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# Effect of ammonium nutrition on the nitrate utilization, nitrate reductase actvity and growth of *Spirodela polyrrhiza*

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## ABSTRACT

The influence of $NH_4^+$ ions on nitrate assimilation and growth of sterile *Spirodela polyrrhiza* cultures was investigated. *S. polyrrhiza* utilises both the nitrate and the ammonium form of nitrogen, it prefers, however, $NH_4^+$. Ammonium ions present in the nitrate medium inhibit the activity of nitrate reductase (NR), but they do not affect enzyme induction and only slightly reduce $NO_3^-$ uptake. These results sugest that the inhibitory effect of $NH_4^+$ on the NR activity is the main cause of the decrease in $NO_3^-$ assimilation by *S. polyrrhiza* cultures growing in nitrate-ammonium medium.

*Key words: nitrate reductase, nitrate utilization, Spirodela polyrrhiza.*

## INTRODUCTION

Plants of the family *Lemnaceae* are capable of utilising both the ammonium and the nitrate form of nitrogen (Ferguson 1969, Joy 1969, Knypl 1976). Ferguson and Bollard (1969) demonstrated an equal mass increment in *S. oligorrhiza* growing on ammonium salts or nitrates, although Joy (1969) claimed a higher increment of *Lemna minor* mass in the presence of nitrates. The growth of plants of the family *Lemnaceae* on media containing both the forms of nitrogen simultaneously leads, however, to limited utilisation of nitrates. Ferguson (1969), Joy (1969) as well as Orebamjo and Stewart (1974) demonstrated that ammonium ions inhibited nitrate uptake and reduced their assimilation. Assimilation of $NO_3^-$ is known to be dependent on the functioning of the inductive enzyme, nitrate reductase. In higher plants this enzyme, with but few exceptions is not sensitive to the ammonium ion (Hewitt 1975). It appeared, however, that in

*Lemnaceae* $NH_4^+$ modified NR, inhibiting in general the activity of this enzyme. Ferguson (1969) demonstrated that $NH_4^+$ inhibitis the NR activity in *S. oligorrhiza*, whereas Joy (1969) and Orebamjo and Stewart (1974) found an inhibitory influence of $NH_4^+$ on NR biosynthesis (induction). Lately Vijayaraghavan et al. (1982) noted that $NH_4^+$ stimulated NR activity in *S. oligorrhiza*. The discrepancy of results concerning the influence of $NH_4^+$ and NR activity and the role of ammonium in regulation of $NO_3^-$ assimilation prompted the authors to undertake studies on the influence of $NH_4^+$ on the level of activity and induction *in vivo* of nitrate reductase and uptake and utilisation of $NO_3^-$ by *S. polyrrhiza* cultures.

## MATERIAL AND METHODS

The experimental material consisted of sterile *S. polyrrhiza* (L.) Schleiden cultures transplanted at 3-week intervals onto fresh sterile medium.

A long-term experiments (18 or 21 days) on the influence of mineral nitrogen on plant growth (number of fronds, dry mas yield, $NO_3^-$ and $NH_4^+$ uptake) was run in Erlenmayer flasks of 300 $cm^3$ capacity filled with 100 $cm^3$ of the respective medium with 3 plants inoculated from the basic culture. The following media were used (mM): $KNO_3$ — 3.0, $Ca(NO_3)_2$ — 2.0, $NaH_2PO_4$ — 1.0, $NaNO_3$ — 1.0, $MgSO_4$ — 1.0, Fe-citrate — 0.045. The ammonium medium consisted of (mM): $(NH_4)_2SO_4$ — 4.0, $CaSO_4$ — 2.0, $K_2SO_4$ — 1.5 with the same remaining components as in the nitrate medium. The nitrate-ammonium media with various $NO_3^-$ to $NH_4^+$ ratios were prepared on the basis of a nitrate and an ammonium medium. Each medium was supplemented with microelements in the composition ($\mu$M): $H_3BO_3$ — 9.70, $MnCl_2 \cdot 6H_2O$ — 2.02, $ZnSO_4 \cdot 7H_2O$ — 0.18, $CuSO_4 \cdot 5H_2O$ — 0.20 and $H_2MoO_4 \cdot H_2O$ — 0.08. Sucrose in a 0.1 per cent concentration was added to the media. All of them were buffered with sterilised $CaCO_3$ in the amount of 50 mg per flask. Introduction of $CaCO_3$ maintained a constant pH level (6.9-7.2) in the medium. The plants grew in a photothermostat room with 18 h light (25 $W \cdot m^{-2}$) and 6-h night at a constant temperature of 21°C.

In short-term experiments concerning N uptake and NR activity measurements (Table 2 and Fig. 3a) the plant material cultured on ammonium medium (18 days) was transferred for 3 days to a medium free of nitrogen and then 250 mg of fresh plant weight was transferred to nitrate, ammonium and ammonium-nitrate medium. After a definite time (marked in the Tables and Figs.) $NH_4^+$ and $NO_3^-$ uptakes were determined as well as NR activity. In the long-term experiments (Table 3, Fig.

3b) the plants were inoculated directly into the suitable medium. After 7, 14 and 21 days part of the plants was discarded after measuring NR activity and nitrogen uptake in the solutions.

Nitrates in the medium and plant material were determined after Cataldo et al. (1975) and ammonium ions after McGullough (1967). The amount of $NO_3^-$ and $NH_4^+$ taken up was calculated from the loss of the given ions as determined in the outset medium and after a definite time of growth of the plant. The $NO_3^-$ and $NH_4^+$ content in the plant material was determined in extracts prepared from fresh plant matter (200-300 mg) by homogenisation in 0.1 M phosphate buffer (pH 7.5) containing 0.5 mM EDTA (Orebamjo and Stewart 1974). The homogenate was placed in a boiling water bath for 30 min and then centrifuged for 15 min at 15 000×g. The combined supernatants, after twofold washing of the sediment with extraction buffer were used for determination of the relevant ions. The amount of assimilated nitrogen was calculated from the difference between its amount taken up and accumulated. The coefficient of N utilisation was calculated by dividing the amount of assimilated N by the amount of N taken up × 100. Total nitrogen in the plant material was determined by the standard micro-method of Kjeldahl.

Nitrate reductase activity *in vivo* was determined by the method of Decleire et al. (1976). The plant material (200 mg of fresh matter) was incubated in solutions containing 0.1 M K-phosphate buffer (pH 7.6), 5 per cent propanol (final concentration) and 0.2 M $KNO_3$ (potential activity) or 0.05 M $K_2SO_4$ (actual activity). The material was incubated in 25-$cm^3$ Erlenmayer flasks placed on a water bath at 25°C. After 1 h 0.5 $cm^3$ samples of the incubation fluid were taken for determining nitrites. The latter were determined by adding to the sample 1 $cm^3$ of 1 per cent (w/v) sulphanilamide in 1 N HCl and 1 $cm^3$ of 0.01 per cent (w/v) of N-(1-naphtyl)ethylenediamine dihydrochloride and distilled water to a final volume of 5 $cm^3$. After 30 min absorption was read at 540 nm. The enzyme activity was expressed in nmoles of $NO_3^-$ per 1 g fresh weight per hour.

## RESULTS

### GROWTH OF *S. POLYRRHIZA* IN DEPENDENCE ON THE FORM OF NITROGEN

The final dry weight increment (Fig. 1a) and the increase in the number of fronds (Fig. 1b) of *S. polyrrhiza* growing on ammonium salts exclusively were significantly higher than the same values for plants receiving nitrates exclusively. Significant differences in growth were noticeable as late as after 15 days of culture. Dry weight of a single

segment was, however, distinctly lower in the presence of $NH_4^+$ (Fig. 1b) as early as after 10 days of growth. Thus, there is no doubt that the growth of single. *S. polyrrhiza* fronds in the presence of $NO_3^-$ was more intensive, the number of fronds, however, and the yield of dry mass were lower as compared with those of cultures growing on ammonium medium.

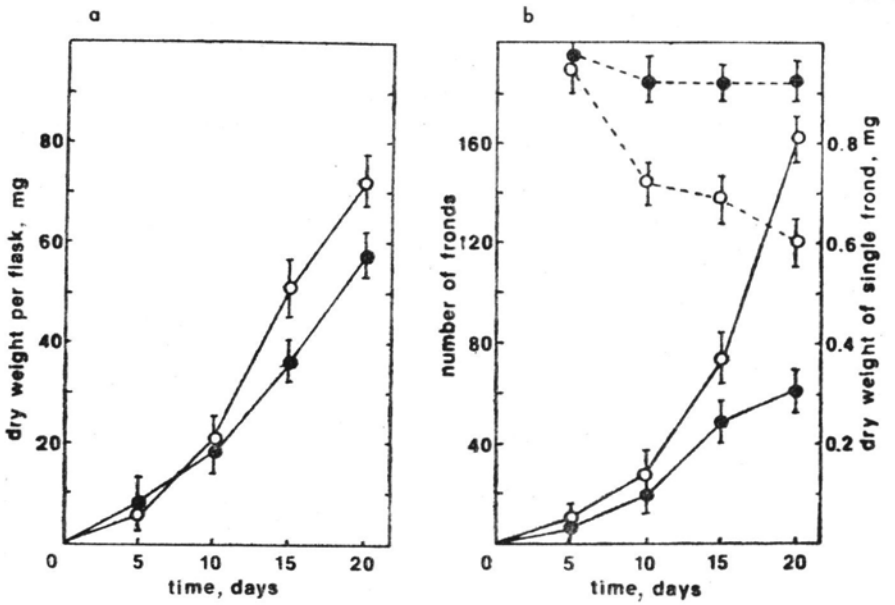


Fig. 1. Growth kinetics of *S. polyrrhiza* in dependence on nitrate (●) or ammonium (o) form of nitrogen in medium (N = 8 mM). a — dry weight, b — number of fronds and dry weight of single frond (dashed line). Results are means from 5 replications for each combination

Introduction into the medium of both nitrogen forms (with maintenance of a constant concentration N = 8 mM) had a significant effect on growth of the plants. Optimal growth (of the plants was obtained after 18 days of culture at an external $NO_3^-$:$NH_4^+$ ratios of 5:5 and 4:6 (Fig. 2), whereas the number of fronds per flask was similar within a wide range of external $NO_3^-$:$NH_4^+$ ratios and did not differ from the number of fronds of *S. polyrrhiza* taking up $NH_4^+$.

### N UPTAKE IN DEPENDENCE ON $NO_3^-$ : $NH_4^+$ RATIO

*S. polyrrhiza* growing in medium containing both forms of nitrogen took up and assimiliated both $NO_3^-$ and $NH_4^+$ (Table 1). There were, however, differences in the degree of utilisation of the nitrate and the ammonium form of nitrogen. It was, namely, found that introduction of a small amount of $NH_4^+$ into the medium ($NO_3^-$:$NH_4^+$ = 8:2) reduced by one half uptake and assimilation of $NO_3^-$. The change in the ratio to

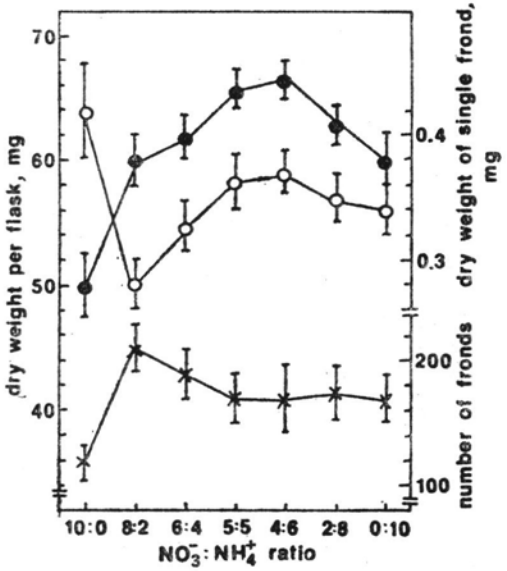


Fig. 2. Influence of $NO_3^-$:$NH_4^+$ ratio (N = 8 mM) in medium on *S. polyrrhiza* growth. ● — dry weight yield, o — dry weight of single frond, x — number of fronds in flask

6:4 did not, however, cause a further reduction of $NO_3^-$ uptake, but nitrate assimilation decreased threefold. The index of utilisation (assimilation/uptake × 100) of the nitrate form of nitrogen continued to decrease. The unchanged index of $NH_4^+$ utilisation may be evidence of the independence of the ammonium N form assimilation of nitrates. The differences found in assimilation and utilisation of $NO_3^-$ and $NH_4^+$ but little affected the total N content in the plants (Table 1), this possibly suggesting the ability of *S. polyrrhiza* of simultaneous utilisation of both these forms of nitrogen.

### KINETICS OF $NO_3^-$ AND $NH_4^+$ UPTAKE AND NR ACTIVITY

Nitrate uptake in the presence of equivalent amounts of $NH_4^+$ in both the tested concentration ranges (4 and 8 mM) was slightly but significantly inhibited after 24 h of plant growth (Table 2). Absorption of $NO_3^-$ in the presence of $NH_4^+$ in long-term experiments (Table 3) continued to decrease, this decrease, however, did not exceed 40 per cent as compared with the control. Nitrates affected to more of less the same degree $NH_4^+$ uptake.

Simultaneous measurement of NR activity in the short-term experiments (Fig. 3a) showed that the activity level of NR in plants transferred to nitrate medium with two ranges of $NO_3^-$ concentrations did not differ, in spite of marked differences in the amount of taken up $NO_3^-$

Table 1

Influence of $NO_3^-$:$NH_4^+$ ratio in nutrient solution (8 mM N) on nitrogen uptake, accumulation and assimilation (mmoles N per gram fresh weight) after 18 days of growth of *S. polyrrhiza*

| $NO_3^-$: $NH_4^+$ ratio in medium | Uptake | | | Accumulation | | | Assimilation | | | Assimilation / Uptake × 100 | | Total nitrogen, mM N per 1 g dry weight of plants |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $NO_3^-$ | $NH_4^+$ | total | $NO_3^-$ | $NH_4^+$ | total | $NO_3^-$ | $NH_4^+$ | total | $NO_3^-$ | $NH_4^+$ | |
| 10:0 | 3.33 a | — | 3.33 a | 0.18 a | 0.03 c | 0.21 a | 3.15 | — | 3.12 | 94 | — | 3.16 a |
| 8:2 | 1.72 b | 1.73 b | 3.45 a | 0.22 a | 0.03 c | 0.25 a | 1.50 | 1.70 | 3.20 | 87 | 99 | 3.47 a |
| 6:4 | 1.25 b | 2.89 a | 4.14 e | 0.32 b | 0.21 a | 0.53 d | 0.93 | 2.86 | 3.61 | 74 | 93 | 3.81 b |
| 5:5 | 0.57 c | 3.91 e | 4.48 e | 0.22 a | 0.26 a | 0.46 d | 0.35 | 3.65 | 4.02 | 62 | 93 | 4.27 c |
| 4:6 | 0.48 c | 4.05 e | 4.53 e | 0.18 a | 0.33 b | 0.51 d | 0.30 | 3.72 | 4.02 | 62 | 92 | 4.57 c |
| 2:8 | 0.06 d | 4.92 e | 4.98 e | 0.05 c | 0.38 c | 0.45 d | 0.01 | 4.54 | 4.55 | 14 | 92 | 4.90 d |
| 0:10 | — | 4.99 e | 4.99 e | — | 0.40 c | 0.40 c | — | 4.59 | 4.59 | — | 92 | 4.97 d |

Mean values with similar letters did not differ significantly at 5 % level. Each mean represents the average of 5 replications.

Table 2

Effect of ammonium ions on $NO_3^-$ and $NH_4^+$ uptake by *S. polyrrhiza* cultures grown for 18 days in ammonium medium (4 mM N), then 3 days in medium free of nitrogen and transferred (250 mg of fresh weigh) to media containing various sources of mineral N. All results are given in µmoles of N per flask (250 mg fresh weight)

| Nitrogen source (mM) | Period of growth, hours | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 3 | | 6 | | 12 | | 24 | |
| | $NO_3^-$ | $NH_4^+$ | $NO_3^-$ | $NH_4^+$ | $NO_3^-$ | $NH_4^+$ | $NO_3^-$ | $NH_4^+$ |
| $NO_3^-$ (4) | 6.9 a* | — | 13.2 c | — | 17.8 d | — | 20.6 b | — |
| $NO_3^-$(4)+$NH_4^+$(4) | 5.5 a | 19.1 b | 12.2 c | 21.2 b | 16.5 d | 26.4 e | 15.5 d | 28.7 e |
| $NH_4^+$(4) | — | 19.1 b | — | 19.8 b | — | 26.6 e | — | 27.1 e |
| $NO_3^-$(8) | 38.4 f | — | 40.0 f | — | 42.7 f | — | 46.8 i | — |
| $NO_3^-$(8)+$NH_4^+$(8) | 36.3 f | 22.1 b | 38.1 f | 27.6 e | 38.4 f | 33.8 f | 39.2 f | 38.4 f |
| $NH_4^+$(8) | — | 29.9 e | — | 35.7 f | — | 39.0 f | — | 40.3 f |

* For explanation see Table 1.

Table 3

Effect $NH_4^+$ on nitrate uptake (μmoles N per flask) by *S. polyrrhiza* growing for 3 weeks in media containing various forms of mineral N

| Nitrogen source (mM) | Period of growth, days | | | | | |
|---|---|---|---|---|---|---|
| | 7 | | 14 | | 21 | |
| | $NO_3^-$ | $NH_4^+$ | $NO_3^-$ | $NH_4^+$ | $NO_3^-$ | $NH_4^+$ |
| $NO_3^-(8)$ | 111.9 a* | — | 327.4 c | — | 339.4 c | — |
| $NO_3^-(8)+NH_4^+(8)$ | 87.1 b | 70.6 b | 216.3 d | 107.9 a | 213.2 c | 231.7 d |
| $NH_4^+(8)$ | — | 94.6 a | — | 176.2 e | — | 299.5 c |

* For explanation see Table 1.

(Table 2). There was, however, a distinct decrease in NR activity in the presence of $NH_4^+$. Significant differences may be observed after as little as six hours of growth. NR activity of plants transferred to the ammonium medium was very low and constant in the course of the whole experiment, independently of the $NH_4^+$ concentration in the medium. After seven days of plant growth in the presence of $NH_4^+$ (Fig. 3b), NR

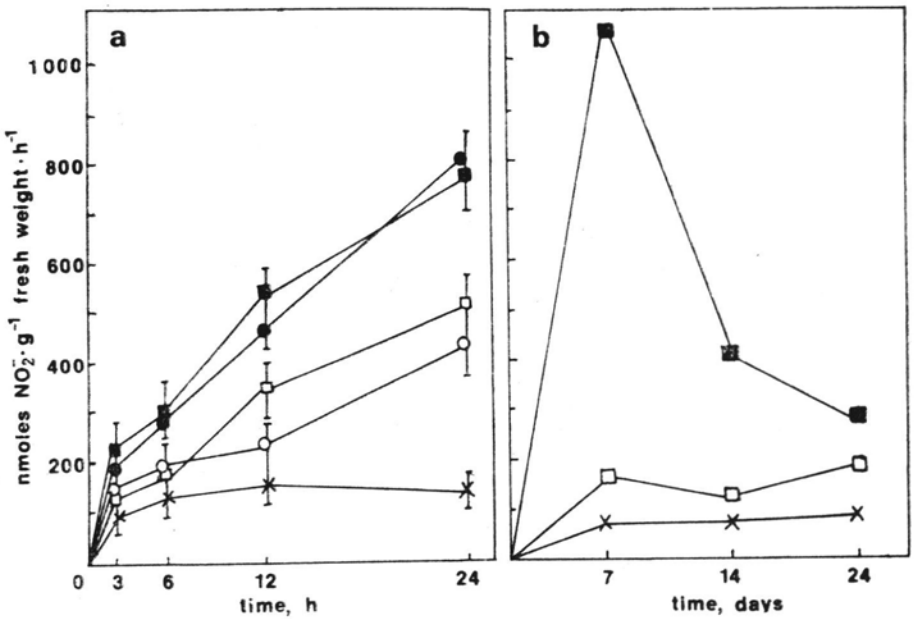


Fig. 3. Effect of $NH_4^+$ on nitrate reductase activity in *S. polyrrhiza* cultures growing for 18 days in ammonium medium (a) (N = 4 mM), the next 3 days in medium without nitrogen and then transferred (250 g fresh weight) to media with various forms of mineral N, (b) NR activity in plants growing for 3 weeks in media containing various mineral nitrogen forms. ● — 4 mM $NO_3^-$, ■ — 8 mM $NO_3^-$, o — 4 mM $NO_3^-$ + 4 mM $NH_4^+$, □ — 8 mM $NO_3^-$ + 8 mM $NH_4^+$, x — 4 mM and 8 mM $NH_4^+$

activity was six times lower than in plants taking up nitrates exclusively. These differences diminished, however, as the cultures aged. It would seem, therefore, that inhibition of $NO_3^-$ assimilation with increasing $NH_4^+$ doses in the medium was rather due to the influence of the latter on NR activity than to the influence on $NO_3^-$ uptake.

The influence of $NH_4^+$ on NR activity *in vivo* is confirmed by the following experiments (Fig. 4). Transfer of 18-day plants from the nitrate medium to $NH_4NO_3$ inhibited NR activity (Fig. 4a). In plants transferred from nitrate medium after previous growth in $NH_4NO_3$ medium (Fig. 4b) NR activity increased. On the other hand, transfer of the plants from ammonium medium to nitrate medium or $NH_4NO_3$ (Fig. 4c) depressed the NR level.

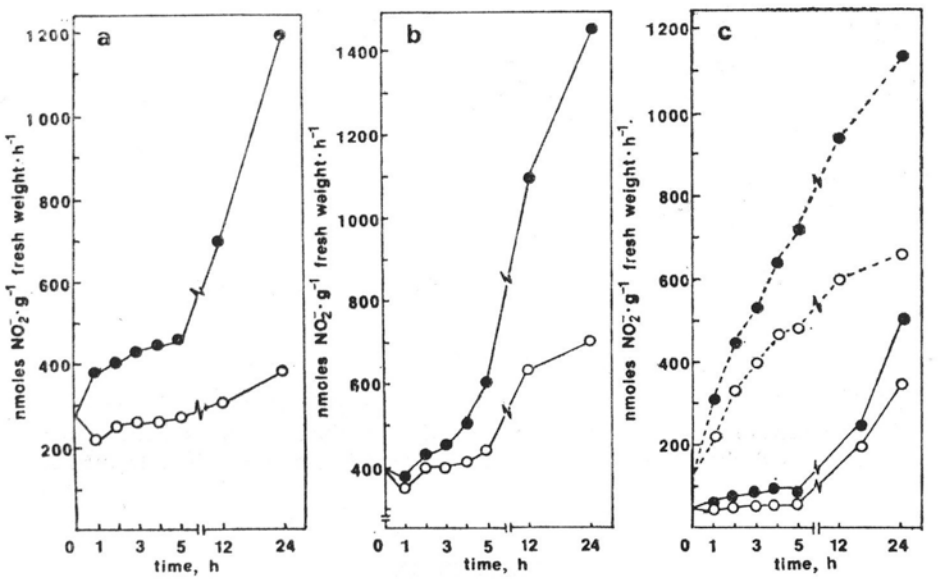


Fig. 4. Influence of $NH_4^+$ on NR in *S. polyrrhiza* cultures growing for 18 days on $NO_3^-$ medium (a), or $NO_3^-$ + $NH_4^+$ (b) or else $NH_4^+$ (c) (N = 8 mM), and then transferred to: ● — 8 mM $NO_3^-$ or o — 8 mM $NO_3^-$ + 8 mM $NH_4^+$. Dashed line denotes NR activity in plants growing for 18 days in ammonium medium (8 mM N), the next 3 days in N-free medium and then transferred to: ● 8 mM $NO_3^-$ or o — 8 mM $NO_3^-$ + 8 mM $NH_4^+$

The NR activity in *S. polyrrhiza* growing 18 days in ammonium medium but placed before transfer for 3 days in medium deprived of nitrogen showed a different course (Fig. 4c, dashed line). Transfer of these plants to $NO_3^-$ produced a drastic increase in NR activity, however, in the presence of $NH_4^+$ the enzyme activity was lower as compared with that in the control and after a certain time NR activity was inhibited.

NR INDUCTION IN THE PRESENCE OF $NH_4^+$

Ammonium ions distinctly depressed the potential and actual activity of NR (Fig. 5) in plants containing active enzyme (previously grown on nitrate medium), whereas in those which had no active NR (grown on ammonium medium) there were only traces of actual activity, but potential (induced) activity remained at a constant, though rather low level during the whole experiment.

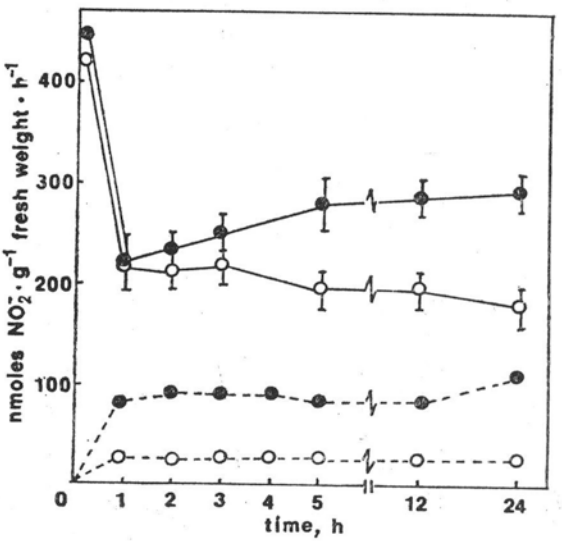


Fig. 5. Potential NR (●) and actual (o) NR activity in *S. polyrrhiza* growing for 18 days in nitrate medium (8 mM N — continuous lines) or in ammonium medium (8 mM — dashed lines) and then transferred to $NH_4^+$ medium (8 mM N)

## DISCUSSION

The present results seem to indicate that assimilation and utilisation of the nitrate form of nitrogen by *S. polyrrhiza* is regulated by $NH_4^+$. The fact that this compound introduced into nitrate medium reduced almost threefold nitrate assimilation and only by one half its uptake may suggest the influence of $NH_4^+$ on NR activity.

A similar decrease of NR activity in *S. oligorrhiza* cultures observed by Ferguson (1969) was interpreted as a reduction of both uptake and assimilation of $NO_3^-$ in the presence of $NH_4^+$. Different results were obtained by Vijayaraghavan et al. (1982) who found that $NH^+_4$ present in the medium stimulated NR activity in the *S. oligorrhiza* culture. In the present experiments the results indicate that, in *S. polyrrhiza* growing in medium containing equivalent amounts of $NH_4^+$ and $NO_3^-$,

NR activity was inhibited as early as after 6 h of growth, whereas, $NO_3^-$ uptake was slightly reduced, inhibition occurred as late as after 24 h. Although after seven days of growth of the plant in $NH_4NO_3$ medium a decrease in $NO_3^-$ uptake was noted, this reduction was relatively small, whereas NR activity was six times lower as compared with that in control plants. These results sugest that $NH_4^+$ inhibits NR activity, while the effect on $NO_3^-$ uptake observed both in our studies and those of other authors (Joy 1969, Ferguson 1969, Ferguson and Bollard 1969) is rather a secondary process.

In keeping with the hypothesis of Butz and Jackson (1977) nitrate reductase is present in tissues of higher plants in a complex with ATPase bound with the plasmalemma and it functions as carrier in active transport of nitrates to the cell and as reductase. Thus, in so far as this hypothesis is correct, the depressed $NO_3^-$ uptake observed in the present experiment might be the result of inhibition of $NO_3^-$ reduction in the NR-ATPase complex. This hypothesis, however, requires confirmation by further detailed investigations.

If plants deprived of active nitrate reductase, owing to growth in ammonium medium are transferred for 1 h to an incubation solution containing the substrate ($KNO_3$), appearance of potential (induction) activity is noted. The same plants when placed in an incubation solution without the substrate ($K_2SO_4$) did not show current activity after 1 h of incubation. This fact may confirm our supposition that $NH_4^+$ does not act on induction, but rather on the NR activity. Our results differ, therefore, from the observations of Joy (1969) who claimed that $NH_4^+$ inhibited NR induction in *Lemna minor*.

The growth of *S. polyrrhiza* measured in terms of dry weight increment and number of fronds depended on the form of mineral nitrogen. Inhibition of NR activity by $NH_4^+$ led to a restriction $NO_3^-$ assimilation, it did not, however, find a reflection in the dry weight or number of fronds, but was expressed in a decrease of the sum of total nitrogen. The presence of $NO_3^-$ in the ammonium medium, on the other hand, had no effect on $NH_4^+$ utilisation, as indicated by the aqual index of ammonium form utilisation in the case of various $NO_3^-$:$NH_4^+$ ratios in the medium. A certain diminution of $NH_4^+$ assimilation was however, noted at higher nitrate doses ($NO_3^-$:$NH_4^+$ = 8:2), this resulting probably from the deficit of these ions in the medium. Since the sum of total nitrogen determined in the plants increased with higher $NH_4^+$ concentration in the medium in relation to $NO_3^-$ it would seem that *S. polyrrhiza* assimilates more readily the ammonium form of nitrogen.

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## *Wpływ odżywiania solami amonowymi na wykorzystanie azotanów, aktywność reduktazy azotanowej oraz wzrost Spirodela polyrrhiza*

Streszczenie

Badano wpływ $NH_4^+$ na asymilację azotanów oraz wzrost sterylnych kultur *Spirodela polyrrhiza*. *S. polyrrhiza* wykorzystuje zarówno azotanową jak i amonową formę azotu, preferuje jednakże odżywianie $NH_4^+$. Jony amonowe obecne w pożywce azotanowej hamują aktywność reduktazy azotanowej (NR), nie mają wpływu na indukcję enzymu oraz w niewielkim stopniu zmniejszają pobieranie $NO_3^-$. Wyniki wskazują, że hamujący wpływ $NH_4^+$ na poziom aktywności NR jest główną przyczyną zmniejszenia asymilacji $NO_3^-$ przez kultury *S. polyrrhiza* rosnące w pożywce azotanowo-amonowej.