

**Phosphorus Absorption by Intact Maize Plants
from Flowing Solutions
Influenced by 2,4-dinitrophenol and Viscosity of Solution**

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Abstract. The investigation of phosphorus absorption by intact plants during a short period has above all confirmed the validity of the results obtained in the foregoing study of the kinetics of absorption by excised roots. Further, the results show the unquestionably important role of mass flow in transporting ions to plant roots, mainly at lower and medium concentrations, that is, from about 0.1 to 10 mM. Under conditions of growth close to the optimum, the supply by means of mass flow can be sufficient even at lower concentrations of phosphorus, such as 1.47 mM KH_2PO_4 , or the absorption of phosphorus by plants can be higher than in the case of ions being transported to roots by diffusion. With a higher absorption the phosphorus distribution somewhat changes as well, relatively more of it being accumulated in the roots. 2,4-DNP applied to the nutrient solution at a concentration of 10^{-5} M reduces the phosphorus absorption.

Mass flow round the maize roots significantly increases the absorption of phosphorus in excised roots (ČÍŽKOVÁ-MACŮRKOVÁ and LAŠTŮVKA 1975) as well as in the roots of intact plants (MACŮRKOVÁ and LAŠTŮVKA 1972, PALÁTOVÁ and LAŠTŮVKA 1974). The experiments with excised roots, in which 2,4-DNP was applied to the medium and the solution viscosity was increased, have shown that phosphorus absorption occurs metabolically. However, these experiments were concerned with phosphorus absorption and accumulation in the cells of excised roots, and the results may be substantially different from those obtained in experiments with intact plants.

Therefore, the present work examines the effect of flowing solutions on the phosphate uptake by intact plants, studying not only the absorption and accumulation in the roots, but also the transport to the shoots, with the application of 2,4-DNP and higher viscosity of solution.

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Material and Methods

Plant Culture

Maize plants (*Zea mays* L. cv. 'Kočovská raná') were used in the experiments. Five days after germination, the seedlings were transplanted from the germinating pots to cultivation vessels containing Richter's solution (with 10 mg Fe l⁻¹ as FeEDTA), with Hoagland microelement solution added. In one half of the vessels the solution was stationary, in the other it was flowing at a rate of 0.162 cm sec⁻¹. In both variants the plants were given the same amount of nutrients (per plant and day). The culture took place in a glass-house with natural illumination, at air temperature varying from 18 °C to 28 °C, from April 26 to May 5, 1973.

Absorption Experiment

On May 4, 1973, the plants were put in the absorption solutions. Richter's medium with Hoagland microelement solution was used. Phosphorus was labelled ³²P, the activity of solutions was 814 kBq l⁻¹ (22 µCi l⁻¹). In addition to the basic variant (control) more of them were prepared: 2,4-DNP (concentration 10⁻⁵ M) was added to the basic solution, potato starch (concentration 1 to 2 %) to others. The solutions were adjusted to 5.3 pH, aerated before use, the temperature of solutions was 24 °C, of the air 25 °C, the illumination was natural. The 1 % starch solution had 3.3 times, and the 2 % solution 14.1 times higher viscosity than water. Dinitrophenol at the given concentration was added to the cultivation solution 1 h before the commencement of absorption, the metabolic activity of the plants being thus reduced at the very beginning of the experiment proper.

The volume of the solution was 1 l for 1 plant. In all variants one part of the solution was flowing, the other was non-flowing. Samples were collected after 4, 8, 10, 12 and 24 h, the roots were washed for 30 min in distilled water, the shoots were separated, both parts weighed and thereafter mineralized by concentrated H₂SO₄.

Measurement of Radioactivity and Evaluation

The method of measurement was the same as that in the previous work (ČÍŽKOVÁ-MACŮRKOVÁ and LAŠTŮVKA 1975). Phosphorus accumulation and the amount of P transported to the shoots were reduced to the 1 g weight (mg P g⁻¹ of fresh matter). The results are the means of four repetitions. The statistical significance of decisive differences was evaluated by the G-test (Fryer 1957).

Results

The results presented in Table 1 clearly show that the flow of the solution of given concentration increases the absorption of phosphorus by maize plants in comparison with the values of absorption obtained in stationary solutions. In the control variant, not only the accumulation in the roots but also, with some delay, the transport of phosphorus to the shoots increase significantly. However, out of the total amount of phosphorus absorbed from the flowing medium, a relatively greater part (as compared with the non-flowing solution) remains accumulated in the roots.

TABLE 1

Phosphorus absorption by intact maize plants from stationary and flowing solutions after Richter as influenced by 2.4-DNP and viscosity of absorption solution

Absorption [h]	Movement of solution	mg P g ⁻¹ of fresh matter of plant material							
		Control		10 ⁻⁵ M 2.4-DNP		1 % starch		2 % starch	
		shoots	roots	shoots	roots	shoots	roots	shoots	roots
4	non-flowing	1.629	2.585	1.079	2.166	1.577	2.637	1.511	2.556
	flowing	1.683	2.592	0.952	2.263	1.700	2.686	1.633	2.667
8	non-flowing	3.157	2.755	1.090	2.256	1.904	2.521	2.205	2.537
	flowing	3.333	3.402 ⁺⁺	1.595 ⁺	2.774 ⁺⁺	2.235	3.380 ⁺⁺	2.420	3.114 ⁺⁺
10	non-flowing	3.264	3.539	1.137	2.418	2.370	2.716	2.979	2.682
	flowing	3.426	3.729 ⁺⁺	1.584 ⁺⁺	2.862	2.981 ⁺	3.716 ⁺⁺⁺	2.809	3.385 ⁺⁺
12	non-flowing	3.320	3.806	1.277	2.916	2.970	3.518	3.604	3.114
	flowing	3.548 ⁺⁺	3.903 ⁺	2.065	2.931	3.217 ⁺⁺⁺	4.612 ⁺⁺⁺	3.170 ⁺⁺	4.137 ⁺⁺
24	non-flowing	3.524	4.541	1.764	4.139	3.544	4.496	3.260	3.842
	flowing	4.021 ⁺⁺⁺	5.759 ⁺⁺	2.220	4.526	3.634 ⁺	5.256 ⁺⁺⁺	3.576 ⁺⁺	5.708 ⁺⁺⁺

Significance of differences in P absorption between plants from non-flowing and flowing solutions is denoted: P 0.05⁺, P 0.01⁺⁺, P 0.001⁺⁺⁺ (n = 4)

Similarly, after the application of 2.4-DNP (1 h before the experiment proper), the values of phosphate absorption from the flowing solution are somewhat higher than those from the stationary medium; the differences are altogether insignificant, the tendencies in accumulation and transport of phosphorus in the plants from the flowing medium being slightly different from those in nonflowing solutions. Generally, the absorption values are lower than those in the control variant; however, the reduction, to g of fresh matter was influenced practically everywhere to the same extent by a lower water absorption, or water content, after applying 2.4-DNP. In the plants from the flowing medium, comparatively less P is accumulated and more transported to the shoots, the relationship thus being reversed in respect to the control variant, of course, in comparison with the plants from the stationary solution with 2.4-DNP. In both last variants the effect of the quicker mechanism of ion transport to the roots, mass flow, was fairly considerable, altogether statistically significant or even highly significant. Even in these variants the phosphorus accumulation in the roots of the plants from the flowing medium was as much as 7 % higher than that in the plants from the non-flowing solution. Thus, in all variants (except that with 2.4-DNP) the plants having absorbed more phosphorus accumulated it rather in the roots; the amount transported was, however, absolutely higher than in the plants with lower phosphate absorption (the non-flowing solution).

Discussion

In reducing phosphorus absorption to 1 g of fresh matter, no account was taken of the growth of the plants in view of the short interval of absorption (*cf.*, *e.g.*, EDWARDS 1970, RUSSELL and MARTIN 1953, RUSSELL and SHOR-

ROCKS 1959). The results do give a picture both of the phosphorus absorption and of its accumulation and transport to the shoots. First of all, all variants have confirmed the foregoing results of experiments with excised roots. The mass flow of the solution increased phosphorus absorption significantly or even highly significantly, except for the 2.4-DNP variant. In the given conditions of concentration, temperature, plant growth, *etc.*, the mass flow brought more P ions to the roots than the diffusion, making its higher absorption by the roots possible. HAI and LAUDELOUT (1966) tried to solve, and justify mathematically, theoretical questions concerning the effect of flowing solutions on ion transport, along with the role of diffusion. On the ground of constructions and calculations they consider diffusion to be the essential mechanism of ion transport. Our results as well as our analysis of the model chosen by HAI and LAUDELOUT are not in agreement with their view.

The spatial arrangement of the root system in the cultivation vessels is considerably complicated and varies with the plant species, shape of the vessel, *etc.* In any case, however, the roots are not always parallel with the direction of the solution flow, the local flowing in this system changing in respect of intensity and direction. Nor is the absorption of the substance evenly distributed over the whole surface of the roots. These and other considerations defy an adequate mathematical treatment. The whole root system can in this case be imagined as a porous environment. A significant role is played here by the tortuosity of the pores, the width of individual streamlines; in a system like this the local direction of the flowing liquid is constantly deviating from the mean direction of flowing. The streamlines divide and combine, the liquid is mixed up and the differences in concentration levelled out. In any case, however, the velocity of flowing round the roots is such that, in a given time unit, the flow brings more ions to the absorption zone than does the diffusion, the former being the dominant mechanism of transport in the given situation. Of course, this is true only in a certain range of concentrations, such as when using Richter's solution (MACŮRKOVÁ and LAŠTŮVKA 1972, PALÁTOVÁ and LAŠTŮVKA 1974). We assume therefore that the model put forward by HAI and LAUDELOUT (1966) is not adequate and, hence, the mathematical consideration and conclusions derived from it are inaccurate.

The function of mass flow is seen quite clearly in the two last variants of the experiment. The increase in the viscosity of solution brought about a decreased diffusibility of phosphorus in the absorption solution; by increasing the osmotic potential of solution the consumption (absorption) of water by the plants was reduced as well (OLSEN and KEMPER 1968). Under these conditions, mass flow fully ensured the phosphorus absorption by the plants, the difference between the two forms of ion supply to the roots being greater, because the movement of the water around the roots is inhibited by the water uptake in the plant and by the subsequent transpiration. In some studies (GREENWAY *et al.* 1969) the effect of osmotics on phosphorus uptake has not been reported. It is our assumption that the authors did not give due attention to these problems, or used well-mixed solutions, which eliminated the influence of osmotically active substances on the rate of ion movement; it may also be supposed that the low ion absorption and the short time interval of measurement made possible differences insignificant. The use

of potato starch in our experiments has been discussed in a foregoing paper (ČÍŽKOVÁ-MACŮRKOVÁ and LAŠTŮVKA 1975).

The presence of 2,4-DNP in the concentration used did not fully inhibit the absorption of phosphorus. Still it corroborated the previous results on the active reception of phosphorus obtained when employing both mechanisms of ion transport to the absorption area (ČÍŽKOVÁ-MACŮRKOVÁ and LAŠTŮVKA 1976). At the same time, its application revealed the differences, or at least a delay, in influencing the phosphorus transport (see RUSSELL *et al.* 1953). It is only in this variant that accumulation in the roots is relatively lower at a higher absorption. We assume that the differences in accumulation and transport between the plants from flowing solutions and those from stationary solutions exist primarily in

- a) the possibility of an increased metabolism in the plant roots from the flowing solution, thus a relatively smaller part being transported,
- b) the inhibition of metabolism in the roots due to DNP, the P transport being less influenced and, thus, a relatively larger amount of it being transported.

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