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Maize Growth and Ion Absorption in Richter's Solution at Different Flow Rates

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Abstract. By comparing maize plants cultivated in standing nutrient solution with those from solutions flowing at different flow rates it has been established that absorption of nitrogen, potassium and especially of phosphorus was increased owing to the flow. There was likewise a relative rise in the distribution of nutrients to the overground parts of the plants. The content expressed per unit dry matter was increased only in the case of phosphorus; with nitrogen and potassium it was slightly lower than in the standing solution. Increasing amounts of iron were required under the conditions of flowing nutrient solutions to prevent chlorosis of the plants. The production of dry matter, *NAR* and *RGR* was also increased because of the flow. The flow considerably changed the habitus of the primary roots of the maize plants. The roots were longer, thinner and on the whole they contained relatively less dry matter (*RWR*). The lengthening of the roots is explained as a response to stimulation by the solution flow — the rheotropism.

The nutrient solution used in the water culture may remain still, or may be stirred, or it may flow through the cultivation vessel round the roots (HAI and LAUDELOUT 1966, LAŠTŮVKA and MINÁŘ 1967).

In the first case it is the diffusion which is the dominant process in ion absorption, in other cases the mass-flow (the stirring of the whole solution) becomes the most important factor (EATON and BERNARDIN 1964, SABET *et al.* 1964, HAI and LAUDELOUT 1966 *etc.*). HAI and LAUDELOUT (1966) found that the ion intake rate is equal to the product of the flow rate and the difference between the concentration of the solutions entering and leaving the cultivation vessel. This relation, however, holds true only within certain limits.

It is clear that the solution flowing round the roots removes the concentration gradient and is of some significance where the ion absorption rate is higher than the diffusion of the corresponding ion. The plant can remove the difference in ion consumption and supply, by the growth of roots and by thus increasing the absorption area. From the published findings, however (LEWIS and QUIRK 1965, 1967, BOULDIN 1961, OLSEN *et al.* 1962), it is clear that there are numerous conflicting opinions on this point.

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In this paper we have presented the results of experiments with maize in Richter's solution in which the solution flow rate round the roots was controlled. We were interested to find out whether and in what way certain physiological values vary at different rates of flow in this solution so well supplied with nutrients.

Material and Methods

Plant Material and Cultivation Technique

Maize (*Zea mays* L. cv. Kočovská raná IE) was used throughout our experiments. After five days of germination the maize seedlings (8 mg of dry root, 12 mg of sprout) were placed in containers and put into cultivation vessels.

These vessels, made of PVC and holding 13 l, were so arranged as to enable the solution to flow through a small tube of a given height and width. 48 plants were placed into each vessel, two of these together forming a series with the same rate of solution flow. In all, these variants of flow were used: 1. without flow, 2. a flow of 0.145 cm s^{-1}, 3. 0.238 cm s^{-1}, 4. 0.833 cm s^{-1}, 5. 2.000 cm s^{-1}. With the exception of the first variant 35 ml min^{-1} of fresh nutrient solution flowed into each vessel. The nutrient solution was completely changed in the first variant twice a day to keep the total amount of solution used per plant and per day identical in all variants. The solution used was adequately aerated.

The experiments started on August 1, 1969. They were performed under the conditions of natural illumination in a greenhouse. The temperature of the air varied between 18 and 30 °C. The nutrient solution was not tempered.

Cultivation Solution and Sampling

In the experiments we used Richter's nutrient solution (1.0 *R*) (Laštůvka and Minář 1967) supplemented by 14 mg l^{-1} of Fe, and a 1.5 times stronger solution (1.5 *R*) supplemented by 22.5 mg l^{-1} of Fe. Iron was supplied partly in the form of Fe EDTA chelate. In the course of the experiments we took samples of 20 plants each for the estimation of dry matter and for the chemical analyses and of 4 plants each for the estimation of chlorophyll content.

Characters Evaluated

Chlorophylls *a* and *b* were estimated according to Šesták (1971, the calculation according to Vernon 1960), nitrogen, phosphorus and potassium according to the methods described by Minář and Laštůvka (1966), the relative growth rate (*RGR*) and the net assimilation rate (*NAR*) according to Laštůvka and Minář (1970a, b). The contents of the elements as well as the relative absorption rate (I_{at}) were calculated per g of dry matter of roots (Laštůvka and Minář 1970b).

The significance of the differences between the variant without flow and the others were estimated by *G*-test (Fryer 1957).

Results

The increasing flow of Richter's nutrient solution (1.0 *R*) influenced, sometimes very markedly, the set of the observed data. First of all the dry matter production was increased and more so in the overground parts of the plant than in the roots (Fig. 1). The maximum length of the root (Fig. 2) was increased by the higher flow in spite of the relatively lower root-weight ratio (*RWR*) of the whole plant. The values of *RWR* and *RGR* decreased in the course of vegetation, flow fastened the decrease of *RWR* more markedly than that of *RGR* (Fig. 3). The values of *NAR* in the distinct intervals tended to drop more in the standing culture (Fig. 4) with the exception of the last sampling in the course of vegetation. The content of chlorophylls *a* and *b* per unit dry matter of the overground part decreased nearly always

Abbreviations used: RGR — relative growth rate; *NAR* — net assimilation rate; *RWR* — root-weight ratio; I_{at} — mean rate of element absorption.

with the increasing flow (Fig. 4), but its total quantity per plant increased.

The content of nitrogen per unit dry matter was extremely well-balanced, tending to decrease in the overground parts with the solution flow, while increasing in the roots (Table 1). Owing to the flow, the content of phosphorus per unit dry matter rose considerably apart from minor exceptions (Table 1). The content of potassium changed in a similar manner as that of nitrogen (Table 1). In all cases, however, the whole content per one plant was higher in variants with the flow than in the culture without flow.

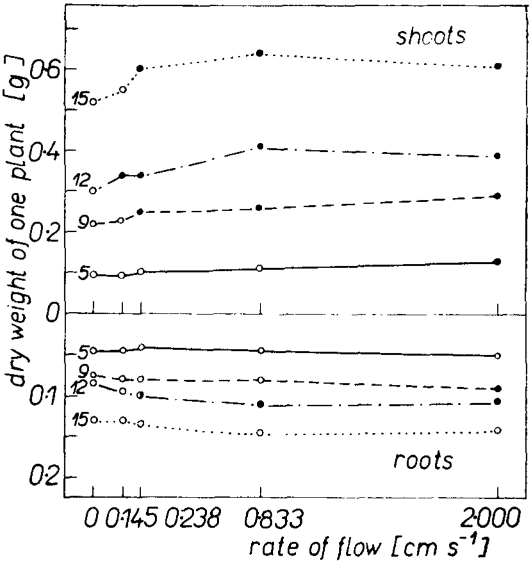

Fig. 1. Dry matter of one plant ($n = 20$). Significant differences between the rates of nutrient solution flow in "zero flow" variant and the others are designated: $P < 0.01$ ◑, $P < 0.001$ ●. The curves are marked with the day of sampling.

The relative absorption rates of the elements per day per unit dry matter of the roots are given in Fig. 5. The absorption of all elements per unit dry weight of roots per day was higher in the flowing solution than in the standing culture. The influence of flow was particularly marked with the absorption of phosphorus. The increased absorption also appeared in the varying distribution to the overground parts. The distribution index was higher in the flowing medium than in the culture without flow. On the other hand the utilization (dry weight produced per 1 mg-at N, P, K) decreased in the flow variants.

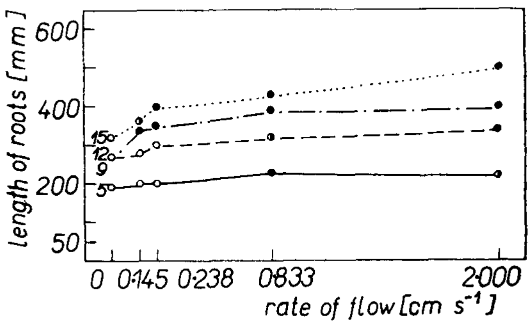

Fig. 2. The length of the roots of one plant ($n = 20$). Significant differences between the rates of nutrient solution flow in "zero flow" variant and the others are designated: $P < 0.01$ ◑, $P < 0.001$ ●. The curves are marked with the day of sampling.

The results of the experiments with the solution of higher concentration (1.5 R) are not mentioned here. Although the values are slightly different from those in the application of Richter's original solution (1.0 R), they have the same tendency and there are practically identical differences between the standing and flow cultures as with the application of the 1.0 R solution.

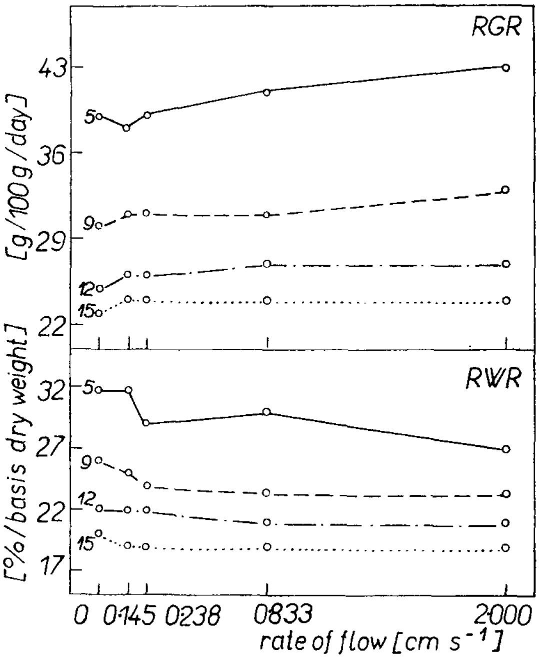

Fig. 3. Root-weight ratio (*RWR*), relative growth rate (*RGR*). The curves are marked with the day of sampling.

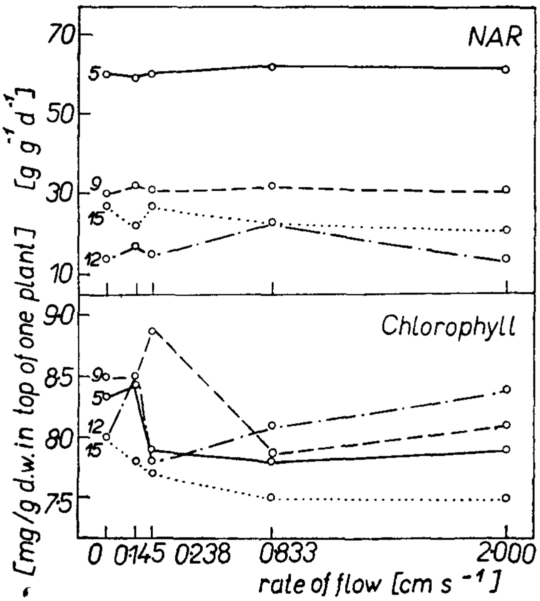

Fig. 4. Net assimilation rate (*NAR*) and contents of chlorophyll *a* and *b*. The *NAR* values are calculated each for a period between two consecutive sampling dates. Chlorophyll contents expressed in mg per g dry weight of the green part (top) of one plant. The curves are marked with the day of sampling.

Discussion

LEWIS and QUIRK (1967) quote three main principles influencing the absorption of nutrients. 1. the stirring of the solution containing ions (massflow), 2. the diffusion of ions, 3. the growth of the root system. They assume that the phosphorus is distributed only by diffusion to the roots of the plants in the soil conditions and also that the sorption area of the roots is sufficient for the full supply of plants with phosphorus. They acknowledge that this statement need not hold good for other elements, *e. g.* for the absorption of nitrogen, magnesium and calcium. Also BARBER *et al.* (1963) consider the mere diffusion of the phosphorus to be a dominant mechanism, BOULDIN (1961), OLSEN *et al.* (1962) assume that the measured uptake of the phosphorus by the plant is about 5—10% higher with the stirring of the solution than without it. On the other hand FRIED and SHAPIRO (1961) suppose that all nutrients are brought to the roots in the soil by massflow of the solution, not by diffusion.

For our work these statements are valuable although they consider these problems from a slightly different point of view. In our experiments we tried to find out whether stirring of the nutrient solution results in an increased absorption of ions, whether it holds good for all ions tested and what the further physiological consequences of such an increased absorption may be.

First of all we tried to ensure the same continuous flow of the fresh solution in all flow variants and to control the different flow rates by means of an aid equipment (variants 2 to 5). It proved completely successful. More than one litre per plant of fresh solution was used within 24 h with the cultivation vessels fully charged by plants. In the variant 1 (zero flow) the plants received the same quantity of fresh solution per day. Only in the informative calculation it can be stated that the plants exhausted less than 1 % of nitrogen, potassium and phosphorus from the used solution. In no case, as is confirmed by the values of *RWR*, did a deficiency of nutrients in the nutrient solution occur, although the possibility of different absorption rates in the standing culture and in the flowing solution is not excluded. Only the claim regarding the flow of the fresh solution into the cultivation vessel in litres per one unit of time fails to state the real solution flow rate. Therefore our cultivation apparatus was constructed in such a way as to force the solution to flow among its lamellae at a certain fixed height

TABLE 1

CONTENT OF NITROGEN, PHOSPHORUS AND POTASSIUM in mg g^{-1} dry matter. Significant differences between the rates of nutrient solution flow in "zero flow" variant and the others are designated: $P < 0.05^{+}$, $P < 0.01^{++}$, $P = 0.001^{+++}$ ($n = 3$).

Days of cultivation	Element	Rate of flow [cm s^{-1}] 0		0.145		0.238		0.833		2.000	
		Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots
5	N	44.50	37.75	46.08^{+}	39.41^{+}	45.73^{+}	38.92^{+}	46.27^{++}	39.50^{+}	46.27^{++}	36.17
	P	12.25	14.44	12.50	15.50^{+}	11.73	17.25^{+++}	12.53	19.25^{+++}	12.53	19.25^{+++}
	K	26.67	25.42	29.17	25.00	28.00	25.42	28.00	27.50	29.00	24.83
9	N	45.73	32.33	45.33	25.00^{+++}	42.00^{+}	29.67	43.00	29.67	41.00^{+++}	28.58^{+}
	P	12.80	18.42	13.60	20.25^{++}	14.33^{++}	19.68^{+}	14.60^{++}	19.42^{+}	15.27^{+++}	22.00
	K	36.00	28.41	34.67	28.33	36.47	27.08	31.67^{+++}	26.67^{+}	32.33^{+++}	26.25^{++}
12	N	41.00	29.00	42.47	31.93^{+}	39.13^{+}	33.33^{+}	37.73^{++}	34.20^{+}	38.20	34.20^{+}
	P	12.53	18.17	14.20^{++}	19.87^{++}	15.13^{+++}	19.73^{++}	15.27^{+++}	19.90^{++}	15.27^{+++}	20.60^{+++}
	K	34.67	30.00	35.87	28.67^{++}	34.33	27.67^{+++}	37.07^{+}	29.00	35.00	28.00^{++}
15	N	39.13	32.80	40.53	33.53	40.53	36.87^{++}	39.60	35.53^{+}	40.53	32.87
	P	10.80	18.60	11.47^{++}	17.07^{++}	11.87^{+++}	18.40	12.13^{+++}	19.13^{+}	12.80^{+++}	20.53^{+++}
	K	35.33	29.33	38.13^{++}	28.33	38.13^{++}	28.67	36.53	26.87^{+}	36.53	26.87^{+}

and width. Thus the rate of the flow can be precisely expressed in cm s^{-1}. The roots of the plants plunged into this flowing solution, bent in the direction of the flow; the equipment is of a different type than that used by HAI and LAUDELOUT (1966). For standing culture the same type of equipment was used, the solution being changed only twice per day. This could also slightly increase the ion absorption, as the movement of ions to the roots by a mere diffusion was limited to less than 20 hours per day.

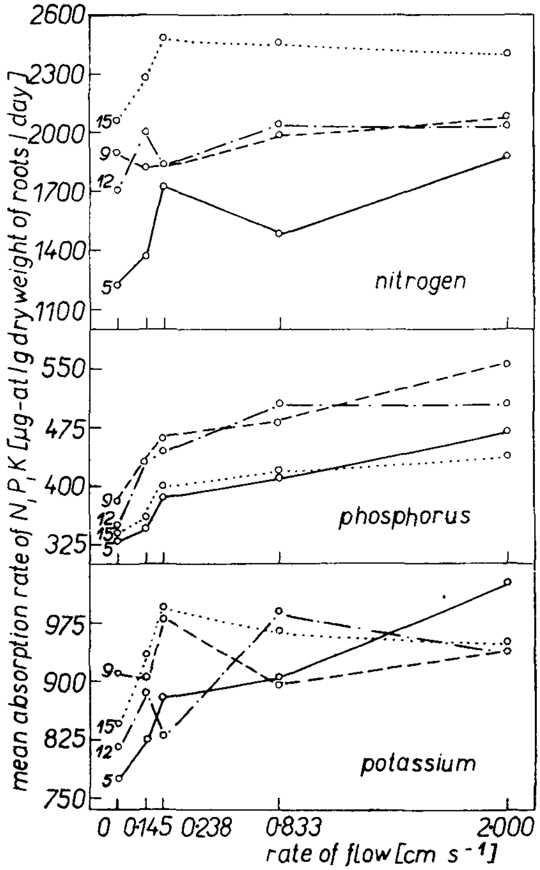

Fig. 5. Mean rate of elements N, P, K absorption per unit weight of roots per day. The curves are marked with the day of sampling.

In spite of the shortcomings mentioned clear cut differences occur in the ion absorption between the standing and the flow cultures. All three elements under discussion — nitrogen, phosphorus and potassium — have a higher average relative absorption rate (I_M) in the flowing solution. There are, however, differences among them: the most obvious increase appears with phosphorus, a certain irregularity with nitrogen and potassium. It appears very improbable to us that the differences should be caused by different diffusion rates of the respective ions as may be the case in the soil. BARBER (1962) has stated that the diffusion of phosphate ions in soil is decreased. We assume that both in the standing culture and in the flow culture inner factors of the plants, particularly their different metabolism, determined the differents ion absorption of phosphate and of other ions.

The absorption intensity of phosphorus is directly dependent on and even determined by, the production rate of the primary products of photosynthesis. Its concentration in photosynthesizing cells (per dry weight) (BROUWER 1963a) is decisive — unless there are other limiting factors of photosynthesis — for the rate and quantity of the phosphorylation processes, or those immediately connected with the photosynthesis, respectively.

In the experiments with different concentrations of the nutrient solution (LAŠTŮVKA and MINÁŘ 1970a, b) and different stand densities (LAŠTŮVKA and MINÁŘ 1970c) the particular role of phosphorus is quite conspicuous.

In our experiments not only a higher relative absorption rate (I_M), but also a higher distribution index and increased content of phosphorus and at the same time, a lower utilization, *i.e.* the production of dry matter per mg-at of phosphorus, are observed in the flow cultures as compared with the standing solution.

From the results it is clear that in the solutions used (1.0 *R* and 1.5 *R*) a small increase in flow rate (to the value of approx. 0.25 cm s^{-1}) is more or less sufficient for a considerable increase of the absorption and further studied characteristics. Any further increase in the flow rate is, however of slight effect.

The absorption and translocation of phosphate anions is known to be closely connected with the absorption and translocation of iron (OLSEN 1935, REDISKE and BIDDULPH 1953). Because of this, we have considerably increased the concentration of Fe in the flowing solutions. Plants from the flow variants with smaller concentrations of iron suffered by chlorosis, as indicated by a lowered production of the dry matter and a subsequent lower absorption of phosphorus and other elements. Even such high concentrations of iron as 14 mg l^{-1} in Richter's solution (1.0 *R*) and 22.5 mg l^{-1} in 1.5 *R* have not ensured in the flowing cultures the same level of chlorophyll production as achieved in the stationary culture. We suppose that even if the production of dry matter (also *RGR*, *NAR*) had clearly risen in the flow culture, the absorbed phosphorus was not effectively used owing to the existence of other limiting factors, *i.e.*, first of all the synthesis of chlorophyll and the thereby influenced absorption, distribution, accumulation, and utilization of nitrogen and potassium.

The overground parts of plants were exposed to the same conditions in all variants. The explanation for the higher absorption of ions and the following changes in the growth of plants in the flow cultures is therefore to be looked for in the formation of the root system and in the conditions in which it occurred. Clearly all three principles described by LEWIS and QUIRK (1967) could participate to a varying degree in the processes of ion absorption and in the subsequent changes. Besides the first two — mass-flow and diffusion — there is the third principle at work. The roots of maize in the standing culture and in the flow culture exhibit a quite different habitus. In the flow cultures the primary roots — one cannot speak of the bunch root system (BERKO 1963) owing to the shortness of cultivation — are substantially thinner and longer than in the standing culture. The storing of the dry matter in them is relatively smaller (*RWR*), which contraindicates any nutrient deficiency (BROUWER 1963b, 1965). As, however the roots were immersed fully in the solution, they were able to absorb the nutrients with their whole surface (RUSSEL 1970) and according to the absorption intensity translocate them differently into the places of consumption (RUSSEL 1970). The flowing solution did not permit the formation of the concentration gradient round the roots (BARBER 1962), thus facilitating the contact of ions with the surface of roots and probably increased even the whole sorption area of the roots. Thus the conditions for the rapid entry of ions into the free space of roots and for their faster absorption and distribution were improved as compared to those in the standing culture. The extension of roots can be caused, indeed, even by means of lower solution concentrations

(MAY *et al.* 1965); but this is not the case in our experiments. We are of the opinion that this is a classical case of rheotropism described by JÖNSSON (1883) in the fungus hyphae, confirmed by a number of research workers even for the root system (see SEN GUPTA 1928/29) and still not quite explained.

The presented experiments show that the absorption and accumulation of ions and numerous subsequent physiological processes are clearly influenced by the flow of solution also in the fairly concentrated Richter's solution. We hope that our results may also contribute to a better understanding of the nutrient uptake by the plants under soil conditions (RUSSEL 1970).

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RADMILA MACŮRKOVÁ, Z. LAŠTŮVKA, Katedra biologie rostlin přírodovědecké fakulty University J. E. Purkyně, Brno: **Růst kukuřice a absorpce iontů v Richterově roztoku o různé rychlosti průtoku.** — Biol. Plant. **14** : 103—111, 1972.

Srovnáním rostlin kukuřice pěstovaných ve stojící kultuře a rostlin pěstovaných v proudícím roztoku o různé intensitě byla zjištěna vlivem průtoku zvýšená absorpce dusíku, draslíku a zvláště fosforu. Relativně stoupla i distribuce sledovaných prvků do nadzemních částí rostlin. Obsah (na jednotku sušiny) se zvýšil pouze u fosforu, u dusíku a draslíku byl více méně nižší než ve stojící kultuře. Zavedení průtoku vyžadovalo zvýšení koncentrace železa v roztoku, aby se zabránilo chlorose rostlin. Vlivem průtoku se zvýšila i produkce sušiny, *NAR* a *RGR*. Průtok kultivačního roztoku značně pozměnil habitus primárních kořenů rostlin kukuřice. Kořeny byly delší, tenčí a celkově se v nich ukládalo relativně méně sušiny (*RWR*). Prodlužování kořenů vysvětlujeme reakcí na dráždění proudem roztoku — rheotropismem.