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Ammonium and potassium effect on nitrate assimilation in cucumber seedlings*

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Abstract

The effect of ammonium present in the induction medium toghether with nitrate on the activity of nitrate reductase (NR), nitrite reductase (NiR), glutamic acid dehydrogenase (GDH) and absorption and accumulation of NO_3^- in cucumber seedlings were investigated. Maximum NR and NiR activity in the cotyledons was observed when seedlings were supplied with KNO_3 as the sole source of nitrogen. When plants were supplied with NH_4NO_3 the presence of NH_4^+ in the induction medium repressed by about 50 per cent the activity of both reductases in the cotyledons. Addition of K^+ to this medium abolished completely the inhibitory effect of NH_4^+. The effect of K^+ cannot be replaced by that Na^+ ions. On the other hand, ammonium has no effect on the level of NR activity in roots, while NiR was almost completely repressed. Under the experimental conditions ammonium, in the presence of nitrates, decreased the activity of GDH, but this diminution did not occur when the plants were supplied with K^+ simultaneously. It has found that NH_4^+ ions reduced NO_3^- absorption but at the same time, the ratio of NO_3^- absorbed to that reduced was increased more than twice. The presumable mechanism of these phenomena is discussed.

INTRODUCTION

In fungi and algae, ammonia and some amino acids are known inactivators of biosynthesis or of activity of nitrate reductase (for review see Hewitt, 1975). In higher plants investigations to demonstrate the repression by ammonia have been negative (Beevers and Hageman, 1969). However, repression of NR was reported for barley roots (Smith and Thompson, 1971), roots of apple seedlings (Frith, 1972) and roots and cotton leaf discs (Radin, 1973, 1975).

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The above cited authors supposed that ammonium has a direct effect on nitrate reduction, while nitrate uptake is unaffected by these ions. In contrast, the results of Minotti et al. (1969) and Rao and Rains (1976) suggest that NH_4^+ can influence indirectly NR activity via its direct effect on NO_3^- absorption. On the other hand, Oaks et al. (1977) supposed that addition of ammonium to induction media interferes rather with the distribution of NO_3^- within the cells than with their absorption, hence it may interfere with the induction of NR.

The effect of NH_4^+ on nitrate reduction is not known, whereas the effect of ammonium on GDH activity was investigated and a number of papers viz. Wakiuchi et al. (1971), Weissmann (1972, Ehmke and Hartmann (1976) have reported that GDH activity was higher in plants supplied with ammonium than with nitrates.

Owing the fact that so far there is no unanimous view concerning the effect of NH_4^+ ions on nitrate reduction, it seemed worthwhile to undertake further studies on the action of ammonium on processes of NO_3^- assimilation in higher plants. The present study was undertaken to investigate the effect of NH_4^+ and other univalent cations on the nitrate- and nitrite reductase and glutamic acid dehydrogenase activity in roots and cytoledons of cucumber seedlings as well as on the absorption and accumulation of nitrates.

MATERIAL AND METHODS

Plant material. Cucumber seeds (*Cucumis sativus* L. cultivar. Monastyrski) were germinated in darkness at 27°C for 2 days on Petri dishes lined with moist filter paper. On the 2-nd day of germination twenty uniform seedlings were transplanted onto perforated aluminium foil stretched over a 600 ml beaker filled with precultured solution, containing 0.22 mM $Ca(H_2PO_4)_2$; 0.37 mM $MgSO_4$ and microelements in μmoles per litre of solution: ferric citrate — 190; H_3BO_3 — 25; $MnSO_4$ — 5; $ZnSO_4$ — 2; $CuSO_4$ — 0.5; H_2MoO_4 — 0.5. The pH in the preculture solutions was adjusted to 5.5 and beakers with seedlings were placed in a growth chamber. Seedlings grew at 25°C (day) and 22°C (night) for 3 days in a 18 hours day cycle (5.83 W/m²) and 6 hours night and 48% relative humidity. After 3 days, the seedings were transferred to the induction medium containing the same macro- and microelements as the preculture solution and nitrogen as 5 mM KNO_3, $NaNO_3$ or NH_4NO_3, or some other combination of potassium, sodium and ammonium salts as indicated in tables. The pH of the induction medium was adjusted to 5.5 and the solutions were aerated continously. The seedlings grew for 24 hrs in the medium in the growth

chamber under constant light (5.83 W/m² at 27°C) and relative humidity. After 24 hrs induction the enzymes activity and the accumulation and absorption of NO_3^- were measured.

Analytical methods. Extracts of nitrate and nitrite reductase were prepared from fresh cotyledons and roots according to the methods described in the previous paper (Buczek 1976). NR was assayed by measuring NADH-dependent production of nitrite (Hageman et al., 1960). NiR was measured by following the disappearance of nitrite with the use of dithionite-reduced methyl viologen as reductant (Joy and Hageman, 1966). Extract of GDH was prepared according to the method of Harper and Paulsen (1969). NADH-dependent glutamate dehydrogenase after Pahlich and Joy (1971) by measuring the rate of oxidation of NADH at 340 nm in the presence of ammonium and α-ketoglutarate. A control lacking ammonium was run simultaneously for each assay. Enzymes activity was expressed in nmoles of products released or in nmoles of substrates used per 100 mg of fresh tissue per hour.

The rate of nitrates absorption were determined by measuring loss of NO_3^- from the ambient solution by the phenoldisulphonic acid method (Johnson and Ulrich, 1950). Cotyledons, hypocotyls and roots dried at 70°C were used for analysis of NO_3^- accumulated. NO_3^- was extracted with 10 ml of hot water at 90°C for 3 hr and subsequent 10 min. in boiling water. After filtration, NO_3^- was estimated by the phenoldisulphonic acid method.

Results are expressed as mean from 4—6 replications. All experiments were repeated three or four times. Test of significance was made according to Buczek (1969).

RESULTS AND DISCUSSION

In order to examine the effect of pH of the ambient solution containing KNO_3 or NH_4NO_3 on the NR activity and NO_3^- absorption, two series of experiments were run. The seedlings grew 24 hours in the induction media at two ranges of pH. The results in Table 1 show that ammonium caused a significant inhibition of NR activity in cucumber roots when induction was tested at pH 7.0, while at pH 5.5 this inhibition did not take place. These results are consistent with the reports of Radin (1975) and Oaks et al. (1977). The above cited authors showed that ammonium inhibits NR activity in cotton and maize roots, respectively, when the induction was performed at pH 7.5. However, in our experiments the inhibitory effect of NH_4^+ on NR activity appeared also in the cotyledons, but only when the seedlings grew at pH 5.5.

Table 1

Effect of pH and univalent cations on NO_3^- absorption and nitrate reductase activity in cucumber seedlings

The enzyme was induced in 5 mM KNO_3 or 5 mM NH_4NO_3 for 24 hr. The values are the average of 4 replicates. The differences between 2 values denoted with different letters within the every column is significant at 5% level

Induction medium pH			NO_3^- absorbed		NR activity	
additions	starting	end	µmoles $NO_3^- \cdot$ seedling^{-1}	µmoles $NO_3^- \cdot g^{-1}$ dry wt.	cotyledons nmoles $NO_2^- \cdot 100\ mg^{-1}$ fr. wt. $\cdot hr^{-1}$	roots
KNO_3	5.5	5.6	14.11 a	731.36 a	952.00 a	88.20 a
NH_4NO_3	5.5	5.4	7.27 b	417.07 b	528.67 b	82.35 a
KNO_3	7.0	7.1	13.50 a	685.21 a	643.50 c	69.75 a
NH_4NO_3	7.0	6.8	6.98 b	366.81 b	738.00 c	24.73 b

Table 2

Effect of univalent cations on the formation of nitrate reductase in cucumber seedlings

The induction time was 24 hr in 5 mM of different nitrate salts at pH 5.5 Each value represents average for 4—5 replicates. Values in brackets reflect the effect of the treatment relative to the control

	Additions	NR activity hours after induction			
		2	6	12	24
		nmoles NO_2^- · 100 mg^{-1} fr. wt. · hr^{-1}			
Cotyledons	KNO_3	20.833 a	481.250 a	841.667 a	1191.667 a
	$NaNO_3$	20.803 a (100)	404.833 b (84)	678.333 b (80)	475.000 b (40)
	NH_4NO_3	28.125 b (135)	306.250 c (64)	531.667 c (63)	416.667 b (35)
Roots	KNO_3	26.042 a	63.542 a	97.917 a	122.917 a
	$NaNO_3$	21.875 b (84)	57.292 a (90)	81.677 a (83)	118.750 a (96)
	NH_4NO_3	15.634 c (60)	59.375 a (93)	75.000 b (76)	104.167 a (85)

The uptake of NO_3^- from the induction medium containing KNO_3 or NH_4NO_3 (Table 1) was dependent mainly on the kind of concomitant cation added to the medium together with NO_3^- and to a smaller extent on the pH of the ambient solution. Ammonium reduced the absorption of NO_3^- by about 50 per cent after 24 hrs induction, however, the differences in uptake of NO_3^- caused by K^+ or NH_4^+ had a little effect on the level of NR activity. Thus, the results suggests that NR activity both in roots and in cotyledons depends on the pH of the ambient solution and the kind of cation added, rather than on the differences in the ratio of NO_3 absorbed.

The data presented in Table 2 show the effect of NH_4 on the induction and on the time-course changes of NR activity in cucumber seedlings. It seems that ammonium has no effect on the induction of NR in cotyledons, however, the activity of NR was markedly inhibited with lapse of time of induction. The effect of NH_4^+ on NR activity in roots was not so clear. After 2 hours of induction with NH_4NO_3 the repression of NR activity reached 40 per cent as compared with that caused by KNO_3 or $NaNO_3$ solutions, but this inhibition disapeared in the next hour of experiment. Recently Frith (1972) demonstrated the inhibition of NR activity by ammonium ions in roots of young apple seedlings, and the ratio of this inhibition was dependent on the concentration of NH_4^+ in the ambient solution. Likewise, Smith and Thompson (1971) found a significant diminution of NR activity in barley roots, when induction was performed in the presence of NH_4^+. The above cited authors suggested a direct effect of NH_4^+ on NR activity.

The experiments listed in Table 3 show that the presence of K^+ ions in the induction medium is essential for maintenance of NR activity in the cotyledons, and the effect of K^+ cannot be replaced by that of Na^+ or NH_4^+. An addition of an equivalent or increased amount (Table 4) of K^+ to NH_4NO_3 induction medium, suppressed completely the inhibition of NR activity by ammonium and caused an increase of NO_3^- absorbed. The above results may suggest an indirect effect of NH_4^+ on the NR activity, at the same time they emphasise the specific role of K^+ (Table 3). However this role of K^+ in the assimilation of nitrates was questioned recently by Frost et al. (1978).

The above results show that, under the experimental conditions, repression of NR activity in the presence of NH_4^+ takes place only when K^+ ions are lacking in the induction medium. The beneficial effect of K^+ ions on reduction and absorption of NO_3^- has been reported by Oji and Izawa (1969), Harper and Paulsen (1969), Sasakawa and Yamamoto (1977), Pflieger et al. (1977) and others. In addition, according to the nitrate transport hypothesis

Table 3

Nitrate reductase activity in the presence of various univalent cations

The NR activity was measured after 24 hr induction of cucumber seedlings by different nitrate salts

Concentration of added salts mM		NR activity	
		Cotyledons nmoles NO_2^- · 100 mg^{-1} fresh wt. · hr^{-1}	Roots
KNO_3	5.0	1156.50 ± 29.37	105.75 ± 4.31
$(NH_4)_2SO_4$	2.5		
$NaNO_3$	5.0	611.00 ± 32.25	104.00 ± 3.12
$(NH_4)_2SO_4$	2.5		
KNO_3	5.0	1003.50 ± 27.12	97.98 ± 4.15
K_2SO_4	2.5		
NH_4NO_3	5.0	905.67 ± 23.31	80.67 ± 3.32
K_2SO_4	2.5		
NH_4NO_2	5.0	301.50 ± 18.17	88.50 ± 2.87
Na_2SO_4	2.5		
NH_4NO_3	5.0	192.83 ± 5.13	81.25 ± 3.95
$(NH_4)_2SO_4$	2.5		
NH_4NO_3	5.0	1126.67 ± 30.92	114.83 ± 2.48
K_2SO_4	2.5		
NH_4NO_2	5.0		
K_2SO_4	0.25	901.33 ± 20.84	140.83 ± 7.96
Na_2SO_4	2.25		
NH_4NO_3	5.0		
K_2SO_4	0.025	625.33 ± 31.47	114.75 ± 3.75
Na_2SO_4	2.475		
NH_4NO_3	5.0	615.33 ± 28.42	123.07 ± 5.22
Na_2SO_4	2.5		

Table 4

Nitrate reductase activity and NO_3^- absorption in the presence of potassium ions in the induction medium

The induction medium (precultured solution) contained 5 mM NH_4NO_3 and different concentrations of K_2SO_4. NR activity and NO_3^- uptake was measured after 24 hr induction. Each value represents the average for 5 replicates

Concentration of K_2SO_4 mM	NR activity		NO_3^- absorbed	
	Cotyledons nmoles NO_2^- · 100 mg^{-1}	Roots fr. wt. · hr^{-1}	µmoles NO_3^- per seedling	per g fr. wt.
0.	750.00 a	60.43 a	13.89 a	487.37 a
0.0025	970.83 b	60.92 a	15.69 a	545.19 a
0.025	1258.33 c	83.34 b	18.38 b	618.12 b
0.25	1312.50 c	100.00 c	22.39 c	724.54 b
2.5	1366.67 c	106.25 c	22.64 c	729.00 b

of Ben Zioni et al. (1971), K^+ may act as a counterion for transport of NO_3^- from roots to shoots. This hypothesis was supported by Frost et al. (1978). These later authors noted, that wheat seedlings absorbed

and accumulated more NO_3^- when supplied with K^+ than when supplied with Na^+ ions.

According to Minotti et al. (1969) ammonium afects the NR activity by direct inhibition of NO_3^- uptake. A detailed analyzis of absorption and accumulation of NO_3^- in cucumber seedlings is given in Tables 5 and 6. Ammonium present in the induction medium

Table 5

Absorption, accumulation and reduction of NO_3^- by cucumber seedlings as affected by univalent cations

Absorption and accumulation of NO_3^- was measured after 24 hr induction of seedlings in precultured medium containing 5 mM of different nitrate salts. The values are average of 4 replicates

Treatment	Absorption	Accumulation	Reduction	Absorbed / Reduced
		µmoles $NO_3^- \cdot g^{-1}$ dry weight		
KNO_3	675.5 a	499.6 a	175.9 a	3.8
$NaNO_3$	531.2 a	418.9 a	112.2 b	4.7
NH_4NO_3	398.7 b	351.6 b	47.1 c	8.5
		µmoles $NO_3^- \cdot$ seedling^{-1}		
KNO_3	13.9 a	10.2 a	3.8 a	3.7
$NaNO_3$	10.4 a	8.1 a	2.3 b	4.5
NH_4NO_3	6.6 b	5.7 b	0.9 c	7.6

Table 6

Accumulation of NO_3^- by cotyledons, hypocotyls and roots of cucumber seedlings

The analysed material from experiment described in Table 5.

Treatment	NO_3^- accumulated		
	Cotyledons	Hypocotyls	Roots
	µmoles $NO_3^- \cdot g^{-1}$ dry wt.		
KNO_3	300.9 a	109.9 a	92.5 a
$NaNO_3$	238.5 b	89.4 a	85.9 a
NH_4NO_3	184.6 c	67.1 c	58.9 b

decreased significantly the amount of NO_3^- absorbed as compared with the control (KNO_3). The fact that the ratio of NO_3^- absorbed to reduced increased simultaneously in seedlings supplied only with NH_4NO_3 may suggest, that NH_4^+ affects reduction of NO_3^- rather than absorption. On the other hand, inhibition of NR activity by NH_4^+ was not observed in roots (Tables 1 and 2) while in cotyledons the inhibition was very distinct. Thus it may be supposed that ammonia reduced the translocation of NO_3^- from roots to cotyledons and thereby decreased NR activity. On the other hand, we noted that ammonium

Table 7

Effect of univalent cations on the NR, NiR and GDH activity in cucumber seedlings

The enzymes activity was measured after 24 hr induction in precultured solution containing different nitrate salts. Values in brackets reflect the effect of the treatment relative to the control

Treatment mM		Cotyledons			Roots		
		NR[1]	NiR[2]	GDH[3]	NR	NiR	GDH
KNO_3	5.0	808.322 a	1746.763 a	473.00 a	197.916 a	855.200 a	630.00 a
$NaNO_3$	5.0	508.280 b (63)	1528.800 a (87)	389.50 a (82)	178.834 a (90)	210.000 b (32)	567.00 a (90)
NH_4NO_3	5.0	366.520 c (45)	1050.000 b (60)	335.83 b (71)	176.334 a (89)	126.000 c (19)	405.00 b (59)
KNO_3	5.0	—	1030.199 c	420.99 a	—	—	602.49 a
KNO_3	5.0	—	966.857 c (94)	457.50 a (107)	—	—	804.00 c (133)
$(NH_4)_2SO_4$	2.5						

NR[1] activity—nmoles NO_2^- formed per 100 mg fresh wt. per hr.
NiR[2] activity—nmoles NO_2^- utilized per 100 mg fresh wt. per hr.
GDH activity—nmoles NADH utilized per 100 mg fresh wt. per hr.

ions present in the induction medium reduced the amount of NO_3^- absorbed (Table 5). However, the amount of NO_3^- accumulated in cotyledons, hypocotyls and roots was more or less proportionally diminished (Table 6), while in roots inhibition of NR was not observed. We suspect that ammonium ions added to the induction medium could interfere with the distribution of NO_3^- within the cells as well as with its translocation from roots to cotyledons.

The experiments of Wakiuchi et al. (1971), Weissmann (1972) and Ehmke and Hartmann (1967) demonstrated that, when plants were grown on nutrient solution containing ammonium as the sole source of nitrogen, the activity of GDH in leaves and roots was higher than in the nitrate solution. In our experiments the activity of GDH was decreased both in roots and cytoledons, when seedlings were grown in minus K^+ medium containing equivalent amounts of NH_4^+ and NO_3^- (Table 7). However, when the solution was supplied with potassium, the inhibitory effect of NH_4^+ declined and the level of GDH activity was the same as in the control plants, likewise as observed by Wakiuchi et al., and Weissmann. The interpretation of these results is difficult, considering that Harper and Paulsen (1969) and Sasakawa and Yamamoto (1977) found that GDH activity was not dependent on K^+ ions. However, it is not excluded, that ammonium ions may also compete with nitrate for NAD/P/H (Radin, 1973; Leech and Kirk, 1968). The fact that, in the presence of NH_4^+, the activity of NR in roots was strongly repressed (Table 7) seems to confirm the above hypothesis.

CONCLUSION

The results presented above show that the activity of NR, NiR and GDH in cotyledons of cucumber was decreased when the induction medium contained equal amounts of NH_4^+ and NO_3^-. The uptake of NO_3^- was also decreased when the ratio of NO_3^- absorbed to reduced increased over two times as compared with the control. On the other hand, ammonium had no effect on NR activity in roots, while NiR activity was strongly inhibited and GDH activity was diminished by about 40 per cent. Since the addition of K^+ ions to the induction medium containing ammonium suppressed completely the inhibition of NR and GDH both in roots and in cotyledons, we may suppose that NH_4^+ affects distribution of NO_3^- processes and translocation within the plants rather than acts directly on reduction of NO_3^-. The indispensibility of K^+ for translocation of NO_3^- in the xylem has been proposed by Ben Zioni et al. (1971), and confirmed by Frost et al. (1978). However, in our experiments, in contrast to those of Frost

et al., K^+ could not be replaced by Na^+ ions. The fact that the activities of the investigated enzymes were not inhibited when the ambient solution contained NH_4^+ and K^+ ions may indicate that the effect of NH_4 on the activity of enzymes involved in nitrate assimilation is indirect rather than direct. Ammonium ions may also compete with nitrates for NAD/P/H, probably by reduction of NO_3^- and NO_2^- or reductive amination of α-ketoglutarate. The fact that NH_4^+ inhibits simultaneously the NR, NiR and GDH activities in cotyledons, while in roots the effect of ammonium appears only in diminution of NiR and GDH activity supports the foregoing hypothesis.

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Wpływ jonów amonowych i potasowych na asymilację azotanów w siewkach Cucumis sativus L.

Streszczenie

Badano wpływ jonów amonowych i potasowych, wprowadzonych do pożywki indukcyjnej łącznie z azotanami, na aktywność reduktazy azotanowej (NR), reduktazy azotynowej (NiR) i dehydrogenazy glutaminianowej (GDH) oraz na pobieranie i akumulację NO_3^- w siewkach ogórka.

Maksimum aktywności NR i NiR w liścieniach uzyskano, gdy rośliny pobierały KNO_3 jako jedyne źródło azotu. Jeżeli roślinom dostarczono azotany w formie NH_4NO_3, obecność jonów NH_4^+ w medium indukcyjnym zahamowało w około 50 procentach aktywność NR i NiR w liścieniach. Dodanie K^+ do roz-

tworu indukcyjnego zawierającego NH_4NO_3, znosiło niemal całkowicie hamujący wpływ NH_4^+ na aktywność NR i NiR. Z drugiej strony jony amonowe nie miały wpływu na poziom aktywności NR w korzeniach, jednakże aktywność NiR była całkowicie hamowana. W warunkach naszych doświadczeń, obecny w pożywce jon NH_4^+ razem z NO_3^- obniżał aktywność GDH, jednakże inhibicja ta nie wystąpiła, jeżeli do medium indukcyjnego dodano jony K^+. Stwierdzono, że NH_4^+ redukował pobieranie azotanów, ale równocześnie zwiększał się stosunek NO_3^- pobranych do zredukowanych.