 5A) but significant uptake was still evident at 100 μM. The increase in P uptake arising from ammonium pretreatment was decreased by AZ pretreatment but it was not eliminated (Fig. 5A, inset). Phosphorous translocation was severely restricted at low AZ pretreatments and was completely eliminated by 50 μM AZ (Fig. 5A). All uptake rates were constant during the 5.5 h uptake period, and there was no indication of a recovery either in the P uptake rate or the P translocation rate in the presence of 100 μM proline. Again, however, the increase in P translocation arising

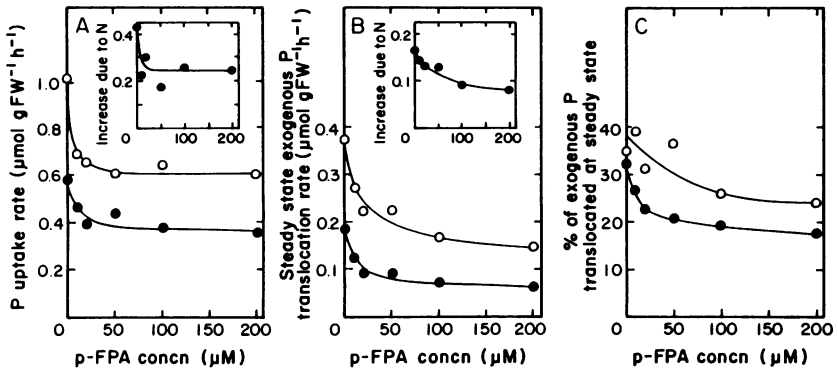

FIG. 4. Effect of pretreatment (20 h) with increasing p-FPA concentrations with (open symbols) and without (closed symbols) 1 mM ammonium on subsequent P uptake rates (A), mean hourly exogenous P translocation rates during the 3 to 4 h period (B), and the percentage of exogenous P translocated during that period (C), by DeKalb XL-45 maize seedlings. The insets in (A) and (B) show the increase in uptake and exogenous P translocation rates, respectively, resulting from ammonium pretreatment.

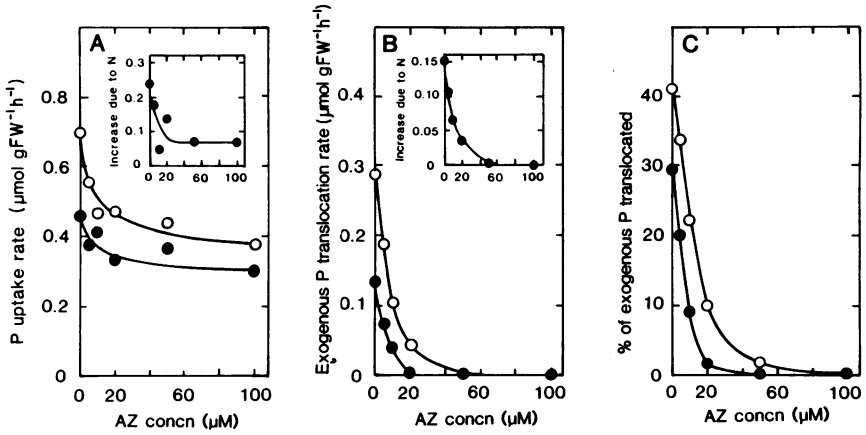

FIG. 5. Effect of pretreatments (20 h) with increasing AZ concentrations with (open symbols) and without (closed symbols) 1 mM ammonium on subsequent P uptake rates (A), mean hourly exogenous P translocation rates during the 3 to 4 h period (B), and percentage of exogenous P translocated during that period (C), by DeKalb XL-45 maize seedlings. The insets in (A) and (B) show the increase in uptake and exogenous P translocation rates, respectively, resulting from ammonium pretreatment.

from ammonium pretreatment persisted until translocation was eliminated and the proportion of the absorbed P which was translocated remained higher for the ammonium pretreated seedlings even when translocation was severely restricted (Fig. 5C).

DISCUSSION

The present results confirm other investigations (5, 21, 22) in illustrating a significant influence of N status of the tissue on P uptake and emphasize the complexity of the manner in which the stimulus is exerted. Capacity of the P uptake system, not its apparent binding efficiency, was increased by ammonium pretreatment (Fig. 1) which also increased root N concentrations (Table I). The stimulus was not specific to P since sulfate uptake was also enhanced (Table II). At this stage of growth, the roots increased in fresh weight at about 1%/h. The presence of ammonium during the pretreatment period did not increase the growth rate. Because both nitrate and ammonium elicit the response (20), differential cytoplasmic acidity resulting from assimilation of the two N ions appears not to be implicated in the observed effects on P transport unless the mechanism of enhancement differs between the two N sources—a possibility which cannot be excluded.

The extent of the stimulation in P uptake was similar in the genotypes Pioneer Sargent and DeKalb XL-45, although the latter consistently translocated a larger proportion of the absorbed P to the xylem (Figs. 2, 3). The stimulus was expressed in roots containing relatively high P concentrations (Table I), *i.e.* under conditions where P uptake presumably was limited by high tissue P status (1, 2, 4, 10–12, 19). A greater stimulation occurred, however, with seedlings grown without P and containing lower tissue P concentrations (Fig. 2; Table I). In seedlings which had not been pretreated with ammonium, growth in 25 μM P did not restrict P uptake (Fig. 2) even though P concentrations in the roots of these seedlings were appreciably higher than those in seedlings grown without external P (Table I). Hence, in the absence of ammonium pretreatment, the P uptake system was restricted to a level that was insensitive to further inhibition by increased tissue P. It is therefore difficult to visualize the stimulation resulting from ammonium pretreatment under the high P conditions to be a consequence of enhanced removal (via metabolic transformation, xylem deposition, or vacuole accumulation) of a P metabolite that acts as a negative effector of P uptake. This reasoning implies a direct enhancement of the activity or synthesis of the transport system or a stimulation in generation of the driving force for uptake.

The complexity of the mechanisms responsible for the ammonium induced stimulus are further evident from the experiment involving divided-root systems and those employing amino acid analogs. The divided-root experiment clearly indicates a requirement for participation of the entire root system in expression of the stimulus of P transport arising from N pretreatment; pretreatment of part of the root system did not result in a significant increase in P uptake by that part unless the other part was also pretreated (Table III). Moreover, when a part of the root system was not pretreated, its uptake was inhibited by pretreatment of the other part. Influences of the nutrient status of regions of the root system remote from those in which uptake was being measured have been reported in studies of sulfate uptake in *Macroptilium atropurpureum* (3), and of phosphate uptake in potato (4) and barley (6). In those instances, it was visualized that creation of a 'demand' for the element of interest in regions remote from the uptake region influenced the uptake of that element by facilitating its deposition into the xylem or otherwise depleting a small feedback inhibitor pool (6). In the present experiments this interpretation would require that the demand originated in the opposite roots because the shoots had been excised. It is conceivable that differential rates of energy supply from the endosperm (8) to the two root parts was affected

by exposure of a given part to ammonium, and that generation of the driving force for P uptake or activity of the P uptake system was directly affected in that way.

Presence of p-FPA and AZ during the pretreatment period decreased subsequent P uptake in seedlings that were pretreated with ammonium and in those not pretreated (Figs. 3, 4A, 5A). Nevertheless, a significant component of the stimulation was insensitive to either amino acid analog (Figs. 4A, 5A, insets). Because these amino acid analogs result in synthesis of nonfunctional proteins (15, 17, 18) or in impaired protein synthesis (15), the data imply a requirement for continual normal protein synthesis for maintenance of a component of P uptake, or the existence of two P uptake systems (14, 25) differentially sensitive to altered protein synthesis.

As in previous studies with other ions (17, 18, 23, 24), translocation of exogenous P was restricted more than phosphorous uptake by the amino acid analogues (Figs. 4B, 5B), with AZ exerting an especially marked effect (Fig. 5, B, C). Translocation of endogenous P was also restricted by p-FPA and AZ (data not shown). The fact that the stimulus in uptake was still evident at 50 μM AZ, a concentration at which exogenous P translocation was essentially eliminated (Fig. 5), further supports the view that the stimulation at least partially involved a specific effect on the uptake process and that it cannot be accounted for totally by enhanced translocation (20). The data further tend to mitigate against the notion that the stimulus resulted solely from the direct lifting of a feedback control on P uptake by enhanced xylem deposition. However, the possibility of an additional direct stimulation of the P translocation process cannot be ruled out. The increase in translocation relative to the increase in uptake (Fig. 5C; *cf.* Refs. 9, 20) supports the view that both processes were stimulated, although the increase in P translocation was not sufficient to account totally for the increase in P uptake.

Acknowledgments—We appreciate the technical assistance of Mr. P. J. Vanden Berg, Ms. C. Grimmer Bowman, and Ms. P. Longmire.

LITERATURE CITED

1. CLARKSON DT, CB SCATTERGOOD 1982 Growth and phosphate transport in barley and tomato plants during the development of, and recovery from, phosphate-stress. J Exp Bot 33: 865–875
2. CLARKSON DT, J SANDERSON, CB SCATTERGOOD 1978 Influence of phosphate-stress on phosphate absorption and translocation by various parts of the root system of *Hordeum vulgare* L. (Barley). Planta 139: 47–53
3. CLARKSON DT, FW SMITH, PJ VANDEN BERG 1983 Regulation of sulphate transport in a tropical legume, *Macroptilium atropurpureum*, cv. Siratro. J Exp Bot 34: 1463–1483
4. COGLIATTI DH, DT CLARKSON 1983 Physiological changes in, and phosphate uptake by potato plants during development of, and recovery from phosphate deficiency. Physiol Plant 58: 287–294
5. COLE CV, DL GRUNES, LK PORTER, SR OLSEN 1963 The effects of nitrogen on short term phosphorous absorption and translocation in corn (*Zea mays* L.). Proc Soil Soc Am 27: 671–674
6. DREW MC, LR SAKER 1984 Uptake and long-distance transport of phosphate, potassium and chloride in relation to internal ion concentrations in barley: evidence of non-allosteric regulation. Planta 160: 500–507
7. GRUNES DL 1959 Effect of nitrogen on the availability of soil and fertilizer phosphorous to plants. Adv Agron 11: 369–396
8. JACKSON WA, RJ VOLK, DW ISRAEL 1980 Energy supply and nitrate assimilation in root systems. *In* A Tanaka, ed, Carbon-Nitrogen Interaction in Crop Production, Japan Society for the Promotion of Science, Tokyo, pp 25–40
9. LAMAZE T, H SENTENAC, C GRIGNON 1984 Effects of nitrate on phosphate accumulation and transport by corn roots. Physiol Veg 22: 155–161
10. LEE RB 1982 Selectivity and kinetics of ion uptake by barley plants following nutrient deficiency. Ann Bot 50: 429–449
11. LEE RB, RG RATCLIFFE 1983 Phosphorous nutrition and the intracellular distribution of inorganic phosphate in pea root tips: a quantitative study using ^{31}P-NMR. J Exp Bot 34: 1222–1244
12. LEFEBVRE DD, ADM GLASS 1982 Regulation of phosphate influx in barley roots: effects of phosphate deprivation and reduction of influx with provision of orthophosphate. Physiol Plant 54: 199–206
13. LEONCE FS, MH MILLER 1966 A physiological effect of nitrogen on phosphorous absorption by corn. Agron J 58: 245–249
14. LIN W 1979 Potassium and phosphate uptake in corn roots: further evidence for an electrogenic H^+/K^+ exchanger and OH^-/P_i antiporter. Plant Physiol 63: 952–955
15. MACKLON AES, D VAUGHAN, A SIM, ID MCFARLANE, BG ORD 1985 Protein dysfunction and inhibition of amino acid incorporation in root segments from wheat and mung bean seedlings caused by some amino acid analogues. J Exp Bot 36: 911–918
16. MILLER MH 1974 Effects of nitrogen on phosphorous absorption by plants. *In* EW Carson, ed, The Plant Root and Its Environment. University Press of Virginia, Charlottesville, VA, pp 643–668
17. PITMAN MG, RA WILDES, N SCHAEFER, D WELFARE 1977 Effect of azetidine-2-carboxylic acid on ion uptake and ion release to the xylem of excised barley roots. Plant Physiol 60: 240–246
18. SCHAEFER N, RA WILDES, MG PITMAN 1975 Inhibition by p-fluorophenylalanine of protein synthesis and of ion transport across the roots in barley seedlings. Aust J Plant Physiol 2: 61–73
19. SCHJORRING JK, P JENSEN 1984 Phosphorous nutrition of barley, buckwheat and rape seedlings. II. Influx and efflux of phosphorous by intact roots of different P status. Physiol Plant 61: 584–590
20. SMITH FW, WA JACKSON 1987 Nitrogen enhancement of phosphate transport in roots of *Zea mays* L. I. Effects of ammonium and nitrate pretreatment. Plant Physiol 84: 1314–1318
21. THIEN SJ, WW MCFEE 1970 Influence of nitrogen on phosphorous absorption and translocation in *Zea mays*. Proc Soil Sci Soc Am 34: 87–90
22. THIEN SJ, WW MCFEE 1972 Effect of nitrogen on phosphorous transport systems in *Zea mays* L. Proc Soil Sci Soc Am 36: 617–620
23. THORNTON B, AES MACKLON 1985 Effects of some amino acid analogues on the uptake and transport of K^+ and Ca^{++} in wheat and mung bean seedlings. I. Cortical cell fluxes and transport to the stele in excised root segments, as affected by *p*-fluorophenylalanine. J Exp Bot 36: 919–929
24. THORNTON B, AES MACKLON 1985 Effects of some amino acid analogues on the uptake and transport of K^+ and Ca^{++} in wheat and mung bean seedlings. II. Uptake and translocation in whole seedling plants. J Exp Bot 36: 930–936
25. ULLRICH-EBERIUS CI, A NOVACKY, E FISCHER, U LÜTTGE 1981 Relationship between energy-dependent phosphate uptake and the electrical membrane potential in *Lemna gibba* G1. Plant Physiol 67: 797–801