

ORGANIC PHOSPHATE IN AMMONIUM- AND NITRATE-FED TOMATO PLANTS

JURINA J. HOFSTRA and T. KOCH-BOSMA

Botanisch Laboratorium, Universiteit Groningen

SUMMARY

The influence of the nitrogen source on the growth and organic phosphate content of tomato plants was studied.

At a very low light intensity ammonium stimulated growth more than nitrate did, at a high light intensity ammonium restricted growth as compared with nitrate.

The damaging effect of ammonium depends more on conditions of light than of temperature.

The leaf growth ratio and the organic P content ratio for the leaves of the nitrate- and ammonium-fed plants were inversely correlated.

1. INTRODUCTION

The differences between nitrate and ammonium as a nitrogen source for plants are well known. Earlier research on this subject dealt mostly with the influence of ammonium on the growth of plants, and with the choice of a suitable pH and nutrient solution in order to overcome the harmful effects of ammonium (NIGHTINGALE 1937, 1948).

In recent years work has been done on the metabolism of ammonium-fed plants. Ammonium is said to be a respiratory inhibitor (VINES & WEDDING 1963) or an uncoupler of photophosphorylation (AVRON 1960; KROGMAN *et al.* 1962; KANDELER 1969). It may cause a restriction in amino-acid synthesis and, consequently, a predominance of protein degradation over protein synthesis (WEISSMAN 1964; PURITCH & BARKER 1967).

Data on the influence of the nitrogen source on the organic phosphate content of the tomato plant are somewhat contradictory. ROUX & LESANT (1962) reported a higher organic P content, in comparing ammonium-fed plants with nitrate-fed plants; WOOLHOUSE & HARDWICK (1966) found a lower content. In both reports ammonium was found to retard the growth of the plants. It is possible, however, to grow ammonium- and nitrate-fed plants under certain conditions with only slight differences in growth or even with equal growth. The question arose whether any influence of ammonium might be found on the organic P-content of these plants, in other words, whether the differences in organic P-content that have been reported in literature might be related to the ammonium ion *per se* or with the retardation in growth due to ammonium. In this paper some data on this problem are given.

2. MATERIAL AND METHODS

Tomato plants (cv. "Moneymaker" and "Monkladex") were grown in nutrient solution in a greenhouse (HOFSTRA 1964, 1966). At the six leaf stage the plants were placed in containers (15 litres). Three containers, each with four plants, were connected with one stock vessel (15 litres). The nutrient solution flowed out of the stock vessel through the containers and back into the stock vessel. In this way each plant was supplied with nutrients out of five litres of the nutrient solution. This solution was made with tap water and the transpired water was replenished by de-ionized water. The nutrients were supplied three times a week, the complete nutrient solution was renewed once a week.

The plants were grown for three weeks from the six leaf stage, either with ammonium or with nitrate as a nitrogen source.

The plants were given:

Once a week (in the tap water)

Ca(CHO₃)₂ 4.5 meq/l

Mg(HCO₃)₂ 0.9 meq/l

NaCl 0.9 meq/l

Three times a week

Nitrate-fed plants

Ca(NO₃)₂ 0.3 meq/l

KNO₃ 0.2 meq/l

MgSO₄ 1.1 meq/l

KH₂PO₄ 1.1 meq/l

(NH₄)₂SO₄ 0 meq/l

KCl 0 meq/l

Fe 1.6 mg/l

and micro nutrients (HOFSTRA 1966).

Ammonium-fed plants

0 meq/l

0 meq/l

1.1 meq/l

1.1 meq/l

0.5 meq/l

0.2 meq/l

1.6 meq/l (Fe rexenol)

The pH was adjusted daily to 5.8. with diluted KOH solution. At night the minimum temperature in the greenhouse was 15°C. In the daytime the maximum temperature in winter was 22°C, in summer it varied with the amount of sunshine between 22°C and 35°C. In the first series of experiments temperature, light intensity and day length varied thus with the season. In a second series of experiments plants were grown in summer with different light regimes. One set of plants was grown under the normal conditions of the greenhouse, another set was shaded with a cheese-cloth filter to about half the light intensity. The shaded and unshaded plants were fed out of the same stock vessel.

After three weeks four plants out of each set were harvested. Leaf, stem and root weight were determined. The leaves, after removal of the big midribs, and the roots, after removal of the tap root, were powdered in liquid nitrogen and stored in plastic jars at -20°C.

Dry weight percentages of leaves and roots were determined by drying at 105°C for 5 hours.

For the determination of the total P content the fresh material was digested with a mixture of concentrated sulphuric and nitric acid (1:1).

The inorganic P content was determined in the TCA soluble fraction.

The colorimetric P determination was after CHEN *et al.* (1956).

The organic P content was calculated as the difference between the total and the inorganic P content.

The mean value of four plants from one container is given.

3. RESULTS

Growing the plants in the greenhouse caused seasonal differences in the influence of ammonium and nitrate on the growth of the plants. In *fig. 1* the leaf and root growth for the ammonium- and nitrate-fed plants is given. In March, April and September the leaf growth of the ammonium-fed plants was better than or about equal to that of the nitrate-fed plants but in summer the leaf growth of the ammonium-fed plants was inferior to that of the nitrate-fed plants. Root growth of the nitrate-fed plants was nearly always better than that of the ammonium-fed plants.

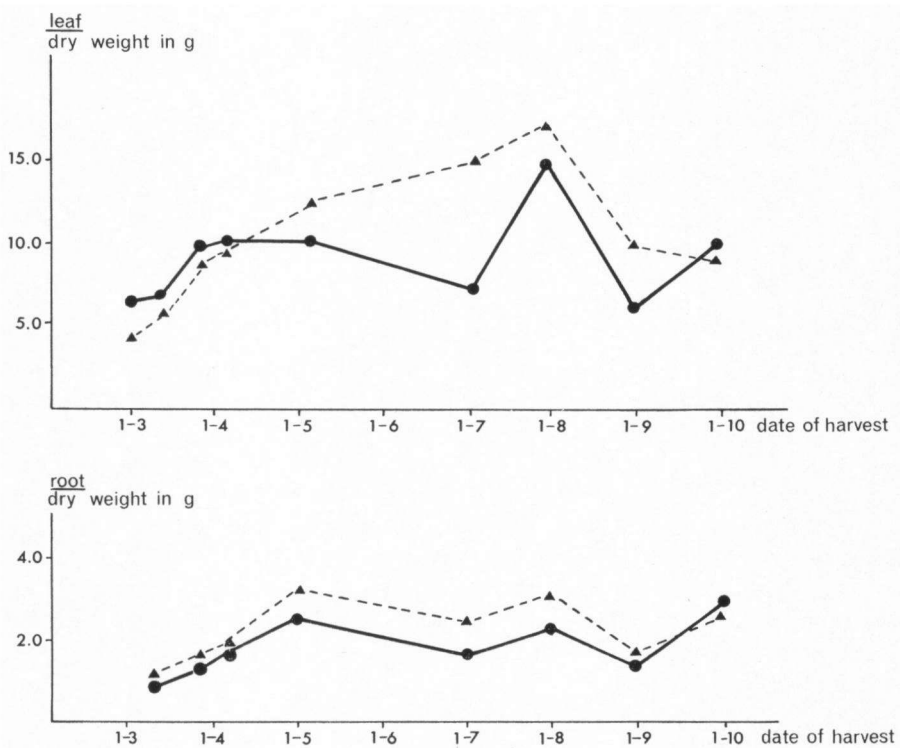
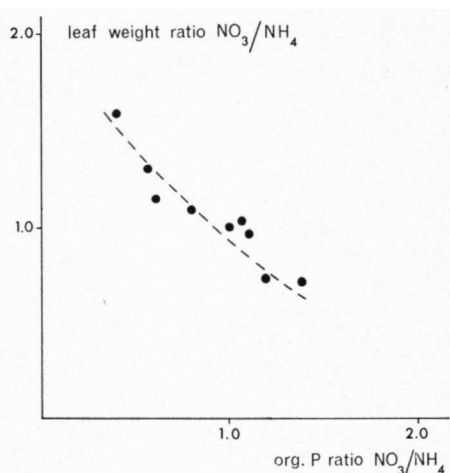


Fig. 1. The seasonal influence on the dry leaf and root weight of tomato plants after a 3 week period with either ammonium or nitrate as a nitrogen source. (NO₃ ▲—▲, NH₄ ●—●). The mean value of 4 plants is given.

Fig. 2.

The inverse correlation between the ratios of the leaf weight and org. P content of nitrate- and ammonium-fed tomato plants. The plants were grown for 3 weeks with either NO_3 or NH_4 as a nitrogen source.



The organic P content of the leaf is given as the ratio for the ammonium- and nitrate-fed plants in order to eliminate fluctuations due to daily shifts in temperature and light. In *fig. 2* this ratio is plotted against the ratio in leaf weight. An inverse correlation is found between them, both on a fresh and dry weight basis. The data for the roots are not so clear. The organic P content of the ammonium-fed roots was increased, but the increase was not inversely correlated with the decrease in root growth.

In these first experiments it is shown that seasonal changes in light and temperature influence the growth of the ammonium- and nitrate-fed plants in a different way. Both light and temperature were interrelated in these experiments. In the second series of experiments, therefore, growth of the ammonium- and nitrate-fed plants was compared under different light regimes but at about the same greenhouse temperature. The results are given in *fig. 3*. The shaded ammonium- and nitrate-fed plants are about equal in leaf growth and in organic P content of the leaves. The growth of both the ammonium- and the nitrate-fed plants was stimulated by a higher light intensity, but the growth of the nitrate-fed plants was consistently more stimulated than that of the ammonium-fed plants. The dry weight percentage of the leaves was higher at the higher light intensity (shaded NO_3 and NH_4 leaves: 12.2%, unshaded NO_3 and NH_4 leaves: 15.5%; mean value of 4 exp.). Under these high light conditions, the organic P content of the ammonium-fed plants increased above that of the nitrate-fed plants, but, as in the first series of experiments, the differences were more pronounced in the leaves than in the roots. The organic P content of the ammonium-fed unshaded leaves rose above that of the shaded leaves and above that of the shaded and unshaded nitrate-fed leaves, whereas hardly any difference was found between the organic P content of the nitrate-fed shaded and unshaded leaves.

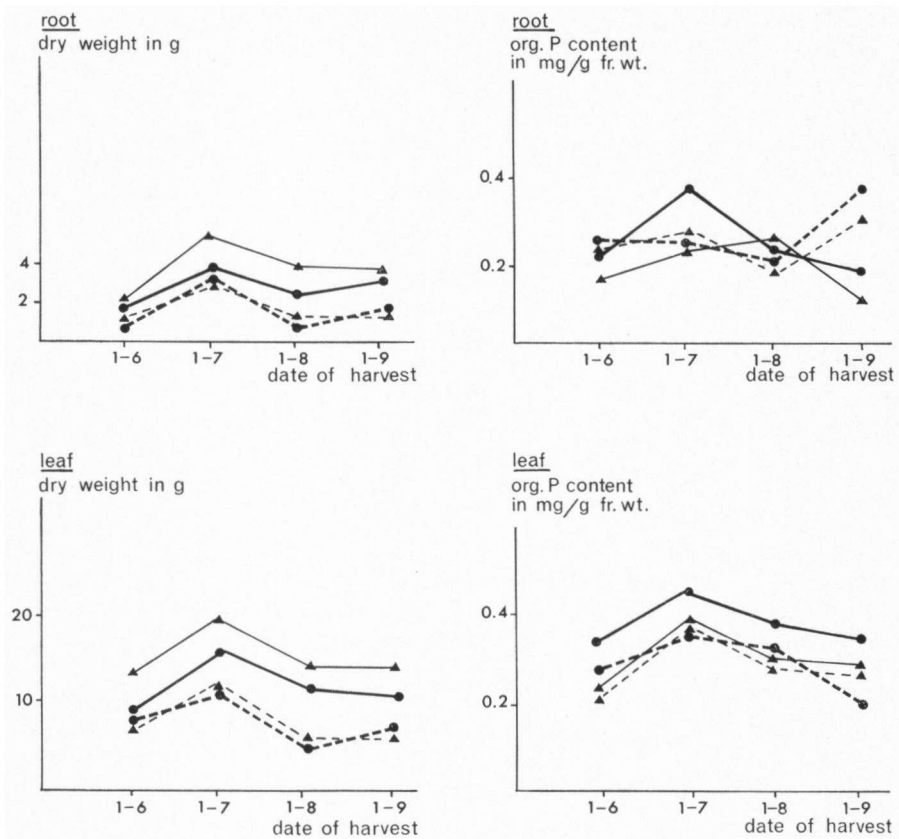


Fig. 3. The influence of the light intensity on the dry weight and the organic P content of the leaves and the roots of tomato plants. The plants were grown for 3 weeks with either NO_3 or NH_4 as a nitrogen source. Half of the plants were under the normal greenhouse conditions (\triangle — \triangle NO_3 , \bullet — \bullet NH_4), the other half shaded by means of a cheesecloth filter (\triangle ---- \triangle NO_3 , \bullet ---- \bullet NH_4). The mean value of 4 plants is given.

4. DISCUSSION

Several factors such as p_{H} , light, ammonium concentration of the nutrient solution, the presence of other ions, may influence the growth of ammonium-fed plants. In varying these factors growth may be retarded, as compared with the growth of nitrate-fed plants (ROUX & LESAINT 1962; WOOLHOUSE & HARDWICK 1966), although growth may occasionally be promoted (BLACKMAN & TEMPLEMAN 1938; TAMM 1956; WEISSMAN 1964).

Fig. 1 shows the seasonal influences on the growth of ammonium- and nitrate-fed plants grown at a low nitrogen level and at a constant p_{H} . In spring and autumn ammonium does not have any harmful effect at all, but even sometimes

a beneficial one as compared with nitrate. In summer, however, a retardation in growth of the ammonium-fed plants is found.

In the greenhouse, light and temperature do vary with the season. One or both of these factors, therefore, may cause these differences in growth. Due to a high temperature in summer ammonium may be taken up too rapidly for a direct conversion into organic compounds, thus damaging the plants. BLACKMAN & TEMPLEMAN (1938) found that shading was beneficial for the growth of ammonium-fed plants. Light, therefore, may also have an effect. In winter the low light intensity may limit the nitrate reducing capacity. Ammonium as a nitrogen source can be used more readily as it is in the reduced state, thus giving better growth. In summer, however, light may not further limit the nitrate reduction but the damaging effect of ammonium may be promoted by a high light intensity. An increase in light intensity to twice its value at about a constant temperature does indeed influence the growth of the ammonium- and nitrate-fed plants to a different degree (*fig. 3*). Growth of the shaded nitrate-fed plants is hardly higher than that of the shaded ammonium-fed plants. At a higher light intensity the growth of both the ammonium- and the nitrate-fed plants is increased. Here, however, the damaging effect of ammonium becomes clear. It is therefore concluded that the retarded growth of the ammonium-fed plants in summer is due to high light intensity rather than to high temperature. The deviation in *fig. 1* for the values found in July may be explained in the same way. After the first ten days the leaf weight ratio of the ammonium- and nitrate-fed plants was 1.4 and the ratio of the organic P content 0.74, these being normal values for high summer. Due to the very cloudy weather in the second half of the experiment, the leaf weight ratio fell to 1.1 and simultaneously the organic P ratio rose to 1.0.

Light may exert its influence, either on the uptake mechanism or, more directly, on the ammonium toxicity in the leaves.

In *fig. 2* is shown that the leaf weight ratio for the nitrate- and ammonium-fed plants is correlated inversely with the organic P ratio. If the ammonium-fed plants surpass the nitrate-fed plants in leaf growth, the organic P content of the ammonium-fed leaves is lower than that of the nitrate-fed leaves. If, however, the nitrate-fed plants surpass the ammonium-fed plants in leaf growth, a higher organic P content is found in the ammonium-fed leaves and an equal growth gives about an equal organic P content. The same is found in the second series of experiments (*fig. 3*). At a high light intensity the ammonium-fed plants are retarded in growth as compared with the nitrate-fed plants. This is correlated with a higher organic P content. In the shaded plants growth is hardly retarded and the organic P content hardly enhanced. Thus the organic P content varies as a result of a variation in growth. Growth may be limited in nitrate-fed plants by a low light intensity or in ammonium-fed plants by a damaging effect of the ammonium. Thus the higher organic P content sometimes found in the ammonium-fed plants may not be caused by the ammonium ion *per se*, but it may be due to the retarded growth of these plants. This is in accordance with the view of Roux & Lesaint. They consider the higher organic P content as storage

material which can be used up if the plants are shifted from ammonium to nitrate nutrition (ROUX & LESAINT 1962).

At a later stage of growth the metabolism of the ammonium-fed plants may be disturbed to such an extent that the organic P content may be lowered, as compared with that of nitrate-fed plants as WOOLHOUSE & HARDWICK (1966) found. They used, however, unequal amounts of nitrate and ammonium in the nutrient solution.

Root growth is nearly always retarded by ammonium (*fig. 1* and *3*). This might be caused by a restricted transport of photosynthates from the leaves to the roots. Simultaneously the organic P content is increased. The inverse correlation, as was shown for the leaves in *fig. 2*, is not found here; other factors, e.g. the shoot/root ratio, may play a role.

ACKNOWLEDGEMENTS

Thanks are due to Prof. Dr. M. H. van Raalte for critical reading of the manuscript and to Miss S. Barker who corrected the English text.

REFERENCES

- AVRON, M. (1960): Photophosphorylation by Swisschard chloroplasts. *Biochim. Biophys. Acta* **40**: 257–272.
- BLACKMAN, G. E. & W. G. TEMPLEMAN (1938): The influence of light intensity and nitrogen supply on the leaf production of frequently defoliated plants. *Ann. Bot. N.S.* **2**: 765–791.
- CHEN, P. S., T. Y. TORIBARA & H. WARNER (1956): Microdetermination of phosphorus. *Anal. Chem.* **28**: 1756–1758.
- HOFSTRA, J. J. (1964): Amino-acids in the bleeding sap of fruiting tomato plants. *Acta Bot. Neerl.* **13**: 148–158.
- (1966): *Amino-acids in the root and bleeding sap of tomato plants*. Thesis, Groningen.
- KANDELER, R. (1969): Hemmung der Blütenbildung von *Lemna gibba* durch Ammonium. *Planta* **84**: 279–291.
- KROGMAN, D. W., A. T. JAGENDORF & M. AVRON (1959): Uncouplers of spinach chloroplasts photosynthetic phosphorylation. *Plant Physiol.* **34**: 272–277.
- NIGHTINGALE, G. T. (1937): The nitrogen nutrition of green plants. I. *Bot. Rev.* **3**: 85–174.
- (1948): The nitrogen nutrition of green plants. II. *Bot. Rev.* **14**: 185–221.
- PURITCH, G. S. & A. V. BARKER (1967): Structure and function of tomato leaf chloroplast during ammonium toxicity. *Plant Physiol.* **42**: 1229–1238.
- ROUX, L. & C. LESAINT (1962): Comparaison de l'influence de la nutrition nitrique et ammoniacale sur la répartition du phosphore chez la tomate. *Ann. Physiol. Vég.* **4**: 235–239.
- TAMM, C. O. (1956): The response of *Chamaenerion angustifolium* (L.) Scop. to different nitrogen sources in water culture. *Physiol. Plant.* **9**: 331–337.
- VINES, H. M. & R. T. WEDDING (1960): Some effects of ammonia on plant metabolism and a possible mechanism for ammonia toxicity. *Plant Physiol.* **35**: 820–825.
- WEISSMAN, G. S. (1964): Effect of ammonium and nitrate nutrition on protein level and exudate composition. *Plant Physiol.* **39**: 947–952.
- WOOLHOUSE, H. W. & K. HARDWICK (1966): The growth of tomato seedlings in relation to the form of the nitrogen supply. *New Phytol.* **65**: 518–525.