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Nitrogen Enhancement of Phosphate Transport in Roots of *Zea mays* L.[1]

I. EFFECTS OF AMMONIUM AND NITRATE PRETREATMENT

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ABSTRACT

The effect of nitrogen status on phosphorous uptake and translocation was examined in 6-day-old dark-grown decapitated maize seedlings exposed to 25 micromolar phosphorous. Transfer to complete solutions containing 1 millimolar ammonium resulted in an increase in phosphorous uptake rate after 6 to 8 hours. The stimulus remained effective for at least 5.5 hours upon subsequent transfer to nitrogen-free solutions. Pretreatments for 16 hours with either nitrate or ammonium resulted in enhanced rates of subsequent phosphorous uptake and in enhanced translocation to the xylem of the exogenously supplied phosphorous. Both processes reached a plateau following pretreatment with 0.1 to 1.0 millimolar concentrations of either nitrogen ion. Further enhancement occurred with 10 millimolar nitrate, but not with 10 millimolar ammonium pretreatment. Although nitrogen pretreatments slightly increased the quantity of exogenous phosphorous retained in the root tissue, most of the extra phosphorous taken up by the nitrogen-pretreated seedlings was translocated to the xylem. The enhanced translocation, however, did not totally account for the increase in uptake implying a specific stimulation of the uptake process.

The stimulating effect of nitrogen on phosphorous uptake by plants (9, 19) may be attributed to increased root proliferation resulting from nitrogen application (6, 8), changes in the availability of soil phosphorous caused by chemical and acidity changes in the rhizosphere (1, 2, 22), and nitrogen-stimulated physiological changes within the plant itself that influence phosphorous transport (5, 13, 26, 27).

The possible importance of the physiological changes in *Zea mays* L. has been indicated by a series of field and glasshouse experiments. The field experiments have consistently shown progressive increases in leaf phosphorous concentrations at anthesis from about 0.2% to more than 0.3% with increasing nitrogen supplied as topdressing (EL Anderson, PhD dissertation, NC State University, 1982). That the response was at least partially a consequence of enhanced capacity for phosphorous uptake was revealed by a glasshouse experiment in which two maize genotypes were grown for 3 weeks in a Dothan loamy sand with adequate and high nitrogen treatments. Following thorough washing of the soil from the root systems, measurements of phosphorous depletion for aerated nutrient solutions (initially 25 μM P) revealed the phosphorous uptake rates were increased 23% by the high nitrogen treatment. The data indicate that soil-grown plants may exibit a nitrogen stimulation of phosphorous uptake as previously demonstrated in solution culture.

Additional attributes of the nitrogen-stimulated phosphorous uptake response are reported in this and the following paper. Phosphorous uptake by root tissue and translocation from it via the xylem were examined in decapitated, dark-grown maize seedlings such that effects resulting from enhancement in shoot functions were eliminated. Results of experiments defining the onset of the stimulus and the concentration-dependence of the stimulatory effects of pretreatments with either ammonium or nitrate are presented herein. Data from kinetic, inhibitor, and split-root studies are included in the second paper (25).

MATERIALS AND METHODS

Seed of the corn genotype DeKalb XL 45 was germinated in the dark at 30° C on paper towels kept moist with 0.1 mM $CaSO_4$. On the d 3 after germination, seedlings were selected for uniformity and all roots except the primary axis removed. Each seedling was supported in a small plastic stopper, transferred to 15 L tanks of aerated basal nutrient solution (pH 6.0), and grown in the dark at 30° C and 98% relative humidity for a further 2 d. Seedlings were again selected for uniformity and the shoots excised 1.5 cm above the endosperm. Thin-walled glass tubes (2.25 mm i.d. × 95 mm long) were attached to the stump of the shoots and sealed with high vacuum grease. These assemblies were then supported with the roots in the same aerated basal culture solutions containing the appropriate ammonium or nitrate pretreatment reagents.

The experimental unit used during the uptake and translocation measurement phase of the experiments comprised four decapitated seedlings (one culture) in 400 ml of basal medium labeled with ^{32}P. There were four replications of this unit for each treatment in all experiments. Cultures were maintained at 28° C during the uptake measurement phase of the experiments. Two basal nutrient solutions were employed. One is referred to as chloride-medium and contained 1 mM $CaSO_4$, 1 mM KCl, 250 μM $MgSO_4$, 25 μM KH_2PO_4, trace elements at two-fifths the concentration in Hoagland solution (10), and 1 mg Fe L^{-1} as FeEDTA. The other, referred to as sulfate medium, was identical except that 500 μM K_2SO_4 replaced 1 mM KCl.

The time required to initiate the nitrogen stimulation of phosphorous uptake was examined in experiment I. Seedlings were grown in sulfate medium and, immediately after attaching the

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exudate collection tubes to the shoot stump, four seedling (one culture) were placed in 400 ml of the same solution labeled with ^{32}P (0.2 μCi μmol^{-1}). Twelve such cultures were prepared. Samples of solution were taken and exudate collected from the glass tubes every 0.5 h to establish basal rates of uptake and translocation of the exogenous phosphorous for each culture. At the fourth h solutions were replaced; four cultures were exposed to the basal uptake medium, four others to the basal uptake medium containing 0.1 mM NH_4^+, and the final four to the basal uptake medium containing 1.0 mM NH_4^+. Ammonium was added as $(NH_4)_2SO_4$. Samplings were continued at 0.5 h intervals (with solutions being replaced every 4 h) for the next 14.5 h, following which samples were taken at hourly intervals for a further 6 h.

Experiment II portrays the pattern of phosphorous uptake resulting from ammonium pretreatment during a subsequent period in nitrogen-free medium. Seedlings were grown in sulfate-medium and, after attaching the exudate collector tubes, were placed for 16 h in 15 L tanks containing either sulfate medium or sulfate medium supplemented with 0.5 mM $(NH_4)_2SO_4$. Following this pretreatment phase, seedlings were transferred back to nitrogen-free sulfate medium for 1 h. Four cultures each from the control and ammonium pretreatments were exposed to sulfate-medium labeled with ^{32}P. Samples were taken from the uptake solutions and exudate collected at 0.5 h intervals over the next 4 h.

Experiments III and IV describe the effects of nitrate and ammonium concentrations during pretreatment on subsequent phosphorous uptake and translocation. Seedlings were grown in chloride medium. In experiment III, 16 h pretreatments of 0, 0.02, 0.1, 1.0, and 10 mM nitrate, established by adding $Ca(NO_3)_2$ to chloride medium, were initiated immediately after attaching the exudate collectors. This experiment also had an ammonium pretreatment of 0.5 mM in which the chloride medium was supplemented with $(NH_4)_2SO_4$. Experiment IV involved 16 h pretreatments of 0, 0.02, 0.1, 1.0, and 10 mM ammonium supplied as $(NH_4)_2SO_4$ to the chloride medium. For both experiments, phosphorous uptake and translocation were measured by sampling the ambient solution and xylem exudate at 0.5 h intervals over a 4 h period after transfer from pretreatment solutions to nitrogen-free chloride-medium labeled with ^{32}P. Exudate volume was also monitored each 0.5 h by measuring the height of the liquid in the exudate collection tubes.

Phosphorous depletion from the uptake solution was used to calculate the exogenous phosphorous uptake rates by dividing the ^{32}P removed by the ambient specific activity. There was no consistent change in specific activity of the uptake solution in any of the treatments. Translocation of exogenous phosphorous to the xylem was calculated by dividing the ^{32}P activity in the xylem exudate by the ambient specific activity. The amount of endogenous phosphorous translocated was determined as the difference between the total phosphorous in the exudate and the exogenous phosphorous translocated; it refers to phosphorous derived from the seed or accumulated in the root tissue prior to the uptake phase, and not in the equilibrium with the ^{32}P from the external solution.

At the conclusion of the experiments, roots were desorbed for 2 min in unlabeled uptake solution. Seed pieces, including the short mesocotyl section to which the exudate collectors had been attached, were separated from the roots which were then blotted, weighed, and analyzed for phosphorous (21) or nitrogen (18). Uptake solution and exudate samples were dried, and the latter ashed at 480° C. All samples were taken up in 0.1 N HCl and ^{32}P activity determined by liquid scintillation counting. Total phosphorous in solutions and exudate was measured by a modification of the method of Murphy and Riley (21). All data are presented per unit fresh weight of root tissue and are the means of four replicate cultures.

RESULTS

In experiment I all seedlings were exposed to nitrogen-free uptake solutions for the first 4 h during which they absorbed phosphorous at 0.458 μmol g^{-1} fresh weight h^{-1} (Fig. 1A). The uptake rate in the seedlings maintained in the nitrogen-free solutions increased slightly at 0.530 μmol g^{-1} fresh weight h^{-1} during the latter part of the 26 h experimental period. Seedlings transferred to solutions containing 1 mM ammonium at the fourth h maintained similar uptake rates as those maintained without nitrogen until about h 10 or 12 following which the uptake rate gradually exceeded that of the control seedlings and ultimately increased to 0.828 μmol g^{-1} fresh weight h^{-1} (Fig. 1A). Seedlings exposed to 0.1 mM ammonium (data not shown) responded identically to those exposed to 1 mM ammonium. Hence the concurrent presence of ammonium at either 0.1 or 1 mM stimulated phosphorous uptake about 50% but, within the limits of detection, the stimulus took from 6 to 8 h to initiate and about 12 h to develop fully. No difference in root fresh weight (1.666 ± 0.007 g fresh weight culture^{-1}) could be detected at the end of the experiment implying that the presence of ammonium increased either the driving force for phosphorous uptake or the activity or net synthesis of the uptake system rather than increasing the surface area for absorption.

When seedlings were pretreated for 16 h in 1 mM ammonium (experiment II), the stimulus was sustained when phosphorous uptake was subsequently measured in N_2-free medium (Fig. 1B). Moreover, the stimulated uptake rate (0.704 μmol g^{-1} fresh weight h^{-1}) remained constant throughout the 5.5 h period in nitrogen-free medium with no evidence of decay to the rate (0.451 μmol g^{-1} fresh weight h^{-1}) measured in seedlings which were not pretreated. A relatively long-lived stimulus is indicated.

All nitrogen pretreatments in experiments III and IV stimulated subsequent exogenous phosphorous uptake and translocation from nitrogen-free medium. Figure 2 illustrates the patterns in seedlings with no nitrogen pretreatment and those pretreated

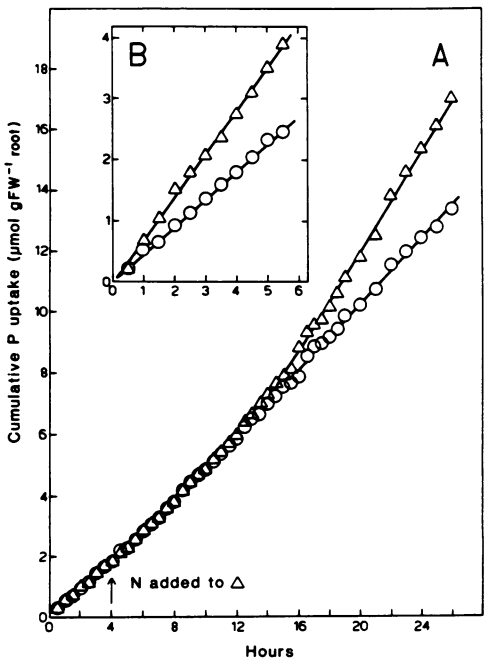

FIG. 1. Cumulative phosphorous uptake by decapitated dark-grown maize seedlings from 25 μM phosphorous during (A) the concurrent presence (△) or absence (○) of 1.0 mM ammonium added at h 4 (experiment I), and (B) exposure to nitrogen-free solutions following a 16 h pretreatment period in the presence (△) or absence (○) of 1.0 mM ammonium (experiment II).

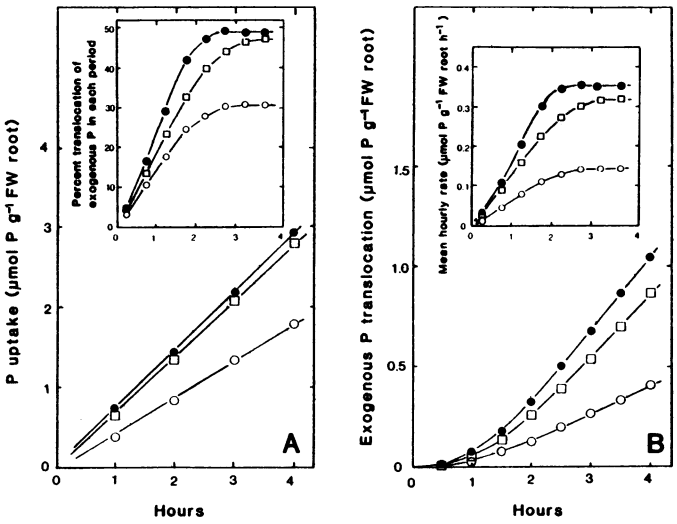

FIG. 2. Effect of nitrate or ammonium pretreatment on the uptake (A) and translocation (B) of exogenous phosphorous in experiment III. No N control (○), 1 mM nitrate (□), 0.5 mM ammonium (●).

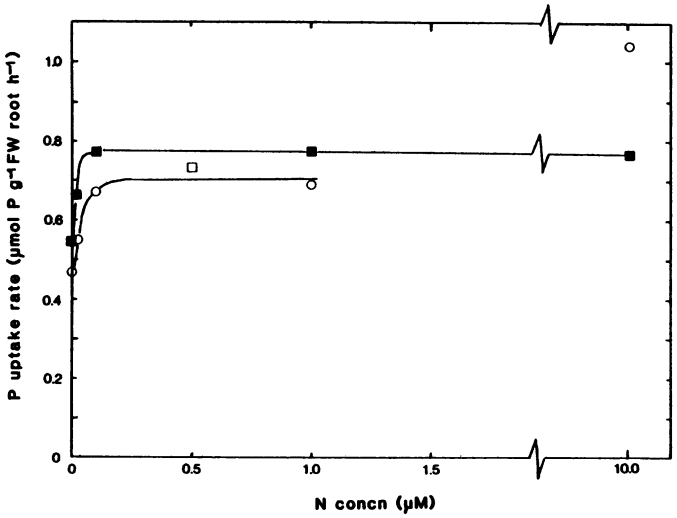

FIG. 3. Effects of nitrogen pretreatments on rates of phosphorous uptake by decapitated maize seedlings. Uptake rates were calculated from linear regressions of exogenous phosphorous uptake *versus* time. Experiment III, ammonium (□); experiment III, nitrate (○); experiment IV, ammonium (■).

with 0.5 mM ammonium or 1.0 mM nitrate in experiment III. Uptake rates were constant (Fig. 2A) and the enhancement resulting from nitrogen pretreatments was sustained throughout the 4 h uptake period. An increase in exogenous phosphorous translocation due to pretreatment (Fig. 2B) was detectable during the first 30 min. and steady state rates occurred by h 3 in all treatments (Fig. 2B, inset). Exogenous phosphorous translocation was increased to a relatively greater extent than uptake such that, at the steady state, nearly 50% of the entering phosphorous was translocated by pretreated seedlings compared to 30% in the seedlings without pretreatment (Fig. 2A, inset). Nevertheless, the increase in the steady state translocation rates for the ammonium and nitrate pretreatments over the controls (0.211 and 0.180 μmol g^{-1} fresh weight root h^{-1}, respectively) did not account quantitatively for the increase in the uptake rates (0.261 and 0.217 μmol g^{-1} fresh weight h^{-1}, respectively), indicating a concurrent stimulation in the rate of accumulation of exogenous phosphorous in the tissue.

All ammonium pretreatment concentrations in experiment IV significantly increased subsequent phosphorous uptake rates, reaching a maximum at 0.1 mM (Fig. 3) with no further enhancement occurring as ammonium concentrations were increased to 10 mM. Within the range 0 to 1 mM, nitrate pretreatments in experiment III resulted in a phosphorous uptake response similar to that of the ammonium pretreatments (Fig. 3), and 0.5 mM ammonium pretreatment data for this experiment agreed well with the results of experiment IV. Translocation of exogenous phosphorous (Fig. 4) responded similarly to the uptake responses, and in all nitrogen pretreatments there was a consistent increase with time in the proportion of the entering phosphorous which was translocated (Fig. 2A, inset). In experiment III, pretreatment with 10 mM nitrate resulted in a substantially increased phosphorous uptake rate (symbol in upper right of Fig. 3). This increase over pretreatment with 0.1 or 1.0 mM nitrate was significant statistically ($P < 0.001$). It thus is not in accord with the patterns established by either the lower nitrate pretreatment concentrations nor the range of ammonium pretreatment concentrations (including 10 mM) in experiment IV. The sizeable stimulation in uptake with 10 mM nitrate was accompanied by a comparable increase in exogenous phosphorous translocation (Fig. 4A) and in the proportion translocated (62% at the steady state).

A decline in water flow to the exudate during the 30 to 60 min period following transfer of seedlings to uptake solutions was noted in most of the experiments we have conducted. After h 2 it returned to values similar to those measured initially. We

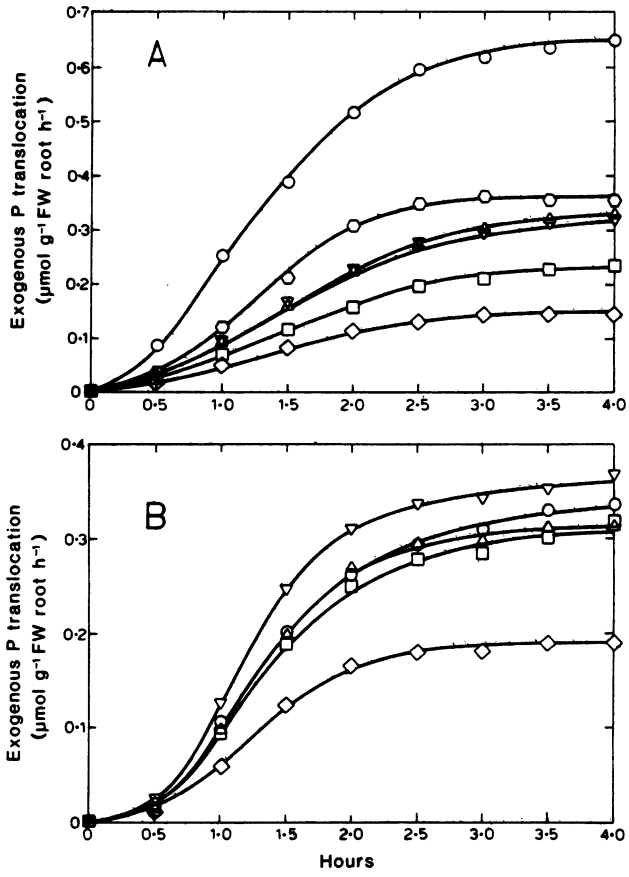

FIG. 4. Effects of nitrogen pretreatment on mean hourly rates of exogenous phosphorous translocation during each 0.5 h measurement period in experiment III (A) and experiment IV (B). A, No N (◇), 0.02 mM NO_3^- (□), 0.1 mM NO_3^- (▽), 1 mM NO_3^- (△), 10 mM NO_3^- (○), 0.5 mM NH_4^+ (○); B, No N (◇), 0.02 mM NH_4^+ (□), 0.1 mM NH_4^+ (▽), 1 mM NH_4^+ (△), 10 mM NH_4^+ (○).

Table I. *Effects of Nitrogen Pretreatment on Rates of Water Flow, Phosphorus Translocation to the Xylem, and Phosphorus Concentration in the Xylem of Decapitated Maize Seedlings*

Values are the means for the period from 2 to 4 h after exposure to nitrogen-free sulfate-medium containing 25 μM P labeled with ^{32}P.

Experiment	Pretreatment	Water Flow	Total P Translocation	Exogenous P Translocation	Endogenous P Translocation	Total P Concentration
		ml g^{-1} fresh wt h^{-1}		*μmol P g^{-1} fresh wt h^{-1}*		*μmol ml^{-1}*
III	No N	0.525	0.601	0.141	0.460	1.14
	0.02 mM NO_3^-	0.509	0.736	0.218	0.518	1.45
	0.1 mM NO_3^-	0.482	0.893	0.303	0.590	1.85
	1.0 mM NO_3^-	0.405	0.805	0.307	0.498	1.99
	10.0 mM NO_3^-	0.381	1.133	0.625	0.508	2.97
	0.5 mM NH_4^+	0.543	0.933	0.356	0.577	1.72
	LSD (0.01)	0.030	0.049	0.034	0.036	0.15
IV	No N	0.636	0.667	0.186	0.481	1.05
	0.02 mM NH_4^+	0.694	0.783	0.296	0.487	1.13
	0.1 mM NH_4^+	0.655	0.850	0.349	0.501	1.30
	1.0 mM NH_4^+	0.674	0.742	0.304	0.438	1.10
	10.0 mM NH_4^+	0.667	0.798	0.317	0.481	1.19
	LSD (0.01)	0.040	0.052	0.033	0.037	0.081

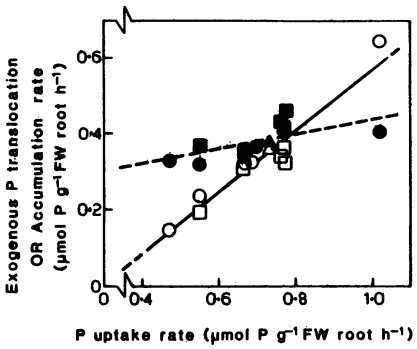

FIG. 5. Relationships between phosphorous uptake rates and steady state rates of exogenous phosphorous translocation (open symbols, $Y = -0.243 + 0.808X$, $r = 0.97$) or rates of accumulation of exogenous phosphorous in the tissue (closed symbols, $Y = 0.243 + 0.192X$, $r = 0.67$). Experiment III, nitrate (○); experiment III, 0.5 mM ammonium (△); experiment IV, ammonium (□).

ascribe the temporary decline to sensitivity of either the solute translocation processes or the hydrolytic conductivity of the root tissue (or both) to plant manipulation during transfer. The transient decline in the water flow had no influence on exogenous phosphorous uptake or translocation (Figs. 2, 4), and differences among nitrogen pretreatments in water and phosphorous flow were maintained throughout the experimental period. Water flow and total phosphorous translocation (presented in Table I as means for the steady state rates after 2.0 h) were both affected by the nitrogen pretreatments, but not in the same way. Nitrate pretreatments tended to decrease water flow, whereas ammonium treatments tended to increase it slightly.

Substantial quantities of total phosphorous were translocated to the xylem in these seedlings (Table I), reflecting the phosphorous supply from the seed and their continual exposure during growth and pretreatment to 25 μM phosphorous. Translocation of endogenous phosphorous, determined for the steady state values by subtracting exogenous phosphorous translocation (Fig. 4) from total phosphorous translocation, was sustained at sizeable rates but was not consistently affected by the nitrogen pretreatments; the increase in total phosphorous translocation for all pretreatments was largely accounted for by the stimulation in translocation of exogenous phosphorous (Table I).

Increased rates of phosphorous transport into the xylem of the nitrogen pretreated plants were reflected in elevated phosphorous concentrations in the exudates (Table I). The increase in concentration with increase in nitrate pretreatment resulted from the combined effects of restriction in water flow and enhancement in phosphorous translocation. The small increase in concentration with ammonium pretreatments was due to phosphorous translocation being increased more than water flow. Variation in water flow across the roots resulting from the nitrogen pretreatments clearly was not directly related to the stimulated phosphorous uptake and translocation.

The relationship between the uptake rates and the steady state exogenous phosphorous translocation rates for experiments III and IV are shown in the open symbols of Figure 5. The regression equation for these values indicates that on the average about 80% of each incremental increase in phosphorous uptake arising from N pretreatment was translocated to the xylem. It is to be

Table II. *Effect of Nitrogen Pretreatment on Total Phosphorus Concentration in Roots of Decapitated Maize Seedlings*

Experiment III		Experiment IV	
Pretreatment	μmol P g^{-1} fresh wt	Pretreatment	μmol P g^{-1} fresh wt
No N	23.4	No N	23.4
0.02 mM NO_3^-	17.3	0.02 mM NH_4^+	23.3
0.1 mM NO_3^-	16.6	0.1 mM NH_4^+	21.5
1.0 mM NO_3^-	15.4	1.0 mM NH_4^+	23.4
10.0 mM NH_3^-	13.8	10.0 mM NH_4^+	20.3
0.5 mM NH_4^+	20.9		
LSD (0.01)	2.3		2.3

noted that the high phosphorous uptake rate resulting from 10 mM nitrate pretreatment did not deviate appreciably from the regression. The closed circles of Figure 5 portray corresponding rates for accumulation of exogenous phosphorous in the tissue. These are more variable but nevertheless illustrate the tendency for a larger proportion of the exogenous phosphorous to accumulate in the root tissue at the lower uptake rates. Total phosphorous concentrations in the root tissue were progressively decreased by increasing nitrate concentrations during pretreatment while this effect was not consistently evident with ammonium pretreatments (Table II).

DISCUSSION

Retention of the endosperm on these dark-grown, detopped seedlings ensured that the root tissue was provided with sufficient energy to sustain both growth and vigorous ion transport processes for many hours following decapitation (11, 12, 16, 17). The nitrogen reserves of the seed also continued to provide the roots of the controls with sufficient levels of nitrogen (>125 μmol g^{-1} fresh weight) to sustain these processes throughout the experiments. In 14 separate experiments, we have been unable to measure any effects on root fresh weight that could be attributed to pretreatment with ammonium although enhanced root fresh weights were observed with nitrate pretreatments in experiment III. Thus, the well established stimulatory effect of nitrogen on growth and proliferation of lateral roots (6) was not observed under these experimental conditions when ammonium was employed. Ammonium pretreatments must therefore have enhanced the capability for phosphorous uptake by the new tissue produced during the pretreatments and/or by the tissue preexisting at the start of the pretreatment period.

Seedlings used in the present experiments were exposed continuously to 25 μM phosphorous and the roots also had a potential supply from the seed. They therefore were at a relatively high phosphorous status as is reflected by their root tissue concentrations (Table II) and high rates of endogenous phosphorous translocation (Table I). Because phosphorous uptake is restricted in roots of high phosphorous status (3, 4, 14, 15, 24), stimulation by nitrogen pretreatment could be due to increased rates of removal of negative effectors by xylem (7) or vacuolar (13) deposition, or by consumption in metabolic reactions (23). Stimulation could also result from a direct action of a nitrogenous metabolite in increasing the activity of the phosphorous uptake system or in increasing the driving force for uptake. Because at least 30% of the entering nitrate is reduced in the roots of these seedlings (16, 20), and because prior exposure to ammonium as well as nitrate elicited the response (Figs. 2, 3), the stimulus may reflect an influence of internal ammonium or a product of its assimilation. However, the requirement of 6 to 8 h for the stimulus to develop (Fig. 1A), its maintenance for at least 5.5 h after transfer to nitrogen-free solutions, and the differential effects of the two nitrogen ions on tissue phosphorous status at the end of the pretreatment period (Table II) all indicate a relative complex response.

The possibility exists that the stimulatory effects of the two nitrogen ions was not brought about by identical means. It has been suggested that concurrent presence of nitrate and phosphorous suppresses phosphorous accumulation in vacuoles thereby enhancing phosphorous transport to the xylem (13). The decrease in root phosphorous concentration during pretreatment with nitrate (Table II) is in accord with that concept, and pretreatment with 10 mM nitrate may have prolonged this effect during the subsequent exposure to nitrate free solutions (Fig. 2). Ammonium pretreatment, however, did not result in decreased root phosphorous concentrations (Table II) implying that preventing diversion to vacuoles was not responsible for the stimulus under these conditions.

The stimulation in phosphorous translocation did not totally account for the stimulation in phosphorous uptake (Fig. 5) which indicates a specific stimulation of the uptake process. Nevertheless, the major source of the extra phosphorous taken up by the nitrogen-pretreated plants was to the xylem, largely bypassing accumulation in storage or metabolic pools in the roots (Fig. 4), and this stimulation of exogenous phosphorous translocation occurred with little effect on translocation of endogenous phosphorous (Table I).

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