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Short Term Studies of Nitrate Uptake into Barley Plants Using Ion-Specific Electrodes and $^{36}ClO_3^-$ [1]

II. REGULATION OF NO_3^- EFFLUX BY NH_4^+

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ABSTRACT

The influence of NH_4^+, in the external medium, on fluxes of NO_3^- and K^+ were investigated using barley (*Hordeum vulgare* cv Betzes) plants. NH_4^+ was without effect on NO_3^- ($^{36}ClO_3^-$) influx whereas inhibition of net uptake appeared to be a function of previous NO_3^- provision. Plants grown at 10 micromolar NO_3^- were sensitive to external NH_4^+ when uptake was measured in 100 micromolar NO_3^-. By contrast, NO_3^- uptake (from 100 micromolar NO_3^-) by plants previously grown at this concentration was not reduced by NH_4^+ treatment. Plants pretreated for 2 days with 5 millimolar NO_3^- showed net efflux of NO_3^- when roots were transferred to 100 micromolar NO_3^-. This efflux was stimulated in the presence of NH_4^+. NH_4^+ also stimulated NO_3^- efflux from plants pretreated with relatively low nitrate concentrations. It is proposed that short term effects on net uptake of NO_3^- occur via effects upon efflux. By contrast to the situation for NO_3^-, net K^+ uptake and influx of $^{86}Rb^+$-labeled K^+ was inhibited by NH_4^+ regardless of the nutrient history of the plants. Inhibition of net K^+ uptake reached its maximum value within 2 minutes of NH_4^+ addition. It is concluded that the latter ion exerts a direct effect upon K^+ influx.

The potential importance of NH_4^+ in the regulation of NO_3^- metabolism has been widely recognized and explored in numerous studies of nitrate assimilation in micro-organisms and higher plants (*e.g.* 2–4, 12, 14). Considering the intermediary role of NH_4^+ in nitrate utilization, the former ion must represent a likely candidate for feedback effects on uptake and/or reduction of nitrate. Both short term (direct) effects of NH_4^+ on the activities of the nitrate transporter, as well as long term (indirect) effects, possibly via transcription-dependent events, might be envisioned. In addition, exposure of tissues to products of NO_3^- assimilation, the amino acids, would be anticipated to influence rates of NO_3^- uptake.

When present in the external medium, NH_4^+ is a potent inhibitor of NO_3^- uptake by barley plants (15, 25), and of NO_3^- accumulation in several other species, including wheat (19, 20) ryegrass (2, 16), apple (10), and corn (23). It should be stressed, however, that a reduction of NO_3^- accumulation by NH_4^+ might be caused by effects upon NO_3^- translocation or reduction rather than via direct effects on NO_3^- uptake *per se*. This distinction has often not been made clear.

In barley, Lewis *et al.* (15), for example, showed that NH_4^+ inhibited NO_3^- accumulation in the root and shoot and NO_3^- translocation to shoots although NO_3^- uptake was not measured directly. Recently, MacKown *et al.* (17, 18) have shown that NH_4^+ inhibits NO_3^- uptake and NO_3^- reduction in corn plants. Their results suggest that almost all the effect of NH_4^+ on uptake of NO_3^- is via its effect on the reduction step. There have also been reports of stimulated NO_3^- uptake arising as a consequence of NH_4^+ pretreatment as in the case of seedlings of wheat (21) and corn (18).

The almost universal choice of relatively long experimental periods (usually 2 to 24 h) for the investigation of effects of NH_4^+ upon nitrate uptake has made it extremely difficult to distinguish between effects on nitrate uptake *per se* and subsequent effects upon the properties (selectivity, turnover, etc.) of the nitrate transporter or effects on nitrate reduction and translocation (*e.g.* 17, 18). Both inhibition (9, 23, 24, 26) and stimulation (21) of *in vitro* nitrate reductase activity, following NH_4^+ pretreatment, have been documented. Other workers using corn have shown that NH_4^+ inhibits NO_3^- reduction *in vivo* (18). However, the possible direct or indirect effects of NH_4^+ on the turnover of the nitrate transport proteins (presuming they are in fact proteins) will remain an open question until such proteins can be biochemically characterized.

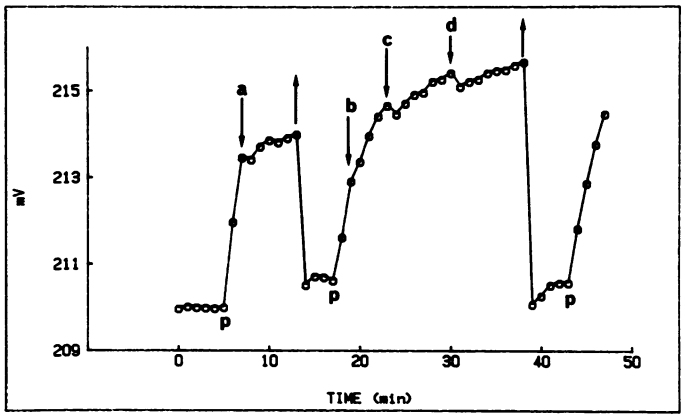

FIG. 1. The effect of NH_4^+ on NO_3^- uptake by barley plants grown in 10 μM NO_3^-. The uptake solution contained 500 μM $CaSO_4$ and 100 μM KNO_3. The increase in mv signal by the NO_3^- electrode corresponds with the decline in NO_3^- concentration of the medium. Plants were added (p) when a stable reading was obtained. At the points marked by ↑, the plants were removed and fresh KNO_3 was added until a stable reading was obtained. The same group of plants was used in all cases. The addition of $(NH_4)_2SO_4$ is marked by arrows, with final NH_4^+ concentration equal to 500 (a, d), 100 (b), and 200 μM (c).

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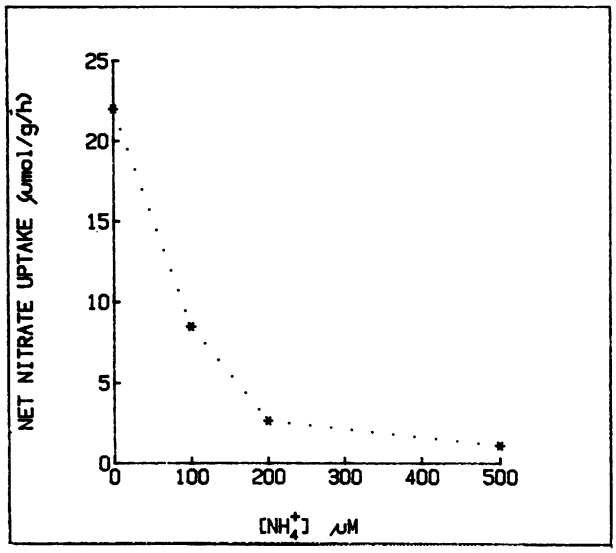

FIG. 2. Nitrate uptake as a function of NH_4^+ concentration, calculated from Figure 1. Coefficients of determination for linear regressions of slopes were ≥0.95 in all cases. Uptake media initially contained 100 μM NO_3^-.

By selecting appropriately short uptake periods, it is possible to gain insight into the nature of the NH_4^+ effects upon NO_3^- uptake. In micro-organisms, net nitrate uptake is usually shut down when NH_4^+ is available, and resumed when the NH_4^+ supply has been exhausted (4, 12). In the latter experiments, these effects appeared to precede effects upon nitrate reductase activity but, even so, maximum inhibition of uptake was not achieved instantaneously. Rather, although inhibition was apparent within 5 min, maximum effects were not evident until 30 to 60 min had elapsed. It might be anticipated that direct effects of NH_4 on the nitrate transporter would be evident immediately. Comparable short term experiments have not been reported for higher plants.

Ammonium ions have also been shown to inhibit potassium uptake (1, 17, 27). Indeed, considering the importance of K^+ in the 'induction' of nitrate uptake capacity (20) as well as the documented interactions between K^+ and nitrate during uptake and translocation (15), it might even be argued that a part of the inhibitory effect of NH_4^+ on NO_3^- uptake could arise from effects upon K^+ uptake. In the experiments described below, we have explored the short term effects of NH_4^+ on NO_3^- influx (using $^{36}ClO_3^-$ as a tracer for NO_3^-) and net NO_3^- uptake and efflux using a nitrate electrode whose output was measured automatically by a computer-controlled digital voltmeter. In addition, the nature of the interactions between NH_4^+ and K^+ influx were investigated in experiments of similar duration. Some longer term experiments were included insofar as the results enabled us to compare our data with that available in the literature.

MATERIALS AND METHODS

Plant Culture. Barley plants (*Hordeum vulgare* cv Betzes) were grown in hydroponic culture as previously described (5) with NO_3^- maintained at 10, 100, or 200 μM. In all experiments, intact barley plants were used after 7 to 8 d of growth.

NO_3^- Influx. NO_3^- influx was measured using $^{36}ClO_3^-$ as a tracer for NO_3^-. The uptake period was 10 min followed by a 5-min desorption in cold (4°C) unlabeled uptake solution. Full details of this method have been described previously (6).

NO_3^- Efflux Method 1. This method has been described previously and involved the measurement of NO_3^- efflux directly, using a Technicon Autoanalyzer (7), which employed a

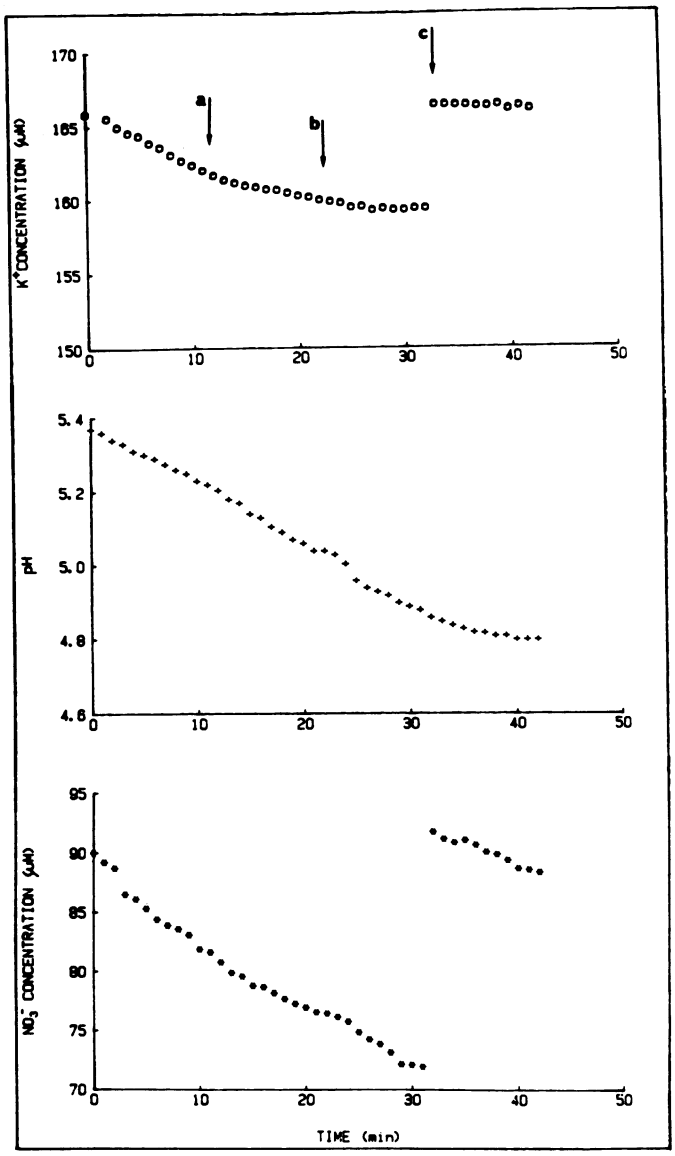

FIG. 3. The effect of NH_4^+ additions on the uptake of K^+ and NO_3^-, and pH reductions from media containing 500 μM $CaSO_4$, 40 μM K_2SO_4, and 100 μM KNO_3. Plants had been grown in identical media. (a, b, and c [shown by arrows]), the additions of $(NH_4)_2SO_4$ to give final concentrations of 100, 200, and 400 μM NH_4^+, respectively. At $t = 31$ min, KNO_3 was added to restore the concentration to that at $t = 0$.

Table I. *Effect of NH_4^+ on NO_3^- ($^{36}ClO_3^-$) Influx by Barley Plants Grown in 10 μM NO_3^-*

Uptake solution contained 100 μM NO_3^-.

[NH_4^+] during Pretreatment	NO_3^- ($^{36}ClO_3^-$) Influx[a] at Durations of NH_4^+ Pretreatment		
	0.0 h	0.5 h	1.0 h
μM		μmol g^{-1} h^{-1}	
0	15.2 ± 1.6	12.2 ± 0.9	13.8 ± 0.8
25	13.7 ± 1.3	13.0 ± 1.0	13.7 ± 0.8
50	11.2 ± 0.3	10.2 ± 1.1	11.6 ± 0.9
100	12.7 ± 1.3	9.2 ± 0.7	13.4 ± 0.7
200	13.5 ± 1.1	13.5 ± 1.3	16.3 ± 0.4

[a] Data shown are means of three replicates ± SE.

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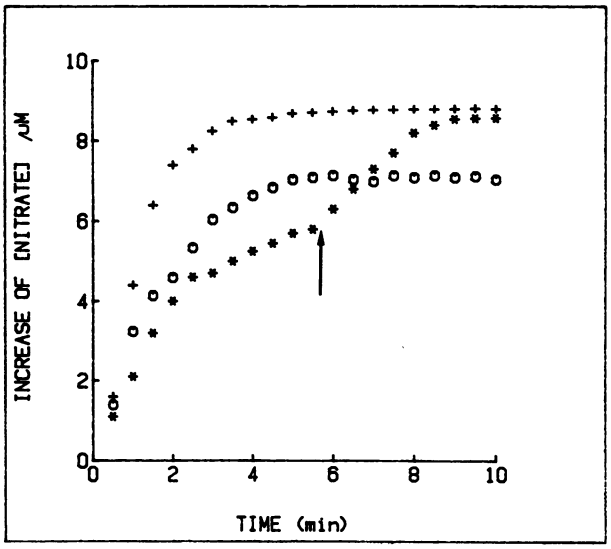

FIG. 4. The effect of NH_4^+ on NO_3^- efflux using barley plants that had been pretreated for 2 d in 5 mM KNO_3, followed by transfer to 100 μM KNO_3 (see "Materials and Methods," method 2). The graph shows the increase in NO_3^- concentration in the external solution when $(NH_4)SO_4$ was added at the start of the experiment (+), after 6 min (*), and in the absence of NH_4^+ (O). The final $[NH_4^+]$ was 400 μM.

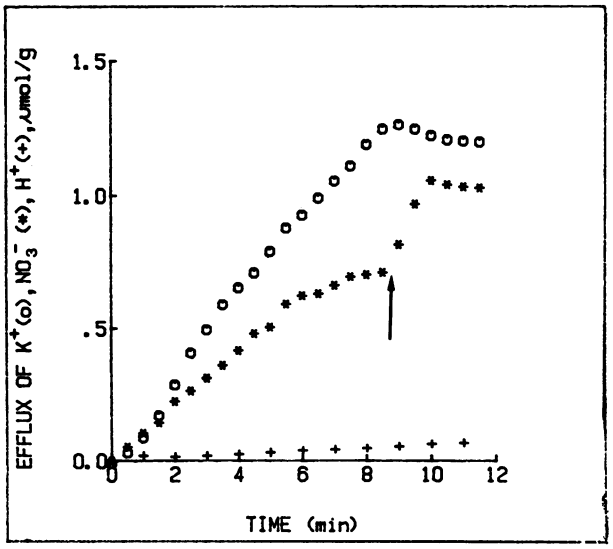

FIG. 5. The effect of NH_4^+ on NO_3^- (*), K^+ (O), and H^+ (+) efflux after pretreatment of barley roots with 5 mM KNO_3, and followed by transfer to 100 μM KNO_3 (see "Materials and Methods," method 2). NH_4^+ (250 μM) was added between 8.5 and 9 min, shown by the arrow.

Table II. *The Effect of NH_4^+ (400 μM) on NO_3^- Efflux Using Plants Grown in the Presence of 200 μM NO_3^-*

Experiment	NO_3^- Efflux[a]		Stimulation
	$-NH_4^+$	$+NH_4^+$	
	μmol g^{-1} h^{-1}		%
I	6.15 ± 0.01	7.92 ± 0.06	28
II	5.46 ± 0.03	6.94 ± 0.01	27

[a] Data show means of three replicates ± SE.

Cd-Cu column for NO_3^- reduction.

NO_3^- Efflux Method 2. Two d prior to efflux measurement, the NO_3^- concentration of the growth medium was increased to 5 mM by additions of KNO_3. After 2 d of further growth, roots were rinsed for 2 min in 500 μM $CaSO_4$ solution followed by transfer to a solution containing 100 μM KNO_3 + 500 μM $CaSO_4$. NO_3^- activity of the medium was measured at 1-min intervals using an Orion specific ion electrode whose voltage was measured and recorded by means of a computer-based system which has been described in detail previously (11). The initial rate of increase of NO_3^- concentration of the medium was taken to represent net NO_3^- efflux.

Table III. *The Effects of Long Term NH_4^+ Provision on Net NO_3^- Uptake and Net NH_4^+ Uptake Calculated from Linear Regression of Net NO_3^- and NH_4^+ Depletion*

The r^2 values of the regression lines are shown in parentheses.

Duration of NH_4^+ Pretreatment	$[NO_3^-]$	Net NO_3^- Uptake		Net NH_4^+ Uptake
		$-NH_4$	$+NH_4^+$	
h	μM	*μmol g^{-1} h^{-1}*		
0–3	100	2.17 (0.87)	2.42 (0.89)	1.97 (0.99)
5–7	200	4.96 (0.97)	1.65 (0.99)	2.03 (0.96)

Table IV. *The Effect of Long Term NH_4^+ Provision on Nitrate Reductase Activity (NRA) Assayed In Vivo in Roots of Barley Plants*

Duration of NH_4^+ Pretreatment	NRA[a]	
	$-NH_4^+$ (controls)	$+NH_4^+$
h	*μmol NO_2^- released/g fresh wt h^{-1}*	
5	0.38 ± 0.05	0.32 ± 0.01
15	0.29 ± 0.04	0.36 ± 0.01

[a] Data show means of three replicates ± SE.

NH_4^+ Effects. NH_4^+ was added as $(NH_4)_2SO_4$ in all cases and the pH was monitored continuously using Corning glass pH electrodes. K^+ was monitored using a K^+-sensitive electrode (Orion model 93-19) and a single junction reference electrode (Orion 90-01), in conjunction with the computer system. NH_4^+ uptake was measured by taking aliquots of the medium which were analyzed by means of an NH_3-specific electrode (Orion model 95-10).

K^+ Influx. K^+ influx was estimated by the use of $^{86}Rb^+$ as a tracer for K^+ in influx periods of 10-min duration, followed by 5-min desorption in (4°C) unlabeled influx solution (5).

Nitrate Reductase Activity. The *in vivo* assay was used, as described previously (5).

K^+ Translocation. Long term effects (5–10 h) of NH_4^+ on translocation of K^+ to the shoots was investigated using $^{42}K^+$. Roots and shoots were weighed into glass vials after prescribed periods in $^{42}K^+$. Half of the samples were preloaded for 4 h with $^{42}K^+$ (4 μCi/mmol) in a medium containing 0.25 mM KNO_3. The other half were pretreated with 0.25 mM KNO_3 and were subject to $^{42}K^+$ at the start of the NH_4^+ treatment. Samples were ashed for 4 h at 600°C, and β-emission was counted by the Cerenkov method in a Searle-Isocap/300 scintillation counter.

RESULTS AND DISCUSSION

As outlined in the "Introduction," there are apparent contradictions in the literature as to the nature of the interactions between NH_4^+ and NO_3^- transport and assimilation. Our results (Fig. 1) show that for plants grown under conditions of low NO_3^- provision (10 μM NO_3^-) there is a marked effect of NH_4^+ on the initial rate of net NO_3^- uptake. The sensitivity of NO_3^- uptake to NH_4^+ (Fig. 2) was similar to that reported for barley by Rao and Rains (25) who used plants that had been grown in the dark in 500 μM $CaSO_4$ solution. In our experiments, the inhibition

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Table V. *The Effect of NH_4^+ (400 μM) on $^{42}K^+$ Uptake, Accumulation in Roots, and Translocation in Barley Plants*

Translocation, as a percentage of uptake, is shown in parentheses. Plants were either provided $^{42}K^+$ at the commencement of NH_4^+ pretreatment (A) or preloaded with $^{42}K^+$ prior to NH_4^+ treatment (B). (In the latter treatment, total uptake and translocation at $t = 0$ was 6.42 ± 0.41 and 2.21 ± 0.2 μmol/g fresh weight, respectively).

	Time	$^{42}K^+$ Uptake, Accumulation, or Translocation[a]			
		A		B	
		$+NH_4^+$	$-NH_4^+$	$+NH_4^+$	$-NH_4^+$
	h	*μmol/g fresh wt root*			
Total uptake	1	2.38 ± 0.10	6.28 ± 0.31	5.51 ± 0.24	6.10 ± 0.65
Accumulated in roots		2.02 ± 0.06	5.28 ± 0.28	2.85 ± 0.15	2.89 ± 0.04
Translocation		0.36 ± 0.04 (15)	0.99 ± 0.03 (16)	2.66 ± 0.09 (48)	3.22 ± 0.61 (52)
Total uptake	3	6.42 ± 0.36	21.54 ± 0.82	6.94 ± 0.22	5.21 ± 0.24
Accumulation in roots		3.07 ± 0.22	11.03 ± 0.36	2.59 ± 0.06	2.38 ± 0.12
Translocation		3.35 ± 0.14 (52)	10.51 ± 0.49 (49)	4.35 ± 0.16 (63)	2.83 ± 0.12 (54)
Total uptake	5	10.39 ± 0.47	39.05 ± 1.18	8.01 ± 0.39	6.49 ± 0.21
Accumulation in roots		4.74 ± 0.16	14.51 ± 0.48	2.29 ± 0.11	2.34 ± 0.07
Translocation		5.65 ± 0.32 (54)	24.54 ± 2.7 (63)	5.74 ± 0.28 (72)	4.10 ± 0.14 (63)

[a] Data show means of three replicates ± SE.

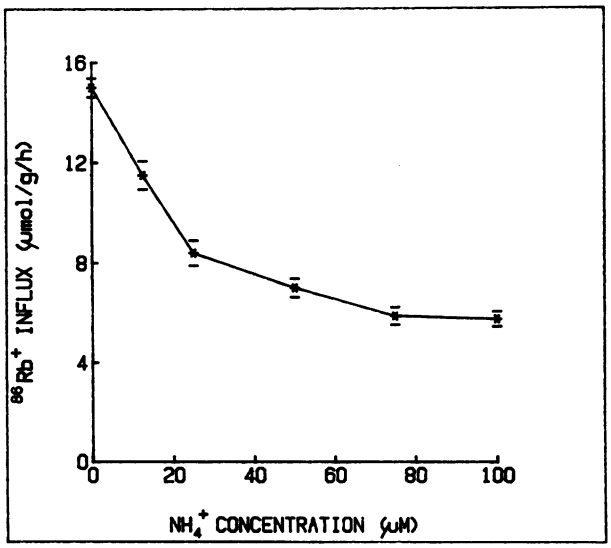

FIG. 6. The effect of NH_4^+ on $^{86}Rb^+$-labeled K^+ influx into barley roots. Potassium concentration of the uptake medium was 100 μM. Points show means of three replicates (SE indicated by bar lines.)

was reversible (Fig. 1), a feature which seems to be characteristic of NH_4^+ effects on NO_3^- transport in *Penicillium* (12) and *Chlorella* (4). Net uptake of nitrate by plants which had been grown in nutrient solution containing 100 μM NO_3^- showed a complete lack of response to the presence of NH_4^+ (Fig. 3). There was also no effect of NH_4^+ or NH_4^+ pretreatment on NO_3^- influx, measured by means of $^{36}ClO_3^-$ (Table I) using plants grown in 10 μM NO_3^-. The experiment was repeated several times using plants grown in different NO_3^- regimes, and in each case there was no effect of NH_4^+ on NO_3^- influx. Our choice of these short uptake periods enables us to distinguish clearly between direct effects of NH_4^+ on NO_3^- uptake and indirect effects which only become apparent in the long term.

How is it possible to reconcile the apparent contradiction contained in the data of Figures 1 and 3? There are several possible explanations. One possibility is that NH_4^+ is the preferred source of N when plants have been grown under conditions of low nitrogen provision. There are several reports documenting this apparent preference in species as diverse as apple (10), ryegrass (2), and barley (15). In the present context, it is possible that the diminution of NO_3^- uptake in the low N plants was a direct effect of NH_4^+ upon the uptake system. The lack of an effect of NH_4^+ on plants provided with adequate nitrate levels may be the result of changes in the sensitivity of the NO_3^- transporter to NH_4^+ as a function of the duration of exposure to NO_3^-. Considering the short half-life of NR decay in corn roots (22), it is not unreasonable to suppose that a similar turnover rate might characterize the NO_3^- transporter. The difficulty remains, however, that NO_3^- influx appears to be essentially unaffected by NH_4^+ treatment during a 10-min influx period even after 1 h of NH_4^+ pretreatment prior to the influx period (Table I). A second possibility, we suggest, is that NH_4^+ stimulates NO_3^- efflux when roots are in a nonsteady state with respect to NO_3^-. We have previously demonstrated that net uptake of NO_3^- or ClO_3^- gradually declines, with time, over a time period of 30 min as low NO_3^- roots are exposed to 200 μM NO_3^- or ClO_3^- solutions (7). This decline is almost certainly the result of an efflux component which increases as a function of the NO_3^- content of the root cytoplasmic compartment (7). It may be that NH_4^+ stimulates NO_3^- efflux until some maximum rate is achieved. Thus, in low NO_3^- roots, efflux is advanced to the rate characteristic of high NO_3^- roots. In high NO_3^- roots, generated by growth at higher [NO_3^-] or by short term loading with NO_3^-, efflux is already at its maximum level for the particular conditions of NO_3^- provision and is therefore not increased by treatment with NH_4^+.

To test the above hypothesis, the effect of NH_4^+ on NO_3^- efflux was investigated in roots which were in a condition approaching a new steady state. This was achieved by pretreating roots in 5 mM NO_3^- for 3 d, followed by transfer to a medium containing 100 μM NO_3^-. NO_3^- efflux following this transfer (Fig. 4) was initially rapid but was reduced after about 10 min. The data clearly reveal that efflux, by comparison to controls, is strongly enhanced by the presence of NH_4^+. Moreover, K^+ efflux to the medium in the absence of NH_4^+ appeared to parallel the observed NO_3^- efflux (Fig. 5). The correlation between NO_3^- efflux and K^+ efflux was statistically significant ($r^2 = 0.9$) with a ratio equal to 1 NO_3^-/1.75 K^+. The addition of NH_4^+, to a concentration of 0.25 mM, caused inhibition of K^+ efflux while NO_3^- efflux was stimulated. These results suggest that there is not an obligatory requirement for K^+ efflux during NO_3^- efflux.

A second method was employed to examine NO_3^- efflux by exploiting the apparent failure of barley roots to discriminate

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between NO_3^- and ClO_3^- (6). We used an analytical method to determine NO_3^- which was unresponsive to ClO_3^- ("Nitrate Efflux Method 1"). Barley plants were pretreated with relatively low NO_3^- (200 μM) for 2 d, after which NO_3^- efflux was examined in the presence and absence of NH_4^+. The results (Table II) demonstrate that there was a significant stimulation of NO_3^- efflux when NH_4^+ was present. Our results seem to contradict those of MacKown *et al.* (17, 18) who showed that there was no apparent effect of NH_4^+ on NO_3^- efflux in corn. However, their experiments were of greater than 2-h duration, so it is possible that more immediate effects of NH_4^+ on NO_3^- efflux were undetected. The alternative explanation is that there are genuine species differences between corn and barley with respect to NH_4^+ effects on NO_3^- uptake and assimilation.

Minotti *et al.* (19) have demonstrated that over 24 h NO_3^- efflux from wheat plants grown in 15 mM NO_3^- was stimulated by 10 mM $(NH_4)_2SO_4$. Similarly, Doddema *et al.* (8) have shown that NO_3^- efflux, from roots of *Arabidopsis* seedlings, is increased by NH_4^+ treatment. In both these cases, the experiments were of several hours duration and subsequent net uptake of NO_3^- was also affected by NH_4^+. We have also found a significant inhibition of net NO_3^- uptake by ammonium after 5 to 7 h of exposure (Table III). However, for exposures lasting up to 3 h, ammonium was without effect. Net NH_4^+ uptake was considerably less than NO_3^- uptake and was apparently unaffected by the external NO_3^- concentration (Table III). It was of interest that when plants were grown with roots maintained at low temperature the sensitivity of net NO_3^- uptake to NH_4^+ was apparent within 30 min (Deane-Drummond and Glass, unpublished data). Thus, it appears the NH_4^+ sensitivity of net NO_3^- uptake by barley plants is a function of nutrient status of the plants and other factors such as growth temperature. In the present context, we suggest that the long term inhibitory effects of NH_4^+ on NO_3^- uptake may, additionally, be mediated indirectly via effects on NO_3^- translocation and/or reduction.

The latter possibility was investigated in more detail. We could detect no apparent effects of NH_4^+ treatment on nitrate reductase activity assayed *in vivo* (Table IV), although it is possible that nitrate reduction rates *in situ* are affected. Our results show that in barley roots, as in barley leaves, NH_4^+ treatment has no effect on rates of nitrate reduction (13). We also examined the effect of NH_4^+ on K^+ translocation using $^{42}K^+$. Because K^+ efflux is inhibited by NH_4^+ (Fig. 5), any changes in $^{42}K^+$ accumulation in the roots reflect effects on K^+ uptake (Fig. 3). It is apparent from Table V that the proportion of absorbed $^{42}K^+$ translocated to the leaves is independent of the presence of NH_4^+ and the inhibition of $^{42}K^+$ uptake.

Regardless of the nutrient status of the plants, net uptake of K^+ was always strongly inhibited by the presence of NH_4^+ (Fig. 3 and unpublished results). Preliminary reports to this effect as well as the lack of effect of NH_4^+ on NO_3^- uptake have been reported previously (11). So far as we are aware, previous investigations of NH_4^+/K^+ interactions have been conducted in experiments lasting greater than 2 h (1, 17, 27). The interaction was therefore explored by the use of $^{86}Rb^+$ as a tracer for K^+ influx determinations. Figure 6 shows the influx of $^{86}Rb^+$, from solutions containing 100 μM K^+, into barley plants in the presence of different external NH_4^+ concentrations. Although K^+ influx was extremely sensitive to the presence of NH_4^+ at concentrations in the 0 to 50 μM range, beyond 50 μM NH_4^+, there was little further reduction. An Eadie-Hofstee plot gave lines characteristic of mixed kinetics of inhibition. It seems likely, therefore, that the mechanism of NH_4^+ inhibition of K^+ influx is complex, based upon both competitive and noncompetitive elements. It should be noted that the effect of NH_4^+ upon K^+ influx and net K^+ uptake (Fig. 3) appears to be instantaneous, unlike the situations described for net NO_3^- uptake.

In previously published work on the interactions between ammonium and nitrate, during nitrate assimilation by plants, the uptake step has been emphasized as the primary site of action. It is apparent from the short term studies reported here that NO_3^- ($^{36}ClO_3^-$) influx is insensitive to the presence of NH_4^+. The evidence also suggests that, where net NO_3^- uptake is reduced, this occurs as a result of stimulation of efflux. The long term effects of NH_4^+ on NO_3^- uptake need not involve a direct action of NH_4^+ or its assimilation products on the NO_3^- transporter, but may be exerted via effects on the translocation of NO_3^-. This might be exerted through a dependence upon available K^+ at the translocation step.

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